NIOZ-RAPPORT 2005 - 5

UNDERSTANDING MARINE FOODWEB PROCESSES: AN ECOSYSTEM APPROACH TO SUSTAINABLE SANDEEL FISHERIES IN THE NORTH SEA

C.J. Camphuysen (editor)

Koninklijk Nederlands Instituut voor Onderzoek der Zee

IMPRESS Final Report Project# Q5RS-2000-30864

Interactions between the Marine environment, PREdators, and prey:
implications for Sustainable Sandeel fisheries

UNDERSTANDING MARINE FOODWEB PROCESSES: AN ECOSYSTEM APPROACH TO SUSTAINABLE SANDEEL FISHERIES IN THE NORTH SEA

IMPRESS Final Report
Project# **Q5RS-2000-30864**

Published: November 2005

C.J. Camphuysen (editor)

THIS PROJECT WAS CONDUCTED WITH FINANCIAL SUPPORT OF THE EUROPEAN COMMISSION, DIRECTORATE GENERAL FOR FISHERIES AND MARITIME AFFAIRS
CONTRACT# Q5RS-2000-30864
(Accepted by the DG Fisheries Research and Scientific Analysis unit, 2 June 2005)

Interactions between the Marine environment, PREdators, and prey: implications for Sustainable Sandeel fisheries

With contributions of principal investigators of all participating institutes:

Royal Netherlands Institute for Sea Research (Royal NIOZ), The Netherlands

Centre for Ecology and Hydrology (NERC), Banchory, Scotland

Danish Institute for Fisheries Research (DIFRES), Denmark

Fisheries Research Services (FRS), Marine Laboratory Aberdeen, Scotland

University of Leeds, England

University of Aberdeen, Scotland

Centre National de la Recherche Scientifique Délégation Alsace (CNRS), France

University of Hamburg, Germany

Netherlands Institute for Fisheries Research (RIVO), The Netherlands

Subcontractors:

Federal Research Centre for Fisheries, Institute for Sea Fisheries (ISF), Germany

Southampton University School of Ocean and Earth Science, Southampton Oceanography Centre, England

This report could be cited as follows:

Camphuysen C.J. (ed.) 2005. Understanding marine foodweb processes: an ecosystem approach to sustainable sandeel fisheries in the North Sea. IMPRESS Final Report, Royal Netherlands Institute for Sea Research, Texel

ISSN 0923-3210

Chapter 0.0 Summary for non-specialists

The industrial fishery for sandeels is the largest single species fishery in the North Sea. **Sandeels** Ammodytidae are important prey for a long list of top-predators, including predatory fish, seals, whales, dolphins, porpoises, and many species of seabirds. In ecologically important sea areas, this **industrial fishery** might or indeed does have an effect on these natural sandeel predators. These effects are often indirect and are generally disputed by the industry. The *IMPRESS* project aimed at tackling a specific part of the conflict: the effect of fishing on breeding success of seabirds and the **risk of overfishing in an ecologically important area** such as the Wee Bankie/Marr Bank complex off the Scottish east coast.

The overall objective of the *IMPRESS* project was to determine the relationship between sandeel population characteristics (i.e. patterns in abundance and age- and size distributions), hydrography (influencing prey availability), and the foraging success and breeding performance of four species of seabirds. A key part of the *IMPRESS* project was to develop and use sophisticated bird-borne loggers suitable for North Sea species in order to collect high quality data on foraging locations, diving depth, and prey capture rates, relative to the physical characteristics of the areas used by these birds for foraging. This information would be combined with data on seabird distribution and foraging behaviour collected at sea, with information on prey stock characteristics, hydrography, and data on breeding performance and population trends at colonies on land. Selected predator species under *IMPRESS* were **Northern Gannet** *Morus bassanus*, **European Shag** *Phalacrocorax aristotelis*, **Black-legged Kittiwake** *Rissa tridactyla*, and **Common Guillemot** *Uria aalge*; all with different foraging strategies, feeding capacities and prey preferences.

Sandeel fisheries, sandeels

On the Wee Bankie/Marr Bank sandbank complex of the Firth of Forth in southeast Scotland, industrial fisheries for sandeels commenced in the early 1990s. Coincident with the increase in the removal of sandeels from areas close to the Scottish east coast, seabird breeding success at colonies along that coast started to decline. Concerned that the fishery was affecting an ecologically sensitive area, fisheries managers prohibited fishing for sandeels close to the coast, from the Farne Islands to Rattray Head, and eastwards to longitude 1°E in 2000 for a period of three years. In 2003, the decision was taken to maintain the fishery closure.

Within the IMPRESS project, sandeel stocks were monitored by acoustic surveys (estimates of the abundance of sandeels active in the water column), by dredging and grabbing (to assess their density in the seabed at night; for population age and length structure analyses). Grab surveys provide point estimates of sandeel density in suitable habitats. Acoustic survey and demersal trawl data, collected prior to and during the project (1997-2003), suggested that the total biomass of sandeels in the study area was significantly higher in the four years when sandeel fishing was prohibited (250 000t-335 000t) than in the three previous years when they had been fished (25 000t-89 000t).

Oceanography

Detailed hydrographical observations and modelling allowed the defining of separate regions within the study area, with different mixing and/or productivity characteristics and bathymetry: "Inner and Outer Banks", the "Shallow sea front" and the "Offshore stratified region", the "Outer Bank region", "Mixed (nearshore) Waters" and "Freshwater Influenced Waters".

The initiation of the annual increase in primary production is presumably the driving factor for the emergence of adult sandeels to feed, and thus the timing and progress of the spring bloom may be important. Spring conditions and their effect on the timing of primary production will have influenced the growth and survival and therefore the availability or profitability of sandeels. Over the last 30 years, meteorological variability (especially spring solar irradiance) drove most of the inter-annual variations in the onset of stratification and the spring bloom. The North Atlantic Oscillation (NAO) played some, but no dominant role.

Seabirds breeding: population trends, reproductive success and diet

Populations of breeding Northern Gannets (Bass Rock) and Guillemots (Isle of May) increased. European Shags declined sharply in 1999, but numbers have increased since. In contrast, there was a continuous decline in breeding numbers of Black-legged Kittiwakes between 1997 and 2003.

Breeding success in Gannets was high. Shags showed an increase in breeding success over 1997-2003, except for 1999 when success was low. Guillemot breeding success declined overall, with values during 2001-2003 being some of the lowest on record. Breeding success in Kittiwakes was variable, but generally higher in 2001-2003 than during the late 1990s. Breeding success was higher in 2003 than in 2002 or 2001 in all four species.

Shags and Kittiwakes were almost completely dependent on sandeels. The main prey brought in by Guillemots for their chicks was Sprats, but adult birds were feeding substantially on sandeels. Gannets, took a wide variety of prey. The different seabirds were apparently sampling from the same sandeel population since in neither year were marked discontinuities found between the length/date relationships for the individual predator species.

Seabirds at-sea

The offshore seabird community comprised at least 37 different seabird species. Within the principal study area, the most species were Common Guillemot (49%), Atlantic Puffin (21%), Black-legged Kittiwake (12%), Razorbill (11%), and Northern Gannet (6%). Clear-cut, generalised seabird distribution patterns were derived, with Gannets far-ranging, Guillemots and Kittiwakes highly concentrated in the western (nearshore) half of the study area at large, and with Shag concentrated in inshore waters (not well covered in these surveys). Seabird densities and species richness declined and species composition altered with increasing distance to the UK coast. The study area, almost entirely within 90 km from land, was part of the areas with the highest mean top-predator densities and diversity of the northwest North Sea. In biomass terms, the seabird community was dominated by Guillemot, Puffin, Razorbill, Gannets and Kittiwakes (98%). For all seabirds within the study area, the energy requirement per unit area was estimated at nearly 120 000 kJ day^{-1} km^{-2}.

Seabird foraging distribution

From a combination of logger data (VHF telemetry, compass loggers, satellite transmitters and GPS loggers) and ship-based offshore surveys, a much more complete picture of foraging trips in seabirds was obtained than ever before. In Shags, three main foraging areas could be identified: inshore, west and north of the colony, and close to the island. Guillemots were foraging much closer to the colony than expected from at-sea surveys, with the furthest distance from the colony estimated at 25.3 km. Kittiwakes used a wide variety of foraging areas, from inshore coastal areas in St Andrews Bay area out to the Wee Bankie/Marr Bank region (foraging range 37.0 ± 16.3km; range 13.6 – 83.5 km). Northern Gannet ranged from West Norway to NE Scotland, into the north central North Sea and the southern North Sea. The mean foraging range was between 165 and 190km, mean trip duration being approximately 24 hours.

Northern Gannets foraging within the study area acquired 59% of their energy over the "Banks". All Shags were foraging in "Freshwater Influenced" waters. Kittiwakes acquired 53% of their energy on the "Banks", and a further 27% in Freshwater Influenced waters. Guillemots acquired 48% of the energy on the Banks, and 24% in Freshwater Influenced Waters. A combination of all data suggests that for these three species the Bank Areas are the most important foraging grounds (49% of the energy acquired) and that Mixed Waters near the coast were relatively unimportant (8%).

Seabird foraging behaviour and flock formation

Most birds that were recorded as feeding participated in feeding flocks and most these flocks comprised several species (multi-species feeding associations, MSFAs). Three major types of MSFAs were recognised: (1) flocks associated with fishing vessels, (2) marine mammal-induced feeding flocks, and (3) 'natural' feeding flocks (seabirds, sometimes with marine mammals, jointly exploiting a shared resource). In the study area at large, in 12 out of 18 common species recorded, at least 80% of the feeding individuals were joining some sort of MSFA. A notable exception was the Shag (23%). 81% of the feeding Guillemots were found in 'natural' MSFAs. Northern Gannets were commonly represented near fishing vessels (43%), with cetaceans (19%), and in 'natural' MSFAs (21%). 69% of the Kittiwakes were feeding in 'natural' MSFAs. Aerial species, such as surface feeding gulls, had a greater tendency to participate in 'natural' MSFAs than expected on the basis of their overall abundance at sea. MSFAs formed around marine mammals occurred primarily in stratified offshore waters, while cetaceans within *c.* 80km from the coast were largely ignored. Feeding Gannets were mostly deep plunge-diving or scooping. Scooping was entirely associated with MSFAs and sandeel feeding. Feeding Kittiwakes were dipping or shallow plunge-diving. Guillemots were observed pursuit diving from the surface mostly.

Seabird foraging depth and time activity budgets

In Shags, the foraging depth was between 21-30, with the mean dive depth being greater in 2003 than in 2002. In Guillemots, the foraging depth varied considerably. Depth distributions peaked between 41-60 m in 2001 and 2002, but in 2003 59% of dives were <20 m deep. In Gannets, dive depth did not differ between years (about 3m). Time activity budgets were obtained for all four species during chick rearing, using a combination of bird-borne data loggers. In Shags, the proportion of time spent foraging was greater in 2002, when less time was spent on land. There was no difference in the number of trips by Guillemots made per day between seasons, but in 2003, they spent more time flying and diving and less time resting on the sea compared with 2002. Kittiwakes made more trips per day in 2003 than in 2002 or 2001, and spent more time in foraging flight. On feeding trips, Gannets spent 0.3%, 43%, and 57% of time respectively diving, flying and resting/swimming on the surface of the water. From gastric temperature loggers, used to measure prey capture rates, it appeared that Shags were successful on 10% of dives and in 55-65% of feeding bouts. In Guillemot, success rates per dive (33%) were much higher.

Seabirds foraging habitat characteristics

Surface feeding seabirds require processes that bring prey to the sea surface and horizontal frontal systems were predicted to provide such opportunities. From at-sea surveys, it was demonstrated that foraging Kittiwakes utilised a broad zone off the Scottish east coast, with peak densities at the shallow-sea front (the seaward side of the mixed coastal zone). This front appeared to form an outer barrier for breeding Kittiwakes, and foraging occurred throughout the area between colony and front. Guillemots were essentially highly widespread in a broad zone along the coast, with relatively low concentrations in mixed coastal waters and beyond the shallow sea front in offshore stratified waters. Isle of May breeding birds utilised only a small part of the principal study area, mainly to the west of the Wee Bankie/Marr Bank complex. The bulk of the (adult)

Guillemots in the eastern part of the study area bred in Kincardine and Deeside and in East Lothian, Berwickshire and or Northumberland.

In contrast to other species, the feeding distribution of benthic feeding Shags was not expected to be associated with fronts or thermoclines. In all three years, Shags were foraging inshore of the Isle of May and the water they foraged in was very mixed. Northern Gannets were by far the furthest ranging species, foraging abundantly within and beyond the principal study area. Behavioural observations during ship-based surveys indicated that the foraging techniques, the tendency to participate in multi-species feeding frenzies, the tendency to join hunting cetaceans as well as the opportunities to scavenge at fishing vessels varied per area.

Continuous oceanographic data from a dedicated cruise in 2003 cruise produced a very detailed ‘snapshot’ of the water column characteristics underneath foraging birds. The mixing properties (as indicated by stratification, using top and bottom temperature differences) of the water column in which different species feed were significantly different. Gannets were found foraging in the most stratified water, while Kittiwakes used water that was less stratified than that of the Gannets, but more so than the water columns over which Guillemots mainly foraged. Decreasing tidal speed during the ebb were phases mostly used by Kittiwakes, while Gannets were targeting the maximal current speeds on both the ebb and flood tides in their preferred foraging region of the Shallow sea front. Guillemots showed almost no difference in foraging abundance with tidal phase. No clear absolute relationship between the density of any seabird species and the density of either sandeels, Herring or Sprats could be determined.

Seabird energetics and energy requirements

Biotic and abiotic factors influencing diving metabolic rates were investigated experimentally, including the effect of prey availability (fish density), prey size, light conditions, fish behaviour, bird condition (body mass), water temperature, and dive depth on prey capture behaviour. Water temperature, dive depth, and digestive phase were important factors affecting the amount of energy which diving seabirds have to expend during foraging. Foraging success depended to a large degree on fish density, while fish behaviour (shoaling or not) had important consequences for predator performance.

Foraging seabirds are constrained by a delicate balance of the time they can allocate towards food acquisition, the energy demands associated with their activities and the food they are able to acquire. Confronted with a decline in availability of a particular prey species (e.g. sandeel), seabirds have a number of potential options. For some it might be possible to switch to other prey, or they may be able to increase their foraging effort in a number of ways. Dietary information suggested that Kittiwakes and Shags were least able to switch to alternative prey. For Kittiwakes, this might be exacerbated by its surface feeding habit that limits its foraging abilities to prey items close to the sea surface. Shags and Guillemots were estimated to have sufficient time and energy to allow them to increase their foraging effort considerably, while Kittiwakes and Gannets appeared more constrained by time and energy respectively.

Prey consumption versus prey stock

Estimates of breeding populations, daily energy requirements, and energy contents of prey fish, revealed a total consumption for June-July of about 16 000t for the four seabird species within the study area. Estimates based on numbers seen foraging at sea in the principal study area yielded a total of >8000t. Both estimates are low compared to the total prey stock estimate averaged over the years: *c.* 197 000t (1/12 to 1/25), but form a significant part of the minimum prey fish stock found between 1997 and 2003 of 27 000t, which is only about 2 to 3 times larger than the estimated consumption of these four top-predator species alone.

Inter-annual variability

The initiation of the annual increase in primary production is presumably the driving factor for the emergence of adult sandeels to feed, and thus the timing and progress of the spring bloom may be important for seabirds targeting 1+ group sandeels. In later phases of chick rearing, seabirds depended more on 0 group sandeels. Spring conditions and the effect on the timing of primary production will have influenced the growth and survival and therefore the availability or profitability of 0 group sandeels.

Breeding success of Kittiwakes increased by 0.13 chicks pair^{-1} for every five days delay in timing of the spring bloom. There was no evidence that the effect of date of the spring bloom on breeding success was different in fishing and non-fishing years, but breeding success higher in years without fishing than in years with fishing. Important climatic variables were more easily identified in the absence of the confounding effects of a fishery.

A high proportion of the variation in the breeding success of three study species of seabirds can be explained when the date of egg laying relative to the timing of the bloom is taken into account. The state of individual birds probably drives the timing of egg laying, while their states are influenced by local environmental conditions affecting food availability during the pre-breeding season. The presence of an industrial fishery in the area has an (additional) adverse effect on seabird reproductive output.

Sandeel biomass was significantly higher in 2000-2003 than it was in the three years prior to the project and the reproductive success of Shags and Kittiwakes was relatively high in these years, albeit variable in Kittiwakes. For the Guillemot, however, the reproductive success declined and relatively few sandeels were brought into the colony in recent years

Changes in numbers of many North Sea seabirds over the last 15-20 years have varied from long-term increases in some to declines in others. Combining information on at-sea distribution and activity (both from visual observations and from data collected with instrumented individuals) with oceanographic data has highlighted the complex interplay between seabird foraging success, feeding location and inter-specific competition and facilitation. Thanks to multi-disciplinary projects such as *IMPRESS*, do we begin to understand the functional links between marine predators, their prey and the marine climate and may we thus come closer to ecosystem-based fisheries management. However, as the results presented here indicate, we are still some way from having all the background knowledge required for such an approach. Given the increasing pressures on the North Sea ecosystem from both fisheries and climate change, using top predators to monitor ecosystem health is an attractive concept. However, simple and seemingly straightforward signals such as the breeding success or population trend of one or few species to monitor the well-being (or prey availability) of a complex and large community do not provide sufficient insight necessary for an adequate management of ecologically important areas.

Sandeel stocks, prior to and following the year 2000 in the principal study area were an order of magnitude different. Many seabirds were under stress when sandeel stocks fell below 100 000t, while breeding success was generally high in 2000-2003, when prey stocks were on average well in excess of 250 000t. A simple advice to stay on the safe side with a sandeel stock of at least 250 000t is not given, however, because several studies demonstrated ecosystem scale effects of climate change in the Northeast Atlantic, likely to alter the spatial distribution of primary and secondary pelagic production, and eventually (if not already) affecting top-predators in the northwest North Sea. Long-term climatic and oceanographic cycles regulate seabird populations on decadal time-scales. The recent concerns about the impact of climate change on the North Sea ecosystem, would call for extreme care when managing an ecologically important area such as the Wee Bankie/Marr Bank complex.

Chapter 0 Summary

- The *IMPRESS* project aimed at tackling a specific part of the (potential) conflict between natural predators and fisheries: the effect of fishing and the risk of overfishing in an ecologically important area.
- The overall objective of the *IMPRESS* project was to determine the relationship between Sandeel Ammodytidae population characteristics (i.e. temporal and spatial patterns in abundance and age- and size distributions), hydrography (influencing prey availability), and the foraging success and breeding performance of four species of seabirds (functional response).
- A key part of the *IMPRESS* project was to develop and use sophisticated bird-borne loggers suitable for North Sea species in order to collect high quality data on foraging locations both in terms of distance from the colony and depth in the water column, the physical characteristics of the areas used by the birds for foraging, and prey capture rates. This information would be combined with data on seabird distribution and foraging behaviour collected at sea, with information on prey stock characteristics, hydrography, and data on breeding performance and population trends at colonies on land.
- Selected predator species under *IMPRESS* were Northern Gannet *Morus bassanus*, European Shag *Phalacrocorax aristotelis*, Black-legged Kittiwake *Rissa tridactyla*, and Common Guillemot *Uria aalge*; all with different foraging strategies, feeding capacities and prey preferences.

Sandeel fisheries, sandeels and other prey fish

- The fishery for sandeels is the largest single species fishery in the North Sea. Part of the explanation for the upward trend in annual sandeel landings over the last decades has been the opening up of new sandeel grounds, such as on the Wee Bankie/Marr Bank sandbank complex of the Firth of Forth in south east Scotland, where fisheries took off in the early 1990s. Although potentially of great consequence to local seabird, marine mammal and fish predators, sandeel landings from this area off the Scottish coast rarely constituted more than 10% of the total North Sea landings. Landings data suggest that, in most years, nearly all the sandeels caught from within the closed area were taken east of the Firth of Tay and Firth of Forth.
- Coincident with the increase in the removal of sandeels from areas close to the Scottish east coast, seabird breeding success at colonies along the coast started to decline.
- Concerned that the sandeel fishery might have influenced the decline in seabird breeding performance, fisheries managers prohibited fishing for sandeels close to the coast, from the Farne Islands in the south to north of Rattray Head in the north, and eastwards out to longitude 1°E. The fishery was closed in 2000, but fishing pressure was very low in 1999. Over the period 2000 to 2003 a limited amount of sandeel fishing was permitted in the area to allow the maintenance of the scientific catch and population structure statistics data-base at the Danish Institute for Fisheries Research. In 2003, when the fishery was to be re-opened, because of the absence of a clear mechanism to close the fishery once more should the problems reoccur, the decision was taken to maintain the fishery closure.
- Based on the most recent estimates of SSB, ICES classifies the North Sea stock as a whole as having reduced reproductive capacity. SSB in 2004 was estimated to be at a historic low value (325 000 t). SSB in 2003 was above B_{lim}, but has in 2004 decreased to below B_{lim} due to a historic low recruitment in 2002.
- In order to estimate prey availability to seabird predators, estimates of the abundance of sandeels active in the water column were required. FRS carried out acoustic surveys to provide such estimates from 1997 to 2003. Acoustic surveys also provided estimates of the abundance of other pelagic fish in the water column, such as Herring and Sprats.
- The alternative to surveying sandeels in the water column is to assess their density in the seabed at night when most sandeels are buried in the sediment. Two techniques have been employed to do this; dredging and grabbing. Dredges cover large areas of ground, taking samples of up to several hundred sandeels per 1000m^2 of seabed covered and are adequate for population age and length structure analyses. Grab surveys provide point estimates of sandeel density in suitable habitats.
- Acoustic survey and demersal trawl data, collected 1997-2003, suggest that total biomass of sandeels in the study area was significantly higher in the four years when sandeel fishing was prohibited (250 000t-335 000t) than in the three previous years when they had been fished (25 000t-89 000t).
- Biomass estimates of Herring from acoustic surveys (1997-2003), were significantly higher during 2000-2003 (4000t-6400t) than in the three earlier years (1700t-3800t). The biomass of Sprats in all years was relatively low (<3000t).
- In all the analyses where the operation of a sandeel fishery was used as a categorical variable to explore the effects of the fishery, 1999 was treated as a "fishery in operation" year. Technically this is correct since the fishery was not

closed until 2000. However, fishing effort in the area was much lower and the total sandeel catch taken was actually no higher than catches made for scientific monitoring when the area was closed to fishing.

- The data collected as a routine during the ICES coordinated international hydro acoustic survey for Herring in 2001-2004 in the study area at large were analysed to provide spatial patterns of sandeels within and beyond the principal study area. Spatial patterns were different in each of the years of survey, with high concentrations of sandeels in the water column much closer to the coast in 2001 and 2004 than in 2002 and 2003.

Oceanography

- Typical of a shallow sea, the water column for the principal study area was well mixed for most of the year. The onset of stratification was usually observed in April and reached a maximum in late July/ early August. The western and/or eastern extremes of the primary study area generally being the more strongly stratified regions. The western region, close to the coast, is influenced by fresh water while the eastern region away from the coast is deep enough for surface thermal stratification not to be mixed by tidal friction.
- Detailed observations allowed the defining of separate regions with different mixing and/or productivity characteristics and bathymetry: Inner and Outer Banks, the Shallow sea front and the Offshore stratified region, the Outer Bank region, Mixed (nearshore) Waters and Freshwater Influenced Waters (Fig. 3.2.8).
- Tides play an important role in the foraging of seabirds, and tidal flag information had to be provided. The speed of tide was defined in six phases: increasing North, maximum North, decreasing North, increasing South, maximum South, and decreasing South.
- Over the last 30 years, meteorological variability drove most of the inter-annual variability of both the onset of stratification (86% of the variance) and the spring bloom (70% of the variance), with variability in the spring solar irradiance being more important than variability in wind stress. The North Atlantic Oscillation (NAO) played a significant, but no dominant, role in generating inter-annual variability in the timing of spring stratification and the spring bloom.
- The daily output of our modelling work allowed relative annual estimates of the sum of primary production before the spring bloom, during the surface bloom and for the subsurface production after the spring bloom. All of these annual variables could be compared to both predator and prey population variables such as breeding success and growth.

Seabirds breeding: population trends, reproductive success and diet

- Breeding population trends differed among the four seabird species studied. There were *c* 45 000-48 000 Apparently Occupied Sites (AOS) of Northern Gannets on the Bass Rock colony during the IMPRESS project. Whole colony counts carried out in 1994 and 2004 suggested a continuous increase. Counts of European Shag nests declined sharply in 1999 due to a large proportion of adults not breeding that year, but numbers subsequently increased. Breeding populations of Common Guillemots increased markedly, but there was a continuous decline in Black-legged Kittiwake numbers between 1997 and 2003.
- Shags showed a general increase in breeding success over 1997-2003, except for 1999 when success was low. Guillemot breeding success showed an overall decline. The number of chicks fledged per pair in Kittiwakes was very variable, with no clear trend. Breeding success of Gannets, only available for 2002 and 2003 was consistently high, as in previous years.
- Breeding success during the three *IMPRESS* field seasons (2001-2003) varied markedly among the species, with that in Shags being the highest recorded at the Isle of May over the last 20 years, but with values for Guillemots being some of the lowest recorded. Kittiwake breeding success fluctuated, but was generally higher than during the late 1990s. Breeding success was higher in 2003 than in 2002 or 2001 in all four species.
- From diet studies, Shags were almost completely dependent on sandeels, with the exception of 1999, the year in which breeding success was low and when a large proportion did not breed. Kittiwakes also depended heavily on sandeels. The main prey brought in by Guillemots for their chicks was Sprats, but adult birds were found to have been feeding substantially on sandeels. Gannets, took a wide variety of prey. Guillemots and Gannets showed contrasting trends in the importance of sandeel in the diet during the period, with the proportion decreasing in the former and increasing in the latter.
- The importance of sandeels in the diet of the seabird predators has been demonstrated and evidence of similarities in patterns of seasonal change has been provided with a consistent shift from 1+ group to 0 group. Guillemots took the smallest 0 group, followed by Kittiwakes and Gannets. Fish were larger in 2002 than 2003, particularly those taken by Gannets, resulting in a significant interaction between species and year. The difference in sandeel size among the species was largely due to interspecific differences in the timing of breeding, rather than selection of different sized sandeels. The different predators were apparently sampling from the same sandeel population since in neither year were there marked discontinuities between the length/date relationships for the individual species.

Seabirds at-sea: distribution and foraging behaviour

- In the study area at large, the offshore seabird community comprised at least 37 different seabird species. Within the principal study area, the most abundant 15 seabird species were Common Guillemot (48.5%), Atlantic Puffin (21.4%), Black-legged Kittiwake (11.9%), Razorbill (10.7%), Northern Gannet (5.9%), Northern Fulmar (0.6%), Herring Gull (0.5%), European Shag (0.2%), Lesser Black-backed Gull (0.1%), Arctic Tern (0.1%), Manx Shearwater (0.1%), European Storm-petrel (0.0%), Common Gull (0.0%), Arctic Skua (0.0%), Great Skua (0.0%), and Great Black-backed Gull (0.0%).
- In comparison with the study area at large, the overall abundance of Guillemots, Puffins, Kittiwakes, Razorbills and Gannets is relatively high, whereas the abundance of Northern Fulmars is fairly low. It should be noted that the number of Shags observed is very low, this being the result of their inshore distribution; coastal areas where sea-going research vessels engaged in offshore censuses seldom venture.
- Clear-cut, generalised seabird distribution patterns were derived, with Gannets far-ranging, Guillemots and Kittiwakes highly concentrated in the western (nearshore) half of the study area at large, and with Shag concentrated in inshore waters (not well covered in these surveys).
- The main feeding area for East Scottish auks and Kittiwakes was found within approximately 100km from the coast, with peak densities usually slightly nearer the coast. Gannets originating from the Bass Rock colony occurred in the entire study area at large. Seabird densities and species richness declined and species composition altered with increasing distance to the UK coast. The principal study area, almost entirely within 90 km from land, was situated within the areas with highest mean top-predator densities and diversity of the northwest North Sea.
- The improved quality of data obtained from more sophisticated loggers is well demonstrated by results from Shags, where VHF telemetry was used in 2001, compass loggers in 2002 and GPS loggers in 2003. European Shags breeding on the Isle of May used three main foraging areas: inshore, west and north of the colony; and close to the island.
- Guillemots carrying compass loggers were foraging much closer to the colony than expected at-sea surveys, with the furthest distance from the colony estimated at 25.3 km. No birds flew to the Wee Bankie/Marr Bank region and some birds foraged close to the coast west of the colony.
- Kittiwakes carrying instruments used a wide variety of foraging areas, from inshore coastal areas in St Andrews Bay area out to the Wee Bankie/Marr Bank region. Mean maximum foraging range per trip was 37.0 ± 16.3 km (range 13.6 – 83.5 km). Mid-July foraging locations became more concentrated on the western edge of the Wee Bankie, but there was no difference in maximum foraging range between incubating and chick-rearing birds.
- From 762 high-quality locations over 147 PTT-days in 2002 and 727 over 110 PTT-days in 2003 Gannet Locations extended to the Bergen/Viking Bank (West Norway), Halibut Bank (NE Scotland), Fisher Bank (north central North Sea), Dogger Bank (south central North Sea) and the Outer Silver Pit (southern North Sea). Gannets made significantly longer trips in 2002 (41.2 ± 2.8 h) than in 2003 (24.6 ± 1.7 h) and travelled further from the colony in 2002 (mea*n* = 312 ± 18 km; Fig 5.5.8) than in 2003 h (mea*n* = 162 ± 15 km). The mean foraging range estimated by GPS loggers in 2003 was 190.4 ± 12.7 km, which was similar to the estimate of 162.2 ± 15.1 km derived from PTTs. Mean trip duration, estimated from GPS loggers in 2003, was 23.3 ± 1.9 h, which was very similar to the estimate of 24.6 ± 1.7h derived from PTTs. Mean uplinks for the PTTs per day in 2002 were 5.1 d^{-1}(± 2.1 SD) and 7.1 d^{-1}(± 1.6 SD) compared to GPS which generated fixes as frequently as every 3 minutes. As such, a much more complete picture of foraging trips was obtained.
- In biomass terms, the seabird community in the principal study area was dominated by auks (Guillemot, Puffin and Razorbill), Gannets and Kittiwakes (98.0% of all birds found in transect). The energy requirements of the seabird community in the principal study area was overwhelmingly dominated by the same species (99.8%). The energy requirements per unit area within the principal study area (118 380 kJ day^{-1} km^{-2}) were on average 3.9x higher than those in the study area at large (30 260 kJ day^{-1} km^{-2}).
- Most birds that were recorded as feeding participated in feeding flocks and most these flocks comprised several species (multi-species feeding associations, MSFAs). In the study area at large, in 12 out of 18 common species recorded, at least 80% of the feeding individuals were joining some sort of MSFA. A notable exception was the Shag (22.6%, n = 190). Within the principal study area, a similar pattern emerged, but with Kittiwakes (56.5%, n = 8452) and Shags (0%, n = 28). showing a lower tendency to participate in MSFAs.
- Feeding techniques were rather diverse in Gannets and Kittiwakes. Feeding Gannets were mostly deep plunge-diving or scooping and the latter activity was much more common within the principal study area than in the area at large. Scooping was entirely associated with MSFAs. Gannets associated with dolphins were typically deep plunge-diving and solitary Gannets were either shallow- or deep plunge-diving. Feeding Kittiwakes were dipping or shallow plunge-diving. Guillemots were observed pursuit diving from the surface mostly, but were occasionally pursuit plunging in attempts to keep up with fast moving fish shoals. Pursuit plunging was only frequently seen in 2004.
- From logger data, diving depth could be analysed. In Shags, the commonest foraging depth was between 21-30 m (50% in 2001, 48% in 2002, 62% in 2003), but mean dive depth was greater in 2003. There was no significant difference in the number of dives per trip between years. In Guillemots, the number of dives per bout varied from 12.2 in 2001 to 4.8 in 2003. In all three years, foraging depth varied considerably (2001: 1.1 – 67.0m; 2002: 0.5 – 68.9m; 2003: 0.7 – 64.0m). Depth distributions peaked between 41-60 m in 2001 (48% of dives) and 2002 (52%), but was

markedly different in 2003, when 59% of dives were <20 m deep. Comparing these data with results from 1997 and 1998 indicated that dive durations were shorter, particularly in 2003, but surface times were longer, such that dive efficiency was generally lower in 2001-2003. Mean foraging depth was between 39m and 43m in all years except in 2003, in which depth was markedly shallower. In Gannets, 1517 and 735 dives were recorded from 18 adults in 2002 and 2003 respectively. Dive depth did not differ between years (2002, mean = 2.50 ± 0.06 m; 2003, mean = 2.96 ± 0.10 m).

- Three major types of MSFAs were recognised: (1) human induced feeding flocks (birds associated with (fishing) vessels), (2) marine mammal-induced feeding flocks (birds attracted to hunting cetaceans or seals), and (3) 'natural' feeding flocks (seabirds, sometimes with marine mammals, jointly exploiting a shared resource).
- Between species, the importance of either MSFA type was very different. Of Guillemots for example, in the study area at large, 80.6% of the feeding individuals (*n* = 19 978) were found in 'natural' MSFAs and 19.0% were feeding solitary or with conspecifics only. Northern Gannets were represented near fishing vessels (42.8%) associated with dolphins or porpoises (18.6%), in 'natural' MSFAs (20.7%), or were feeding solitary or with conspecifics only (18.0%, *n* = 15 961). Kittiwakes were closer to Guillemots with 68.9% in 'natural' MSFAs and 19.7% as solitary or at least single-species feeders.
- Within the principal study area, relatively more birds joined 'natural' MSFAs in Guillemots (88.2%, *n* = 6567) and Gannets (56.0%, *n* = 2913), and with a slightly stronger tendency to feed among conspecifics in Kittiwakes (43.5%, *n* = 8452; 49.4% in 'natural' MSFAs).
- 'Natural' MSFAs were generally formed in coastal waters of very high seabird density and were nearly all encountered within 100km from the nearest coast. Flock size varied with distance to the coast, with numerous but relatively small MSFAs formed within 20km from the coast, fewer and larger flocks at 20-50km distance, and with numerous relatively small flocks at 50-70km distance.
- By comparing snapshot observational data of MSFAs, with the results of a model from probability theory, in which the formation and dissolution of the flock is entirely based on independent and random events, possible deviations between data and model would point to more complicated underlying mechanisms of flock formation and dissolution. The average ('natural' MSFA) flock size equalled 16.6 ± 0.75 (SE), with Guillemot and Kittiwake as by far the most abundant participants. The proportions in the flocks were not accordance with the relative densities at sea and the most aerial species, surface feeding gulls (both Kittiwakes and larger species), had a greater tendency to become recorded as flock participants than expected on the basis of their overall abundance at sea. The frequency distribution of flock size based on the field data deviated from the model expectations: for small flocks the decrease in (log) frequency with increasing flock size is faster than expected, whereas for large flock sizes it is much slower. This implies that small groups dissolute relatively easily.
- MSFAs formed around marine mammals mainly occurred in stratified offshore waters, and within c. 80km from the coast, cetaceans were largely ignored by seabirds.
- Time activity budgets were obtained for all four species during chick-rearing, using both PreciTDs and locational loggers (Shag), compass loggers (Guillemot), a flight activity sensor combined with a saltwater switch (Kittiwake), and PTTs, PreciTDs and GPS-TDs (Gannet). Shags made similar numbers of trips per day in 2001 and 2002, but the proportion of time spent foraging was greater in 2002, and less time was spent on land. The number of foraging trips per day was greater in 2003 than in 2002 or 2001, although the difference was not significant. There was no difference in the number of trips by Guillemots made per day between 2002 and 2003. In 2003, birds tended to spend more time flying and diving and less time resting on the sea compared with 2002. Kittiwakes made more trips per day in 2003 than in 2002 or 2001, and birds spent a higher proportion of time in foraging flight and consequently less time on the water. The percentage time spent at sea in Gannets did not vary between years. There was a significant positive correlation between time spent in flight and overall trip duration. On trips, Gannets spent 0.3%, 43.1%, and 56.6% of time respectively diving, flying and resting/swimming on the surface of the water.
- Gastric temperature loggers were used to measure prey capture rates in all four study species. However, major methodological problems were encountered with Kittiwakes and even after technical adjustments, the birds regurgitated their loggers before they were recaptured. It had to be concluded that this method was not appropriate for this species. Dives of Gannets, as well as feeding events, occurred all along the foraging trips, with the first dive of a trip performed at a median distance of 137.8 km from Bass Rock (range 21.7 – 167.1 km) in 2002, and of 57.42 km (range 1.29 – 275.92 km) in 2003. The first feeding events occurred at distances of 43.9 km (range 6.7 – 64.0 km) and 46.0 km (SD ± 16.2) respectively. The distances of the first dive and feeding event from the colony did not differ significantly between years. Shags were successful on approximately 10% of dives and in 55-65% of bouts. In Guillemot, as with Shags, ingestions could be associated with individual dives in some cases, and bouts in other cases but recorded success rate per dive (33%) was much higher than in Shags. Prey captures for chick provisioning will not be measured by the logger, since chick prey are carried in the bill, so success rate is likely to be even greater than measured.

Seabird energetics

- We investigated how biotic and abiotic factors influenced diving metabolic rates (water temperature, depth, digestive phase, bird condition), and we experimentally investigated the effect on cormorant prey capture behaviour of prey availability (fish density), prey size, light conditions, fish behaviour, bird condition (body mass), water temperature, and dive depth.
- Water temperature, dive depth, and digestive phase we demonstrated to be important factors that strongly affect the amount of energy which cormorants have to expend during foraging (dive depth not investigated in Shags).
- Abdominal temperatures remained fairly stable during shallow diving in European shags, which would indicate that they did not employ a strategy of regional hypothermia to prolong dive duration.
- Foraging success of cormorants foraging on live fish (Rainbow Trout) depended to a large degree on prey availability (fish density), while fish behaviour (shoaling or not) had important consequences for predator performance.
- Prey size, light conditions, bird condition (body mass) and water temperature had little impact on cormorant foraging behaviour within the range tested. Dive depth greatly affected dive duration of cormorants but had little effect on the overall success rate of dives.
- Foraging seabirds are constrained by a delicate balance of the following three components: (a) the time they can allocate towards food acquisition; (b) the energy demands associated with their activities and (c) the food they are able to acquire. Confronted with a decline in availability of a particular prey species (e.g. sandeel), seabirds have a number of potential options to maintain their DFI at a sustainable level. For some it might be possible to switch to other prey. Alternatively, they might be able to increase their foraging effort in a number of ways.
- Dietary information suggested that Kittiwakes and Shags may be less able to switch to alternative prey compared to Guillemots and Gannets. In the case of Kittiwakes this might be exacerbated by its surface feeding habit that limits its foraging abilities to prey items at, or close to, the surface.
- Shags and Guillemots were estimated to have sufficient time and energy to allow them to increase their foraging effort considerably, Kittiwakes and Gannets appeared more constrained by time and energy respectively. This study suggested that during chick-rearing Gannets are working at the highest metabolic level of all species considered and hence, have the least physiological capacity to increase foraging effort. Therefore, Gannets could potentially be very sensitive to reductions in prey availability. To compensate for their energetically costly life, however, Gannets use a highly profitable foraging niche.
- Estimates of breeding populations from Kincardine and Deeside in the north to Northumberland in the south, on DEE for adults and chicks, an energy content of 5 kJ g^{-1} fish and an absorption efficiency of 0.8, reveal a total consumption for the period June-July of about 16 000t for our four study species within the principal study area. Estimates based on numbers seen foraging at sea in the principal study area yield a total of at least 8000t. Both estimates are low compared to the total prey stock estimate averaged over the years: *c.* 197 000t (1/12 to 1/25). Yet, they form a significant part of the minimum prey fish stock found between 1997 and 2003 of 27 000t, which is only about 2 to 3 times larger than the estimated consumption of these four top-predator species alone.
- Insufficient knowledge has become available on the functional reponses to fully apply the 'individual based static approach'. Using the maximum intake rate (while foraging) observed in the experiments with cormorants, a prey density of about 40 mg m^{-3} is required. Acoustic surveys over the years 1997 until 2003 estimated the total biomass of 1+ group sandeel in the *IMPRESS* study area to be on average 135 000t, or on average 300 mg per m^3. The estimate is much higher than the required 40 mg m^{-3}, the prey density at which for example Shags should be able to meet their energy requirements.

Seabirds, foraging habitat characteristics from a combination of methods

- The density of MSFAs per unit area surveyed within the principal study area, and the mean numbers of seabirds within such flocks were very low in (nearshore) Mixed Waters. Freshwater Influenced Waters and Offshore Stratified Waters were found to "produce" many more and consistently larger flocks, while by far the largest MSFAs were found in the Bank Areas.
- Within the principal study area, corrected for the size of the respective zones defined by bathymetry and hydrography, Northern Gannets acquired 24% of their energy in Freshwater Influenced Waters, 11% in Mixed Waters (mostly in deeper waters), 59% over the Banks and 7% in Offshore Stratified Waters. Kittiwakes acquired 53% of their energy on the Banks, 18% in Offshore Stratified Waters, 27% in Freshwater Influenced waters and only 2% in Mixed Waters. Guillemots acquired 48% of the energy on the Banks, 20% in Offshore Stratified Waters, 24% in Freshwater Influenced Waters and only 8% in Mixed Waters. A combination of all data suggests that for these three species the Bank Areas are the most important foraging grounds (49% of the energy acquired) and that Mixed Waters near the coast were relatively unimportant (8%). All Shags were foraging in waters that have been categorised as Freshwater Influenced and this is the area where these birds seemingly acquire most (if not all) the energy required.
- Surface feeding seabirds require processes that bring prey to the sea surface. Horizontal frontal systems are predicted to provide such opportunities. From at-sea surveys, it was demonstrated that Kittiwakes broad zone off the Scottish

east coast during the breeding season, with peak densities to the shallow-sea front (i.e. the seaward side of the mixed coastal zone). Dipping, shallow plunge-diving, and surface pecking were typical forms of feeding behaviour observed in Kittiwakes. Kittiwakes were commonly seen to join type 3 ('natural') MSFAs and most were feeding in freshwater-influenced coastal waters and over the banks. Kittiwakes were seemingly constantly searching for social feeding large auks (Guillemots or Razorbills) that were driving fish balls towards the surface in a concerted effort. The foraging distance of instrumented Kittiwakes originating from the Isle of May accorded well with the distance from the breeding colony to the shallow sea front, which runs parallel to the coast in the principal study area. The front appears to form an outer barrier for breeding Kittiwakes, and foraging occurred throughout the zone between the colony and the front. Thus, the colony-based results from the activity loggers accord fairly well with at-sea surveys and telemetryand demonstrate a consistent pattern of distribution of Kittiwakes and other surface feeders at, and westwards of, the front, with very few east of the front. However, the shallow sea front was not favoured by breeding Kittiwakes over other habitats within their foraging range. This result may reflect intrinsic constraints of breeding individuals.

- The shallow sea front is important for mid-water divers too, but in addition, these species can exploit the water column, and would be expected to target depths where prey are concentrated. At-sea surveys suggested Guillemots were essentially highly widespread in a broad zone along the UK coast, with relatively lower concentrations of feeding individuals in mixed coastal waters and beyond the shallow sea front in offshore stratified waters. Foraging locations from Isle of May breeding birds equipped with compass loggers in 2002 and 2003 suggested that Guillemots from this colony foraged considerably nearer the colony than these overall densities would suggest. A subsequent analysis of directions of flight of birds carrying fish in the principal study area, suggested a high degree of overlap between logger data and at-sea data with regard to feeding range, such that birds flying towards the Isle of May were exclusively seen in and immediately around the area where instrumented birds were found foraging in 2002 and 2003. This suggested that adults catching prey for their chick rarely did so on the Marr Bank (Outer Bank area and adjacent offshore stratified water) and it implied that Isle of May breeding birds utilise only a small part of the principal study area and mainly the west side of the Wee Bankie/Marr Bank complex. The data suggest that the bulk of the (adult) Guillemots in the eastern part of the principal study area breed in Kincardine and Deeside and in East Lothian, Berwickshire and or Northumberland. Estimated maximum foraging ranges for Guillemots from the Isle of May from sightings during ship-based surveys are in the range of 50km, whereas those from St Abb's Head can be estimated at *c.* 55 km, for Guillemots nesting on the Farne Islands at 70 km, and for birds nesting at Fowlsheugh at at least 110 km.
- In contrast to other species groups, the feeding distribution of benthic feeding species was not expected to be associated with fronts or thermoclines. In all three years, Shags were foraging inshore of the Isle of May and the water they foraged in was very mixed. Ship-based surveys contributed little useful material for this inshore species. The lack of a preference for different phases of the tide by Shags suggests that there are patterns in the behaviour of (adult) sandeels that are more important in determining the timing of foraging than reduced distance between sea surface and foraging habitat apparent during low tide.
- Compared with the other three species, Northern Gannets were by far the furthest ranging species, foraging abundantly within and beyond the principal study area. Behavioural observations during ship-based surveys indicated that the foraging techniques, the tendency to participate in multi-species feeding frenzies, the tendency to join hunting cetaceans as well as the opportunities to scavenge at fishing vessels varied considerably. From activity recorders, attached to the Gannets, diving locations and 'shallow-feeding' locations could be pin-pointed. Gannet behaviour labelled as 'surface feeding' was observed in exactly the areas where type 3 MSFAs were joined most frequently by Gannets and where scooping behaviour was observed during surveys.
- The continuous oceanographic data from the *Pelagia* 2003 cruise produced a very detailed 'snapshot' of the water column characteristics underneath foraging birds. The mixing properties (as indicated by stratification) of the water column in which different species feed were significantly different. Gannets were found foraging in the most stratified water, while Kittiwakes used water that was less stratified than that of the Gannets, but more so than the water columns over which Guillemots mainly foraged. Within the principal study area, Guillemots were relatively evenly distributed across the regions, but were most abundant in the Inner Bank region. Nearly half of all Kittiwakes seen foraging were observed within the Outer Bank region and two thirds of all Gannets were found in the Offshore stratified region. This separation of bird species determined mainly by the difference in stratification (using top and bottom temperature differences) indicates that their foraging habitat can be defined using rather straightforward and predictable physical characteristic of the water column.
- The need for stratified water implies that Kittiwakes are more limited in the locations in which they can forage than Guillemots and at times of greater mixing they may have to fly greater distances to deeper water where stratification is more likely to be present. Guillemots were found to be able to exploit a greater range of water mass characteristics but do not select to forage in water that is strongly stratified. preferentially foraged in the strongly stratified waters seaward of the Shallow sea front.
- Kittiwakes and Gannets responded significantly different at various tidal phases. Decreasing tidal speed during the ebb were phases mostly used by Kittiwakes and Gannets targeting the maximal current speeds on both the ebb and flood tides in their preferred foraging region of the Shallow sea front. Guillemots showed almost no difference in foraging abundance with tidal phase.

- No clear absolute relationship between the density of any seabird species and the density of either sandeels, Herring or Sprats could be determined. High densities of each of the major sandeel, or small pelagic fish, predators could be linked to patches of one or other, or all three, of the prey species.

Inter-annual variability

- The output from the finalised 1- D physical-biological model was evaluated for the period 1974-2003 and this could be used in conjunction with the long-term data from seabirds nesting on the Isle of May to propose mechanisms linking meteorological conditions and the effect on primary production to higher trophic levels. The timing of stratification and spring bloom were used as possible indicators of sandeel availability. The initiation of the annual increase in primary production is presumably the driving factor for the emergence of adult sandeels to feed, and thus the timing and progress of the spring bloom may be important for seabirds targeting 1+ group sandeels. In later phases of chick-rearing, seabirds depended more on 0 group sandeels. Spring conditions and their effect on the timing of primary production will have influenced the growth and survival and therefore the availability or profitability of 0 group sandeels.
- During 1997-2003, the onset of stratification occurred between 7 April and 30 April (23 d difference between seasons at most) and was very early in 2002 (7 April) and very late in 2001 (30 April) (Table 3.1). Spring bloom (when modelled chlorophyll exceeded 5 mg m^{-3}) lasted between 5.8 (2001) and 7.5 weeks (2000) and commenced between 14 April (2002) and 1 May (2001), or a two-week difference between seasons.
- Breeding success of Kittiwakes increased by 0.13 chicks $pair^{-1}$ for every five days delay in timing of the spring bloom. There was no evidence that the effect of date of the spring bloom on breeding success was different in fishing and non fishing years, but breeding success was 0.66 ± 0.098 (SE) chicks higher in years without fishing than in years with fishing. The final model containing both the effects of spring bloom date and the sandeel fishery explained 74% ($P< 0.001$) of the variance in breeding success. Separating years with or without a fishery, the effect of climate alone explained 56% of the variance in breeding success in years without a fishery and 10% of the variance in years with a fishery. This suggests that important climatic variables are more easily identified in the absence of the confounding effects of a fishery.
- Surface feeding Kittiwakes are more dependent on prey present in the upper water column, and this finding suggests that a later spring bloom may have increased the availability of prey in the upper water column during the breeding season through a slowing down in the growth of juvenile sandeels, possibly coupled with a delay in the emergence of adult sandeels. With elevated levels of food occurring relatively late in the season, the trade off between predation and feeding may force fish to take longer to acquire adequate levels of food needed to survive the next winter.
- For Guillemots, annual variation in breeding success was not explained by the timing of spring blooms, nor stratification in either oceanographic region or the sandeel fishery. Guillemots are pursuit divers, less constrained in their foraging depths than Kittiwakes, and Guillemots are probably less likely to encounter food limitation. This would explain why annual variations in breeding success of different species at the same colony utilising similar prey may not be in phase and that Guillemot and Kittiwake breeding success on the Isle of May are not correlated
- A high proportion of the variation in the breeding success of three study species of seabirds can be explained when the date of egg laying relative to the timing of the bloom is taken into account. The results indicated that for Kittiwakes and Shags there is an interaction between the timing of events and the effect of the fishery. The best model explaining breeding success for Guillemots used the difference in days between the timing of the bloom and the median date of egg laying as the explanatory variable. We hypothesise that the state of individual birds drives the timing of egg laying and that their states are influenced by the local environmental conditions which affect food availability earlier in the year during the pre-breeding season.
- Comparing annual estimates for the amount of production during the bloom period and the duration of the bloom to the breeding success of each of the three species breeding on the Isle of May, it appeared that for both Guillemots and Kittiwakes, the addition of the pre-bloom and bloom production or length of bloom provided better models for breeding success than models simply using variables linked to timing. For Shags the timing variables remained the better explanatory variables. However, the best models for all three species include fishing as a variable or an interaction term which helps to explain the variance in annual breeding success. These results provide further evidence that the presence of a fishery in the area has an additional adverse effect on seabird reproductive output.
- Between years, in the study area at large, the density of Guillemots was fairly consistently four times the density of Kittiwakes which was in turn about twice the density of Gannets at sea. Within the principal study area, however, a rather erratic pattern in the relative abundance of Guillemots was found. It is most likely that the variability has been caused by non-breeders that were more abundant within the principal study area in some years than in others.
- The proportion of Guillemots and Kittiwakes foraging in natural MSFAs in the study area at large was generally very high, but notably lower in 2002 and 2003. In Gannets, the interest to join these frenzies in the area at large was substantially lower. All species showed a remarkable variability in their tendency to forage within natural MSFAs in the principal study area, with very high values for all three species in 1997 and 2001 and a high figure for Guillemots and Kittiwakes in 2004.

- There was considerable inter-annual variability in most parameters measured. The year 1999 came out as an extreme season, with very low prey fish stocks (all species), a low presence of sandeels in the water column, much reduced breeding success in Shags, Guillemots and Kittiwakes, and low numbers of seabirds at sea in the principal study area. It was a year when stratification developed rather late, but spring bloom occurred as normal, and there was no commercial fishery for sandeels of significance. Rather few Kittiwakes were observed to participate in natural MSFAs, probably in the absence of (suitable) Guillemots in the area. By contrast, 2001 was a season in which rather high prey-fish stocks were found, with abundant sandeels in the water column, substantial amounts of Herring and Sprat, with a late development of stratification and spring bloom, high densities of Guillemots and a very strong tendency by Gannets and Kittiwakes to join these birds in natural MSFAs.
- Sandeel biomass was significantly higher in 2000-2003 than it was in the three years prior to the project and the reproductive success of Shags and Kittiwakes was relatively high in these years, albeit variable in Kittiwakes. For the Guillemot, however, the reproductive success declined and relatively few sandeels were brought into the colony in recent years
- Despite several significant correlations, the variability of the material collected from year to year is substantial and the predictive value of the parameters measured is relatively low. Mechanisms influencing prey availability are clearly species-specific, but other factors must have influenced breeding populations and reproductive success, given the contrasting trends in the seabird population monitored on the Isle of May.
- The year 2004 was a season when no fieldwork under *IMPRESS* was scheduled. However, in response to concerns raised in the northwest North Sea, notably in Shetland, that breeding was seriously delayed and that breeding success would be low again, a ship-based survey was scheduled to be able to evaluate any differences with previous seasons. We have evidence that nesting was seriously delayed in some species (notably Guillemots), but with timing of nesting and fledging near normal in others (for example in Razorbills). On the nearby Farne Islands, alternative prey fish were fed to terns, suggesting a scarcity of sandeels. In the North Sea as a whole, sandeel stocks were exceptionally low and substantial non-breeding (or breeding failures) of seabirds occurred at the Northern Isles of Britain. During the ship-based surveys in July 2004, a highly different feeding method was observed, described as ‘drive hunts’. Natural MSFAs in 2004 were different from any of the (9) preceding years in that neither avian nor mammalian predators seemed to be the driving force, but that large schools of fish occurred near the surface, travelling fast, with seabirds and marine mammals following an trying to keep up. Wee Bankie, normally packed with foraging seabirds, few birds were seen, and chicks of Guillemots (later than normal) appearing at sea were smaller than in any previous year.
- Observations were done on breeding success of seabirds on several study plots including the Isle of May and a very poor breeding season was reported for Shags (as bad as 1999), all three auks on the Isle of May had a very low success (Guillemot lowest on record, Razorbill second lowest), Kittiwakes reproduced less than the long-term average, and Fulmar production was the lowest ever recorded. These results should be put into the context of a much larger area with the productivity for most species being the lowest in recent history and sandeel shortages were evident from dietary studies in several areas (Wilson 2004).
- Changes in numbers of many North Sea seabirds over the last 15-20 years have varied from long-term increases in some to declines in others. Combining information on at-sea distribution and activity (both from visual observations and from data collected with instrumented individuals) with oceanographic data has highlighted the complex interplay between seabird foraging success, feeding location and inter-specific competition and facilitation. Thanks to multi-disciplinary projects such as *IMPRESS*, do we begin to understand the functional links between marine predators, their prey and the marine climate and may we thus come closer to ecosystem-based fisheries management. However, as the results presented here clearly indicate, we are still some way from having all the background knowledge required for such an approach. Given the increasing pressures on the North Sea ecosystem from both fisheries and climate change, using top predators to monitor ecosystem health is an attractive concept. Simple signals such as the breeding success or population trend of one or few species to monitor the well-being (or prey availability) of a complex and large community do not provide sufficient insight necessary for an adequate management of ecologically important areas.

Prey fish stocks, notably sandeels, prior to and following the year 2000 in the principal study area were an order of magnitude different. Many seabirds were under stress when sandeel stocks fell below 100 000t, while breeding success was generally high in 2000-2003, when prey stocks were on average well in excess of 250 000t. A simple advice to stay on the safe side with a sandeel stock of at least 250 000t is not given, because several studies demonstrated ecosystem scale effects of sea surface warming in the Northeast Atlantic, likely to alter the spatial distribution of primary and secondary pelagic production, and eventually (if not already) affecting top-predators in the northwest North Sea. Long-term climatic and oceanographic cycles regulate seabird populations on decadal time-scales and seabirds in the North Sea have been increasing for decades, apparently in response to a combination of reduced persecution and greatly enhanced prey availability. Their success may be about to change, if we understand the signals well and the recent concerns about the impact of climate change on the North Sea ecosystem, coupled with the largely unexplained crash in North Sea sandeel stocks in 2002-2004 would call for extreme care with an important area such as the Wee Bankie/Marr Bank complex.

Chapter 1 Introduction

World fisheries have expanded, diversified, intensified and made technological advances. Overfishing has been a concern for at least several centuries (Pauly *et al.* 1998; Pauly & Maclean 2003; RCEP 2004), and Jackson *et al.* (2001) concluded that ecological extinction caused by overfishing precedes all other pervasive human disturbance to coastal ecosystems, including pollution, degradation of water quality, and anthropogenic climate change. As the current crisis of global fisheries worsens, solutions need to be found not only to resolve the fisheries problems, but more so to protect our natural resources and marine ecosystems for future generations (Jackson *et al.* 2001; Pauly & MacLean 2003; Kaschner & Pauly 2004; Rattcliffe 2004).

Seabirds are increasingly viewed as an important component of marine ecosystems, particularly in temperate and polar regions (Croxall 1987). They feed at a variety of trophic levels but, in general, are usually at the top end of food chains, preying chiefly on small pelagic fish, crustaceans, cephalopods and young stages of demersal fish. The competition between apex predators - apart from seabirds also pinnipeds, whales, dolphins, and sharks - and fisheries is an issue still triggering heated debate (Bailey 1986; Duffy *et al.* 1987; Bailey 1989; Houston 1992; Ichii *et al.* 1996; Furness 1999; Víkingsson & Kapel 2000). The impacts of fisheries on seabird communities are indeed complex and varied (Tasker *et al.* 2000; Camphuysen 2001; Furness 2003). While by-catches in fishing gear have caused direct mortality and major reductions in certain seabird populations, other fisheries enhance foraging opportunities and may help increase seabird numbers. It has been argued, that the vast amounts of fish consumed by apex predators could otherwise - perhaps - have been available to the fisheries (Houston 1992; Stefanson *et al.* 1997; Schweder *et al.* 2000; Cowx 2003; but see Kaschner & Pauly 2004). It has been argued that the overfishing of large predatory fish has led to increases in the survival and stocks of young fish with seabirds generally profiting from this newly established and abundant food resource (Jones 1983; Bailey *et al.* 1989; Camphuysen & Garthe 2000; Camphuysen 2001). As a result, and apparently against all odds, while catches from the fishing industry rose sharply and while more and more fish stocks became harvested unsustainably, most seabird populations – overall – increased (Cramp *et al.* 1974; Lloyd *et al.* 1991; Mitchell *et al.* 2004).

Still, from the marine ecosystem's perspective, there were sufficient reasons for concern. Ecosystem effects of prey stock collapses influenced or caused by the fishing industry were often identified to negatively affect top-predator survival or reproductive success (Duffy 1983; Avery & Green 1990; Furness 2003; Rattcliffe 2004). Depletions of predatory fish stocks in the North Sea may perhaps have more than compensated for quantities of small fish removed by modern industrial fisheries, but high levels of fishing have altered the makeup of marine ecosystems, leading to increased ecosystem instability. The impacts of fisheries are often difficult to assess against a background of environmental and anthropogenic influences (Furness 2003). However, there is growing evidence that the effects of fisheries on targeted resources go well beyond those imposed by apex predators (Trites *et al.* 2004).

The *IMPRESS* project has not been designed to solve world fisheries issues, but aimed at tackling a specific part of the (potential) conflict between natural predators and fisheries. In the North Sea, the Lesser Sandeel *Ammodytes marinus* is a major prey item for many seabirds, particularly during the breeding season (Furness & Tasker 1997, 2000; Wanless *et al.* 1998; this report). Within the North Sea, sandeels are a principal prey also for pinnipeds, cetaceans as well as for many large predatory fish. Sandeels are currently the target of the largest single species fishery in the North Sea (Figure 1.1-1-2) and this has led to high profile concerns being raised about the potential impact of this fishery on seabirds (Monaghan 1992; Huntington *et al.* 2004; ICES 2004). Although the extent to which sandeel abundance is influenced by industrial fishing is uncertain, large catches taken from restricted geographical areas may affect sandeel densities and so influence food supply to other predators (Anon. 2004). There is increasing evidence that sandeels in the North Sea do not constitute a single homogenous stock, but may consist instead of several discrete stocks (Proctor *et al.* 1998; Pedersen *et al.* 1999). Fishing effort for the species is also patchily distributed and there is concern that over-exploitation of sandeel stocks may have occurred at local spatial scales. Several studies pointed out that seabirds performed less well in years or periods of sandeel shortages, whether or not exacerbated by industrial fisheries (Monaghan *et al.* 1992; Rindorf *et al.* 2000). The industrial fishery off the Firth of Forth in southeast Scotland was a reason for concern; so much so that a fishing moratorium became established (Box 1).

The concerns about the effects of fisheries on marine ecosystems in general, and on seabirds in particular, have been the stimulus for a series of major research projects to investigate the interactions between seabirds, sandeels and the industrial fishery, initially in Shetland (Monaghan 1996, Wright 1996) and more recently off the coast of mainland Britain. The *IMPRESS* project was designed to build on work performed under the *ELIFONTS* (Effects of Large-scale Industrial Fisheries on Non-target species) and *MIFOS* (Modelling the Impact of fisheries on seabirds) projects (Rindorf *et al.* 2000; Ollason 2000). The *MIFOS* and *ELIFONTS* projects took a comparative approach and used seabirds with contrasting breeding and feeding ecologies to determine species-specific relationships between predator performance and sandeel availability (e.g. Monaghan 1996, Rindorf *et al.* 2000). They also sought to investigate some of the behavioural mechanisms underpinning these population responses by deploying data loggers and other electronic devices on breeding adults (e.g. Monaghan *et al.*

1994, Hamer *et al.* 2000). However this approach was severely limited by the lack of off-the-shelf, low mass loggers suitable for many of the small-bodied seabird species in the North Sea seabird community.

The data on seabird abundance, distribution, diet and foraging behaviour collected as part of IMPRESS between 2001 and 2003 differed from comparable data from the *ELIFONTS* and *MIFOS* projects in one crucial way, namely that the industrial sandeel fishery on the Wee Bankie and Marr Bank was closed throughout this period. The *IMPRESS* results therefore reflect responses of seabirds in this area in the absence of any direct effects of a commercial fishery taking place during the breeding season. It should however, be noted that a limited fishery was carried out for scientific purposes.

The overall objective of the *IMPRESS* project was to determine the relationship between sandeel population characteristics (i.e. temporal and spatial patterns in abundance and age- and size distributions), hydrography (influencing prey availability), and the foraging success and breeding performance of four species of seabirds (functional response). Traditionally, seabirds have either been studied at-sea or at the breeding colony and few studies have attempted to combine the two approaches. However, such integration was a key objective for the IMPRESS project. Accordingly, long-term data on at-sea abundance and habitat usage were combined with long-term colony-based data on breeding population size, vital rates, breeding phenology and diet.

A key part of the *IMPRESS* project was to develop and use sophisticated bird-borne loggers suitable for North Sea species in order to collect high quality data on foraging locations both in terms of distance from the colony and depth in the water column, the physical characteristics of the areas used by the birds for foraging, and prey capture rates. This information would be combined with data on seabird distribution and foraging behaviour collected at sea, and with data on breeding performance and population trends at colonies on land. The two approaches provided complementary data on foraging behaviour: colony-based work using data loggers provided detailed information on foraging location and behaviour of individuals of known origin and status; at-sea work provided insights into the importance of conspecific and interspecific interactions and links between foraging activity and hydrographic characteristics.

Box 1. Sandeel fisheries and a commercial fishing ban

Simon Greenstreet

Sandeels constitute important prey for many seabird species foraging in the North Sea. Some of the major sandeel fishing grounds are situated in the vicinity of seabird colonies and there is considerable overlap between the distributions of post-settlement sandeels, seabirds at sea and the activities of the industrial fishery. This has led to concern over the potential impact of the fishery on seabirds. During the late 1980s and early 1990s, attention focused on interactions between seabirds, sandeels and industrial fishing around the Shetland Islands in the northern North Sea. The breeding success of several seabird species on Shetland declined, coincident with a reduction in the amount of sandeels in their diets, apparently in response to variation in sandeel availability. More recently the region of greatest concern for seabird ecologists has switched to the fishing grounds off the Firth of Forth, southeast Scotland, in particular the Wee Bankie, Marr Bank, Berwick's Bank and Scalp Bank. The fishery for sandeels on these banks first occurred, to any significant extent, in 1991, and by 1993 exceeded 100 000t, dropping back to around 50 000t annum^{-1} in subsequent years. Nine major seabird colonies in and around the Firth of Forth are home to over 150 000p of breeding seabirds. During the breeding season the diet of several species consists almost entirely of sandeels, and their requirements may be as much as 17 000t each summer. Several species are heavily dependent on the sandeels on the banks where this fishery has developed.

The effects of the Wee Bankie industrial fishery on the seabirds and marine mammals have not been the only concerns raised. Sandeels feature strongly in the diets of several important commercial fish species, such as Whiting, Cod, Haddock and Mackerel. Local fishermen operating out of ports in the Firth of Forth and along the coasts of southeast Scotland and northeast England have been concerned that the sandeel fishery has reduced feeding opportunities for these piscivorous fish, and helped to contribute to a decline in their abundance on local fishing grounds. A fishing ban was introduced in 2000 and was intended to be put in place until 2003. In 2003, because of the absence of a clear mechanism to close the fishery once more should problems reoccur, the decision was taken to maintain the fishery closure. At present it appears that commercial sandeel fishing in this area will remain prohibited until a formal management protocol for opening and closing the fishery in response to sandeel stock management issues or marine wildlife conservation concerns can be introduced.

Bailey R.S., Furness R.W., Gauld J.A. & Kunzlik P.A. 1991. Recent changes in the population of the Lesser Sandeel, *Ammodytes marinus* Raitt, at Shetland in relation to estimates of seabird predation. ICES Mar. Sc. Symp. 193: 209-216.

Danchin É. 1992. Food shortage as a factor in the 1988 Kittiwake *Rissa tridactyla* breeding failure in Shetland. Ardea 80: 93-98.

Furness R.W. 1996. A review of seabird responses to natural or fisheries-induced changes in food supply. In: Greenstreet S.P.R. & Tasker M.L. (eds). Aquatic predators and their prey: 166-173. Fishing News Books, University Press, Cambridge.

Heubeck M. (ed.) 1989. Seabirds and sandeels: proceedings of a seminar held in Lerwick, Shetland, 15-16th October 1988. Shetland Bird Club, Lerwick.

Monaghan P., Uttley J.D. & Burns M.D. 1992. Effect of changes in food availability on reproductive effort in Arctic Terns *Sterna paradisaea*. Ardea 80: 71-81.

Poloczanska E.S., R.M. Cook, G.D. Ruxton & P.J. Wright 2004. Fishing vs. natural recruitment variation in sandeels as a cause of seabird breeding failure at Shetland: a modelling approach. ICES Journal of Marine Science 61: 788-797.

Wright P.J. 1996. Is there a conflict between sandeel fisheries and seabirds? A case study at Shetland. In: Greenstreet S.P.R. & Tasker M.L. (eds). Aquatic predators and their prey: 154-165. Fishing News Books, University Press, Cambridge.

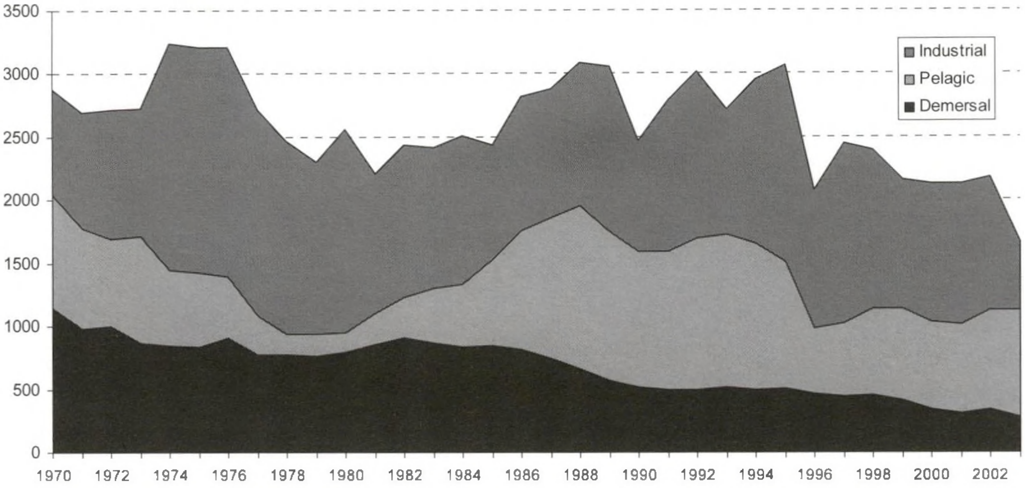


Figure 1.1. Estimated landings ('000 tonnes) in the North Sea from demersal, pelagic and industrial fisheries, 1970-2003 (ICES 2004)

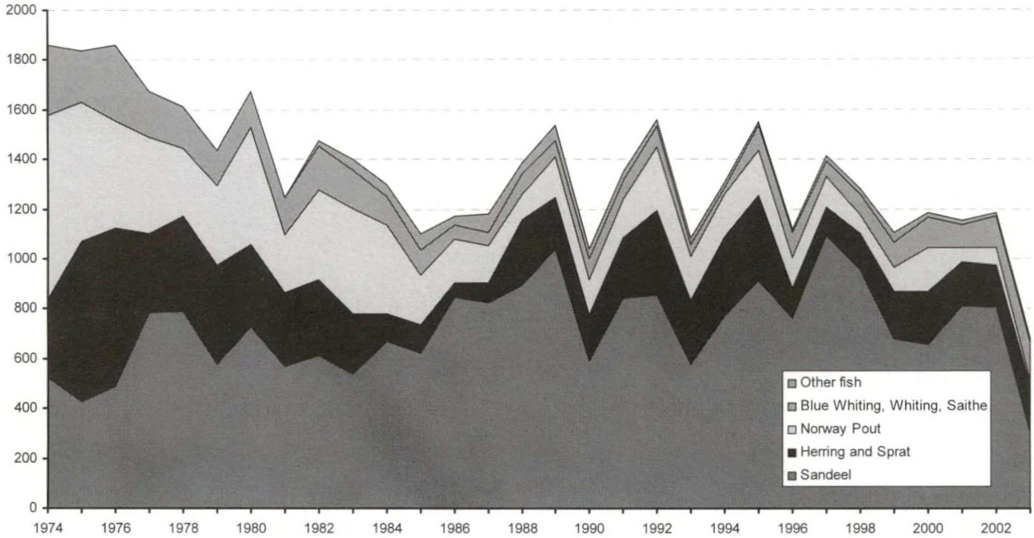


Figure 1.2. Species composition in the Danish and Norwegian small-meshed fisheries ('000 tonnes) in the North Sea, 1970-2003 (ICES 2004)

Detailed specific knowledge of hydrography, sandeel abundance and foraging strategies of top-predators has been obtained in a small, rich study area, previously targeted by industrial fisheries, but where a (industrial) fishing moratorium was kept in place throughout our work (Wee Bankie, W North Sea). The predicted geographic distributions of seabird sandeel consumption based on habitat characteristics, the constraints and opportunities faced by breeding seabirds utilising sandeels in the North Sea (feeding range, timing), and specific information on prey selection (age- and size classes), could be used to model natural fluctuations and the effects of oceanographical conditions on prey availability and, hence, seabird reproductive success. This should enhance our understanding as to exactly how and where seabirds forage, and ultimately how and where potential conflicts with industrial fisheries may arise. This knowledge should be used to define exploitation strategies of the industrial sandeel fisheries that mitigate the impact on the top-predators of the marine ecosystem.

Oceanographic data were obtained by using moored instruments recording temperature, salinity, current direction and speed. Dedicated ship-based surveys were conducted measuring hydrography, age- and size-structured sandeel abundance, as well as foraging activity and foraging interactions of seabirds. Breeding performance and foraging activity was studied at the same time from seabird colonies and the link between hydrography, predators and prey has been evaluated by spatial statistical approaches (GIS) and by modelling the mechanisms of the foraging process. The behaviour and physiology of seabirds has been studied in controlled laboratory experiments to provide the modelling work with additional information.

Selected predator species under *IMPRESS* were **Northern Gannet** *Morus bassanus*, **European Shag** *Phalacrocorax aristotelis*, **Black-legged Kittiwake** *Rissa tridactyla*, and **Common Guillemot** *Uria aalge*; all with different foraging strategies, feeding capacities and prey preferences. Being a follow-up project in which several key-researchers were able to continue their data series, *IMPRESS* could make use of a much longer time-series of material than would otherwise have been possible. The actual spin-off of a large, multi-disciplinary project such as *IMPRESS* is comprehensive, with numerous oral presentations and peer-reviewed publications appearing, or having appeared, in a variety of scientific conferences and journals. A substantial part of the work has been reported and reviewed at and following a conference organised by *IMPRESS* and the Sea Mammal Research Unit (St Andrews) at the Zoological Society in London, 22-23 April 2004, as the second phase of consultation. Much of that work will be published in the conference proceedings (Boyd *et al.* 2006), but this material was extended and re-used in the present document. Future analyses will no doubt lead to a further stream of publications and presentations yet to come.

Kees Camphuysen

with contributions from Simon Greenstreet and Sarah Wanless

Sandeels (courtesy Marine Laboratory Aberdeen)

1.2 Report structure

This is the final report of the *IMPRESS* project and as such a summary of work done and results obtained. The report is structured as follows:

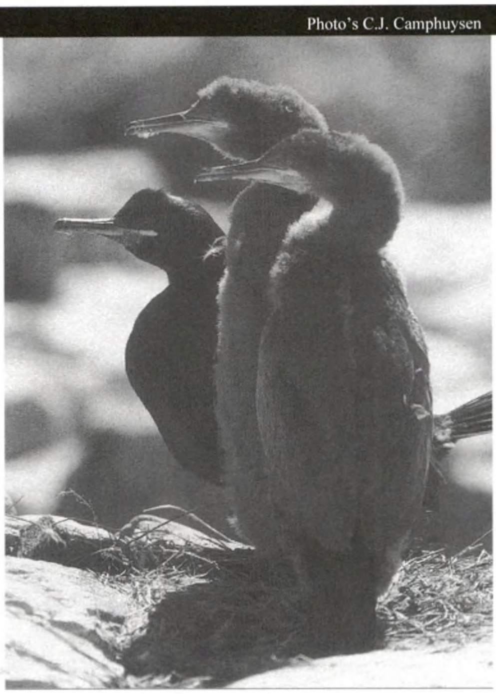
Chapter 1.	A general introduction followed by sections on report structure, descriptions of study area(s) and study species, summaries of existing data made available to the project, methods and planning of field studies, logger development, experiments with birds in captivity and consultation (with contributions from each of the chapter authors).
Chapter 2.	Sandeels and industrial fisheries for sandeel (S Greenstreet)
Chapter 3.	Oceanography (B. Scott, J. Sharples and O. Ross)
Chapter 4.	Sandeels in the Wee Bankie area (S. Greenstreet, E. Armstrong, H. Fraser, G. Holland and I. Gibb)
Chapter 5.	Seabirds in the northwest North Sea (S. Wanless, F. Daunt, C.J. Camphuysen, S. Greenstreet, and Liz Humphreys)
Chapter 6.	Modelling and experimentation (J. van der Meer, J. Ollason, M. Enstipp and D. Gremillet)
Chapter 7.	Local/daily scale hydrography, prey and seabird interactions (S. Wanless, F. Daunt, C.J. Camphuysen, B. Scott. J. Sharples, O. Ross, S. Greenstreet, E. Armstrong, H. Fraser, G. Holland & I. Gibb)
Chapter 8.	Interannual scale hydrography, prey and seabird interactions (S. Wanless, S. Greenstreet, B. Scott, J. Sharples, C.J. Camphuysen)
Chapter 9.	Synthesis (C.J. Camphuysen & J. van der Meer)
Chapter 10.	Conclusions (C.J. Camphuysen & J. van der Meer)

Box 1.3. Seabird species under study

Photo's C.J. Camphuysen

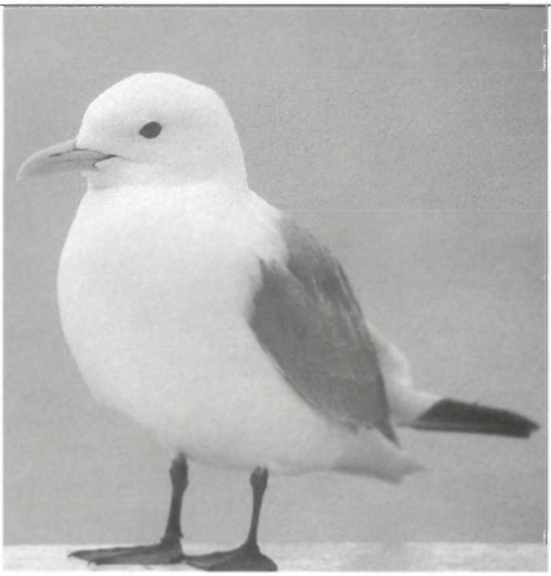
Northern Gannet *Morus bassanus*

Family Sulidae. Largest indigenous seabird in west Palearctic, wingspan 165-180cm, body mass 2500-3600g. Breeding Quebec and Newfoundland, Iceland, Norway, Faeroe Islands, British Isles (including Channel Islands), northern France, Helgoland (Germany) and incidentally in the Mediterranean. West Palearctic breeding population winters from NW Africa to the North Sea (migratory). Mean adult annual survival *c.* 94%. Plunge pursuit diver and surface feeder, almost entirely piscivorous.



European Shag *Phalacrocorax aristotelis*

Family Phalacrocoracidae. Medium-sized, slender-billed marine cormorant, with a wingspan of 90-105cm, body mass 1600-1900g. Breeding Iceland, Norway, Faeroe Islands, British Isles, France and Iberian Peninsula (race *desmarestii* in Central Mediterranean and Black Sea). Dispersive, but adults largely resident in southerly breeding areas. Mean annual survival after 1st year *c.* 85% (variable from year to year). Foot-propelled surface diver: pursuit diving benthic feeder, almost entirely piscivorous.



Black-legged Kittiwake *Rissa tridactyla*

Family Laridae. Small to medium-sized and essentially pelagic gull, wingspan 95-120cm, body mass 350-460g. Breeding North Pacific and North Atlantic, including Iceland, Svalbard, Norway, Faeroe Islands, British Isles, northern France, Helgoland (Germany) and Iberian Peninsula. West Palearctic breeding population winters from NW Africa to the Norwegian and Barents Seas (migratory). Mean adult annual survival >81%. Surface feeder, feeding entirely on marine fish and invertebrates obtained offshore.

Common Guillemot *Uria aalge*

Family Alcidae. Commonest large auk in west Palearctic, wingspan 64-70cm, body mass 800-1100g. Breeding North Pacific and North Atlantic, including Iceland, Norway, Faeroe Islands, British Isles, France, Helgoland (Germany), Iberian Peninsula and Baltic. West Palearctic breeding population winters from Portugal to the Norwegian Sea (migratory). Mean adult annual survival *c.* 88%. Wing-propelled mid-water pursuit diver, almost entirely piscivorous.

Figure 1.3.1. Isle of May as viewed from the northeast (top) and from the southwest (bottom), June 2003 (C.J. Camphuysen).

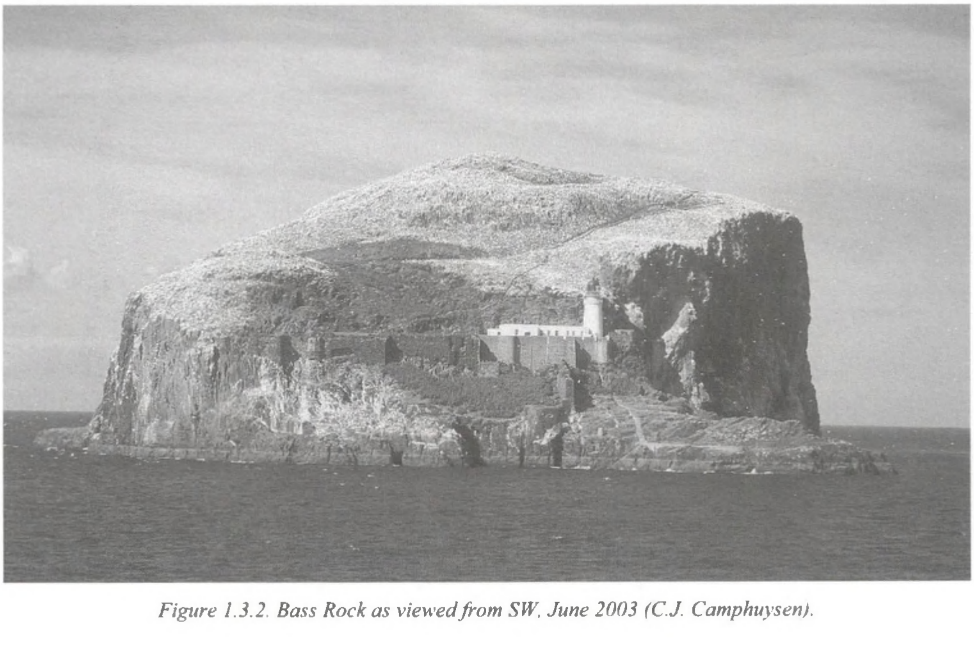


Figure 1.3.2. Bass Rock as viewed from SW, June 2003 (C.J. Camphuysen).

Following the general introduction and within **Chapter 1**, material and methods for each of the working packages are outlined in rather comprehensive sections §1.3 - §1.7. By doing this, it was possible to address methods only briefly in the remaining chapters and to focus rather on results and major outcomes in the following chapters. For most of the work-packages, even more detailed information on methods, calibrations and standardisations is provided in the appendices. The development of data loggers is outlined in §1.6 and further details are provided in Appendix 1.

Chapters 2 and 3 set the scene and describe the conditions in which the project was conducted. What are sandeels, exactly how did the industrial fishery for sandeels develop in the North Sea and how significant have catches been within the principal study area prior to the fishing moratorium are aspects addressed in **Chapter 2**. **Chapter 3** is meant to describe the study area in hydrographical terms and to produce some base-line data that have been vital in later phases of the work. A comprehensive document on hydrographic surveys and long-term mooring work (1997-2003) has been provided as Appendix 3 of this report.

Chapters 4-6 report on specific results of the project, including major outcomes of each of the working packages. **Chapter 4** is a description of the major outcomes of the work on prey density, prey distribution and the size of prey fish performed prior to and during the project in the Wee Bankie/Marr Bank region. It was believed important to not just focus on sandeels, as a major but single prey of the seabirds that have somehow a mixed diet, but to include information on clupeids, collected simultaneously and kindly supplied by the Fisheries Research Services in Aberdeen. Appendix 4 give even more details than already provided in this chapter.

In **Chapter 5** the major (basic) outcomes of the various seabird studies are described, including breeding population trends, breeding success, diet, the offshore seabird community, mean densities of birds at sea, offshore foraging behaviour and flock formations (from visual observations), and foraging locations, depth utilisation, activity budgets and prey capture rates of seabirds (from instrumented birds). **Chapter 6** is an outline of important outcomes of the modelling work and describes the empirical data obtained during experiments with birds in captivity. Chapter 6 also provides the rationale of the statistical approach of the foraging energetics of North Sea birds confronted with fluctuating prey availability.

Chapters 7 and **8** integrate material on different scales: daily/local and inter-annual. It is in these chapters that the various datasets merge and that the benefits of a multi-disciplinary approach are most profound.

Chapters 9 and **10** the results are discussed, and compared with findings in the literature or in nearby areas as measured more or less simultaneously, as a synthesis and to reach overall conclusions.

A CD associated with this volume contains data, (unpublished) material and stand-alone reports that underpin the discussions and presentations within the report, but that were considered too bulky for inclusion in a printed text.

In two consultation phases, international conferences organised in Hamburg (2001) and London (2004), ideas (Hamburg) and results (London) have been presented to a forum of external experts and stake-holders and the comments received have been incorporated in the work done during the project as well as in the analysis phase and in this final report. Before the report went to print, the text has been reviewed by representatives of the European Commission.

1.3 Study species and study area

Study species

IMPRESS focussed on four abundant seabirds nesting in the northwest North Sea: the **Northern Gannet** *Morus bassanus*, a plunge-pursuit diver, the **European Shag** *Phalacrocorax aristotelis*, a pursuit-diving benthic feeder, the **Black-legged Kittiwake** *Rissa tridcatyla*, a surface-feeder, and the **Common Guillemot** *Uria aalge*, a pursuit-diving midwater feeder (Box 1.3). Hereafter these species are referred to as Shag, Guillemot, Kittiwake and Gannet. As well as differing in their feeding methods, these seabirds differ in body size, clutch size, reproductive period and method of transporting food back for the chick.

Study area

Colony based (WP2) studies of seabird breeding populations, seabird diets, and reproductive success on Shags, Guillemots and Kittiwakes were carried out on the **Isle of May** (56°11'N, 02°33'W; Figure 1.3.1). Work on Gannets took place out on the nearby **Bass Rock** (56°06'N, 02°36'W; Figure 1.3.2). The *IMPRESS* **primary study area** was bounded by 56°00'N to the south, 56°30'N to north, 3°00'W to the west and 1°00'W to the east, covering the fishing grounds off the Firth of Forth, southeast Scotland, in particular the Wee Bankie, Marr Bank, Berwick's Bank and Scalp Bank (Figure 1.3.3).

Ship-based surveys studying the distribution, abundance and behaviour of seabirds at sea (WP3) were conducted within and beyond the primary study area, with surveys on board of FRV *Clupea* (2001-2003) and RV *Pelagia* (2003) concentrating on the primary study area and with surveys on board FRV *Tridens* (2001-2004) concentrating on a much larger area (54°N-59°N, 3°W-2°E; Figure 1.3.4). This second area, the larger area around the primary study area, will be referred to as the **study area at large**, throughout this report. The principal study area had a total surface of approximately 6089 km^2, whereas the study area at large measured *c.* 138 362 km^2.

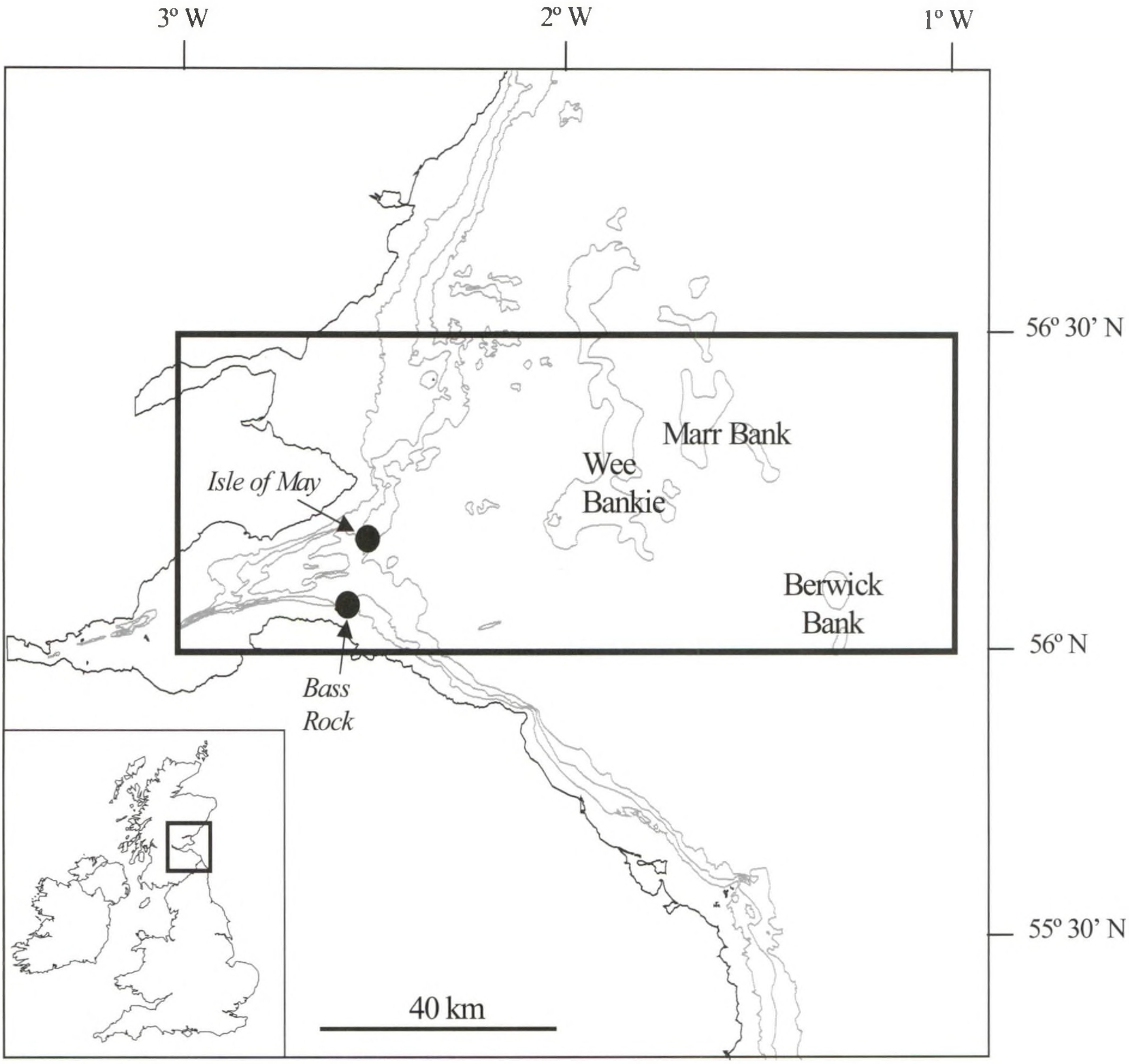


Figure 1.3.3. Map showing coastline, bathymetric contours down to 50m, boundary of study area (denoted by the thick line), and study colonies on the Isle of May and Bass Rock.

Seabird surveys on board **FRV *Clupea*** were carried out between 4 June and 5 July 2001-2003 over major sandeel fishing grounds within the primary study area (Figure 1.3.5). In addition to this, a mini-survey was steamed in June 2001, centred on the Isle of May and a small-scale repeated survey was steamed in June 2002 to examine the effects of day, time of day, and tidal state on seabird usage of the Wee Bankie area. Details of these surveys are to be found in Appendix 2 (see Figs. 3.3 and 3.4 in Appendix 2 for areas surveyed in these mini-surveys).

Dedicated surveys onboard **RV *Pelagia*** covered 4.4% of the principal area and 0.5% of the area at large in June 2003 (624 km^2 in all) (Figure 1.3.6) and these included three 25 hour mini-surveys (each consisting of 12 runs of 125 minutes each) to study the effect of tidal state in hot-spot feeding areas on foraging activity of seabirds. Details of this surveys are to be found in Appendix 3.

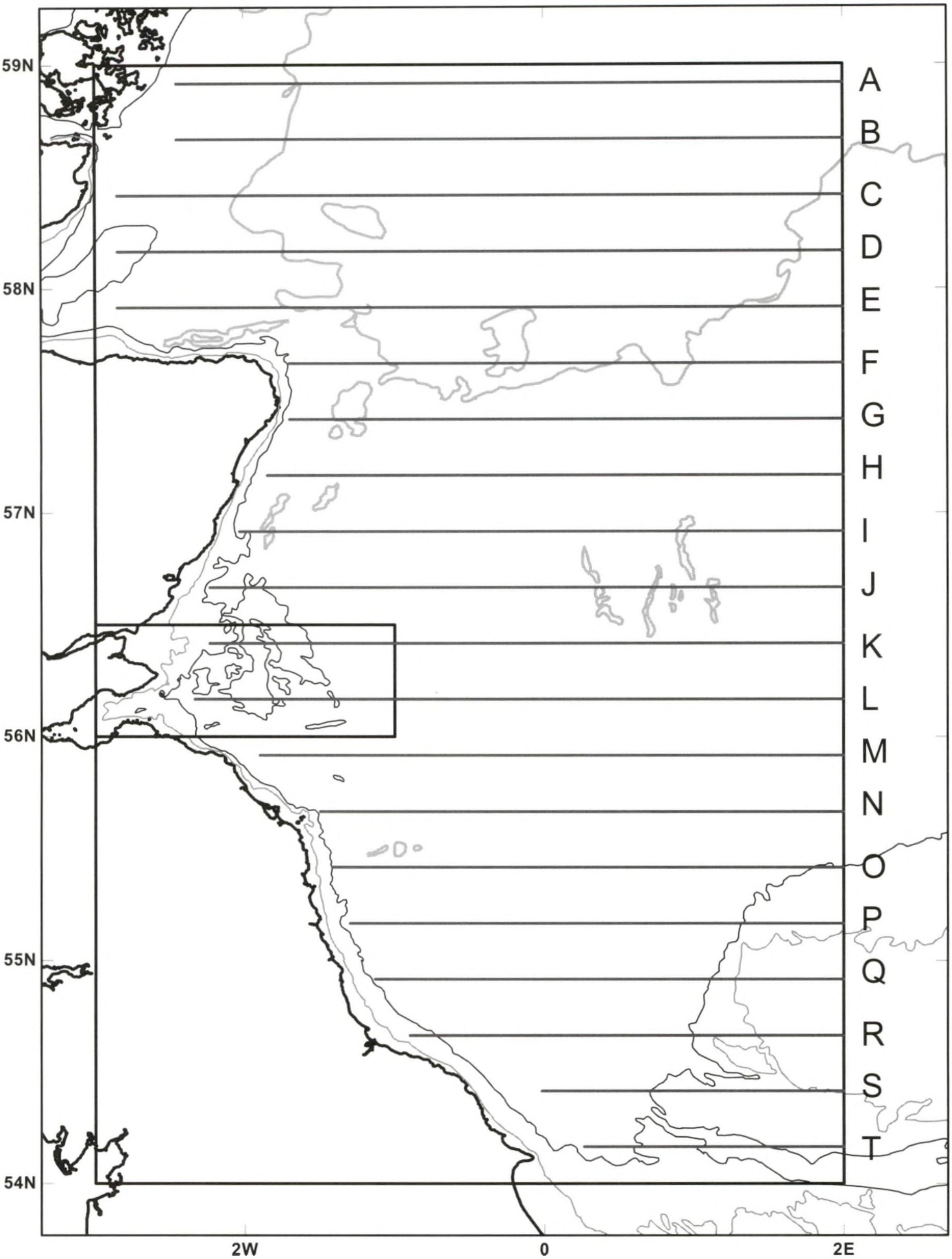


Figure 1.3.4. Map of the study area at large (principal study area as inset) and transects A-T sailed onboard FRV Tridens. The transects are a sailing plan rather than actual coverage and due to light conditions and weather in any one year, variable bits of these transects could not be completed. During the IMPRESS project, the ship travelled deeper into the principal study area, providing more coverage near the breeding colonies and in the Firth of Forth.

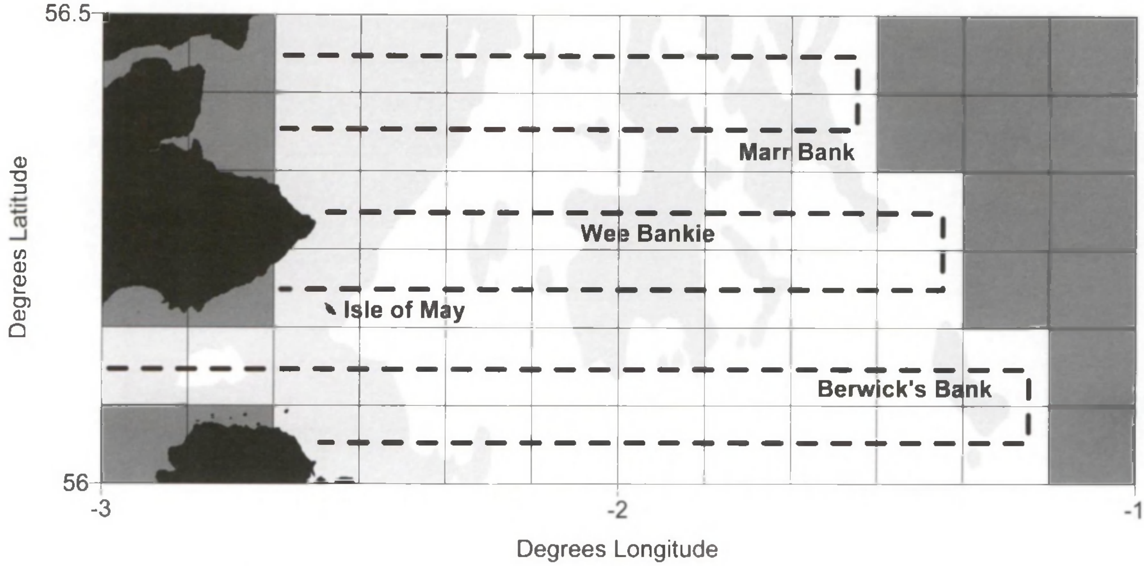


Figure 1.3.5. Chart of the study area showing 5' latitude by 10'longitude rectangles and six main seabird survey transects used by FRV Clupea, June0July, 1997-2003. Areas outside the main study area are indicated by dark shading, while light shading indicates areas with a sea depth of 50m or less. The main sand-banks are indicated, as is the Isle of May.

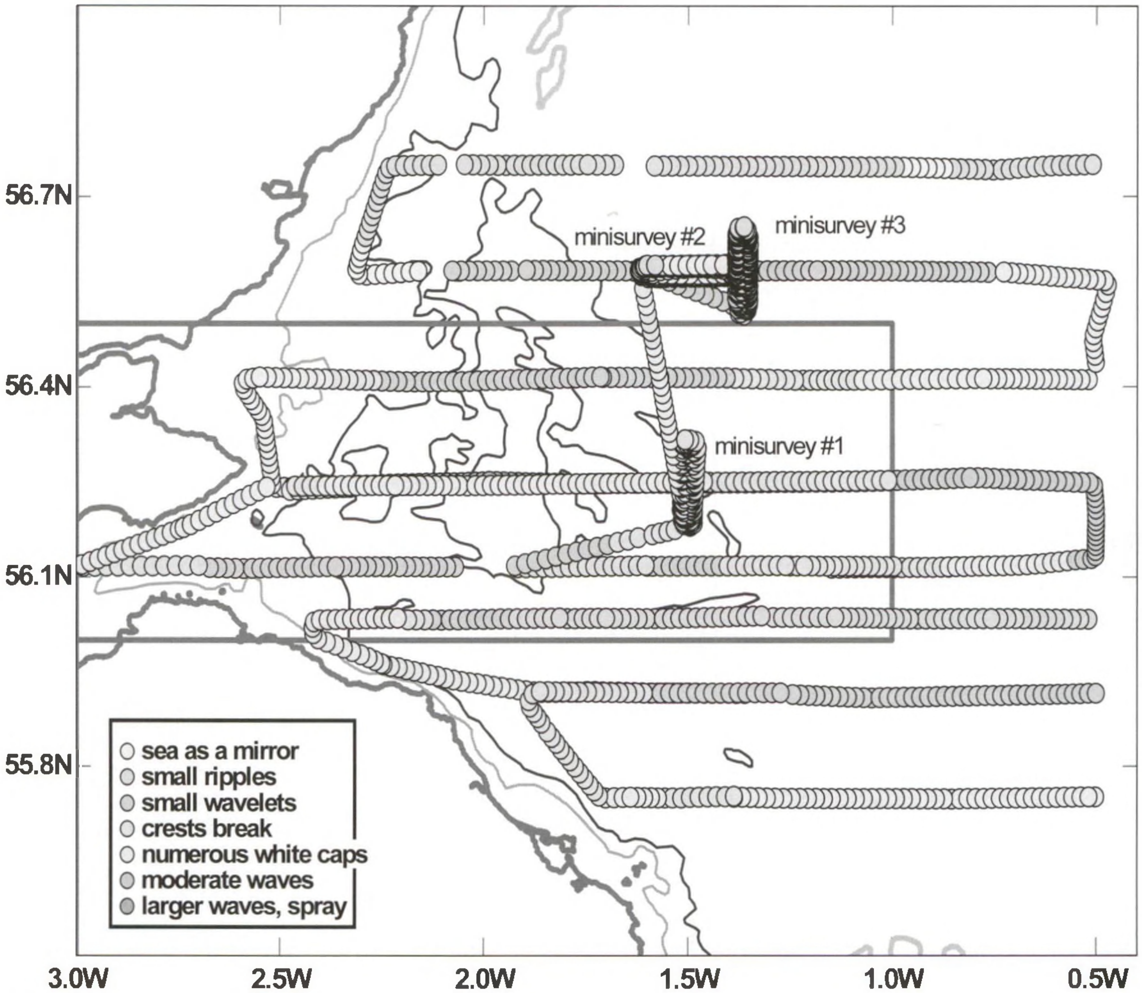


Figure 1.3.6. Survey area for ship-based surveys within and beyond the principal study area in June 2003 onboard RV Pelagia, showing observer effort as centre point locations of each five minute survey period.

1.4 Summaries and collation of available data

As indicated in the general introduction. the *IMPRESS* project was designed to build on work performed under previous projects and monitoring schemes such as the EU-funded *ELIFONTS* (Effects of Large-scale Industrial Fisheries on Non-target species) and *MIFOS* (Modelling the Impact of fisheries on seabirds) projects (Rindorf *et al.* 2000; Ollason 2000). Here we briefly summarise the type of data made available by various partners, as a result of which we were able to put the results obtained during our three years of fieldwork into a wider geographical and temporal context.

Pre 2001 oceanographic / meteorological data

At the start of the IMPRESS project, a review was made of all relevant data sources that could provide the oceanographic and meteorological data for the long-term analyses of the primary study area. This was compiled into Appendix 3. The most consistent collection of oceanographic data began with the survey of the area by FRS in 1997 taking up to 20 CTD cast within the study area 3 times a year (generally in March, June and October – see Appendix 3 for details). Meteorological observations were available as daily means from two weather stations: Leuchars (56.377°N, 2.861°W) and Mylnefield (56.458°N, 3.072°W). These sites were chosen because of their close proximity to the study area, and also as both are surrounded by low-lying land. The relevant data was available back to 1974.

Seabird surveys

Between 1991 and 2004, **FRV *Tridens*** surveyed on average 0.7 ± 0.5% (mean ± SD) of the principal study area and 0.7 ± 0.1% of the study area at large (941 ± 118 km^2 surveyed in all; Figure 1.4.1). All these data, summarised by Camphuysen (2005) and provided as Appendix 5, were made available to the IMPRESS project. Survey tracks (a plan is shown in Figure 1.3.4) were similar, but not identical in each year and due to occasional night coverage of some transects, seabird surveys occasionally had to be discontinued. Seabird surveys on board **FRV *Clupea*** were carried out between 4 June and 5 July in each of seven consecutive years (1997-2003) over major sandeel fishing grounds within the primary study area, and again, all results could be used in the *IMPRESS project* (Appendix 5).

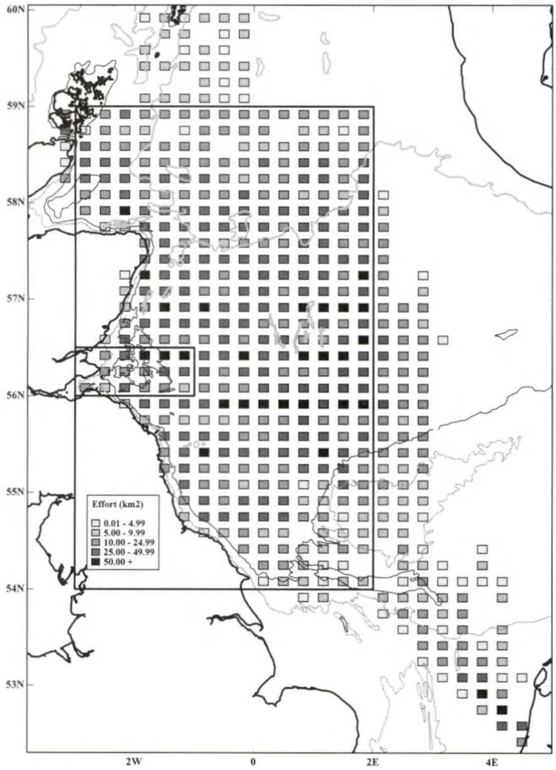


Figure 1.4.1. Survey area for ship-based surveys in the northwest North Sea, showing observer effort in the area at large (km^2 surveyed per 10' latitude x20' longitude rectangle; 54°N-59°N, 3°W-2°E) surveyed by FRV Tridens between 1991 and 2004 and by RV Pelagia in 2003, relative to the primary study area (rectangle as in Figure 1.3.1).

Breeding populations, diet and reproductive success

Whole colony counts of Shags, Kittiwakes and Guillemots were carried out each year by Scottish Natural Heritage on the Isle of May between 1997 and 2000, using standard methods (Walsh *et al.* 1995), and these data were made available to the IMPRESS project. Whole colony counts of gannets on the Bass Rock were carried out at ten-year intervals, most recently in 1994 (Murray & Wanless 1997) and these data were compared with the most recent census in 2004 (Wanless *et al.* 2004) and made available to the IMPRESS project.

Breeding success was recorded for all species nesting on the Isle of May between 1997 and 2000, using standard protocols by Scottish Natural Heritage (Walsh *et al.* 1995). There was no recent information on breeding success of Gannets on the Bass Rock (from years just before IMPRESS commenced), and therefore, we have only data for 2002 and 2003, collected by our own field teams.

Diet samples were obtained annually between 1997 and 2000 for the three Isle of May study species by Scottish Natural Heritage and made available to the IMPRESS project. Only in 1998 is dietary information available for Gannets on Bass Rock and there is therefore little material to compare with, when evaluating our own samples. Samples collected prior to the IMPRESS project were collected and analysed using standardised methods, similar to those used during the project (IMPRESS Report 2001.004).

1.5 Field studies (workpackages 2-6)

1.5.1 Sampling prey availability: assessing the abundance, size and distribution of sandeels and clupeids

Quantifying the abundance and distribution of prey is a major requirement of any predator-prey interaction study. A principal objective to the programme of research carried out in the Wee Bankie/Marr Bank/Berwick's Bank area has been to monitor changes in the sandeel population from year to year, and over the course of each year (FRS contributions; WP 4). Sandeels spend much of their time buried in the seabed sediment, moving out into the water column to feed during daylight hours, mainly in the months of May and June in the Wee Bankie area. Assessment methods based on fisheries catch statistics are presumed to provide estimates of the total population size in an area, as do assessment methods based on sampling sandeels in the sediment during the hours of darkness (see accompanying reports). However, seabirds are dependent on finding their prey at various levels in the water column, and the entire population of sandeels is rarely, if ever, all up in the water column simultaneously. In order to estimate prey availability to seabird predators, estimates of the abundance of sandeels active in the water column are required. **Acoustic surveys** can provide such estimates. FRS has carried out acoustic surveys, timed as far as possible to coincide with the seabird chick-rearing period. Acoustic surveys also provide estimates of the abundance of other pelagic fish in the water column, such as herring and sprats. In the event of a shortage of sandeel prey, these species could provide suitable alternative prey resources. Sandeels are a particularly difficult species to assess using acoustic survey techniques. Their low target strength means that small errors in acoustic integral attributed to sandeels in the water column can lead to large errors in the density estimate (Armstrong, 1986). Nevertheless, even if one is uncertain about the target strength, variation in the total acoustic integral can provide an index of variation in abundance. However, their habit of burrowing in the sediment causes problems with acoustic survey methods, since at any one time, an unknown fraction of the population may in fact be buried in the sediment, and so not available to acoustic census.

The alternative to surveying sandeels in the water column is to assess their density, or abundance, in the seabed sediments. Two principal techniques have been employed to do this, dredging and grabbing; both carried out at night when the vast majority of sandeels are believed to be buried in the sediment (Winslade 1974a-c; Wright & Bailey,1993). Both techniques have their advantages and disadvantages. **Dredge surveys** cover large areas of ground, taking samples of up to several hundred sandeels per 1000m^2 of seabed covered. Such samples are more than adequate for population age and length structure analyses. However, catches are integrated over large areas that may include suitable, as well as unsuitable, sandeel habitat. Thus, in most cases, such samples actually underestimate the real density of sandeels in the suitable habitats. Furthermore, catchability in dredges is low, since many sandeels appear to escape ahead of the dredge, perhaps through the stimulation of an escape response caused by the vibration of the dredge along the seabed (P.J. Wright, unpublished data). In addition, relatively large mesh sizes are required (10mm) in order to prevent the dredge clogging up with sediment. As a result, catch rates of the smaller and younger sandeels tend to under-represent their actual abundance in an area.

Grab surveys provide point estimates of sandeel density, which, in suitable habitats, always exceed dredge density estimates by up to a couple of orders of magnitude (S.P.R. Greenstreet, unpublished data). Sandeel catchability in grabs must therefore be relatively high, and this is particularly true for the smaller size classes, under-sampled by dredges. Another major advantage of grab surveys is that a sediment sample is always associated with each sandeel density estimate. Thus, the suitability of the habitat at each sample location can be assessed directly, at least in terms of depth and sediment particle size distribution. The principal drawback with grab surveys is that only a very small area in total is sampled. For example, a survey of 500 grab samples will only cover 50m^2 of seabed area, compared with the 1000m^2 covered by a single dredge sample. Consequently, the total number of sandeels sampled in any complete grab survey will be much smaller, and rarely sufficient to assess adequately the full age structure of the sandeel population.

Assessment of sandeel biomass in a given area through the use of grab surveys relies on a detailed knowledge of the location and extent of suitable seabed habitat. Grab samples can provide estimates of the mean density of sandeels in suitable sandeel habitat which when multiplied by the area of such habitat can provide estimates of the biomass of sandeels in the region. To do this, however, a precise definition of what exactly constitutes suitable seabed habitat for sandeels is required, so that this can be adequately mapped. Sandeels are known to be extremely selective in the types of sediment that they occupy, preferring coarse, sandy substrates containing a minimum of silt (Macer 1966; Pinto *et al.* 1984; Reay 1970; Wright *et al.* 2000). In this study we use a sediment map, derived using the acoustic survey technique RoxAnn (ELIFONTS 1999), to target our grab sampling preferentially towards sand, slightly gravely sand and gravely sand (Folk 1954), which include these preferred sediment types. These samples are then analysed to provide a precise definition of sandeel habitat within the Wee Bankie, Marr Bank and Berwick's Bank region of the North Sea, off the Firth of Forth, south-east Scotland.

We also present data obtained from a **groundfish survey** (see Appendix 8). This survey was primarily directed towards assessing variation in the populations of piscivorous fish predators of sandeels in the area. However, the codend mesh size used, at 10mm, was small enough to take good samples of sandeels, herring and sprats. The consistent survey design each year meant that these data could also provide potentially useful indices of abundance that would reflect inter-annual variation in the abundance and distribution of these forage fish. Furthermore, this index can be expected to be closely correlated with the fishery dependent CPUE index of sandeel abundance.

Acoustic surveys

The biomass of herring, sprats and sandeels in the water column in the Wee Bankie/Marr Bank area off the Firth of Forth, south-east Scotland, between latitudes 56°N and 56°30'N and longitudes 3°W and 1°W in the north to 1°30'W, was assessed by acoustic survey (WP4). Surveys were carried out using the Scottish FRV *Clupea* between early June and early July of each year during a seven-year period, 1997 to 2003 (Table 1.5.1). The study area, approximately 4720km^2 in extent, was divided into fifty 5' latitude by 10' longitude rectangles (approximately 9.27km by 10.30km). Transects were steamed through the centres of these rectangles in an east-west direction (Figure 1.5.1), approximately perpendicular to the general orientation of the coastline, and so tending to run across depth contours rather than parallel to them (MacLennan & Simmonds 1991). In June 1998 poor weather prevented the two most northerly transects from being surveyed. In 2000 and 2001 sufficient time was available to allow additional part-transects to be steamed in the areas of most interest. These part-transects were either placed between the main transects over the major sand-banks, or focused around the major seabird colony in the area, the Isle of May. The actual transects steamed in each year are shown in Appendix 4. The differences in the proportion of the study area covered by each survey needed to be taken into account in order to compare biomass estimates in each year (Table 1.5.1). Raising factors were therefore determined, which were used to raise the biomass estimates calculated for all cruises undertaken after 1997, to the biomass that might have been expected, had the same area covered in 1997 been covered in each subsequent cruise (Table 1.5.1). Implicit in this is the assumption that the average density of each species in the area covered in each survey equalled the average density in the parts of the study area not covered.

Table 1.5.1. Acoustic survey dates, median Julian date of survey, actual area covered in each survey, and raising factor used to raise total biomass in area surveyed in each cruise to equivalent biomass had the area covered in June 1997 been surveyed.

Year	Dates	Median Julian Day	Area Surveyed (km^2)	Raising Factor
1997	21st to 25th June	174	4721	1.00000
1998	13th to 16th June	165	3392	1.39180
1999	2nd to 5th July	184	4645	1.01636
2000	14th to 19th June	167	4612	1.02363
2001	4th to 9th June	157	4671	1.01070
2002	15th to 19th June	168	4529	1.04239
2003	14th to 17th June	166	4529	1.04239

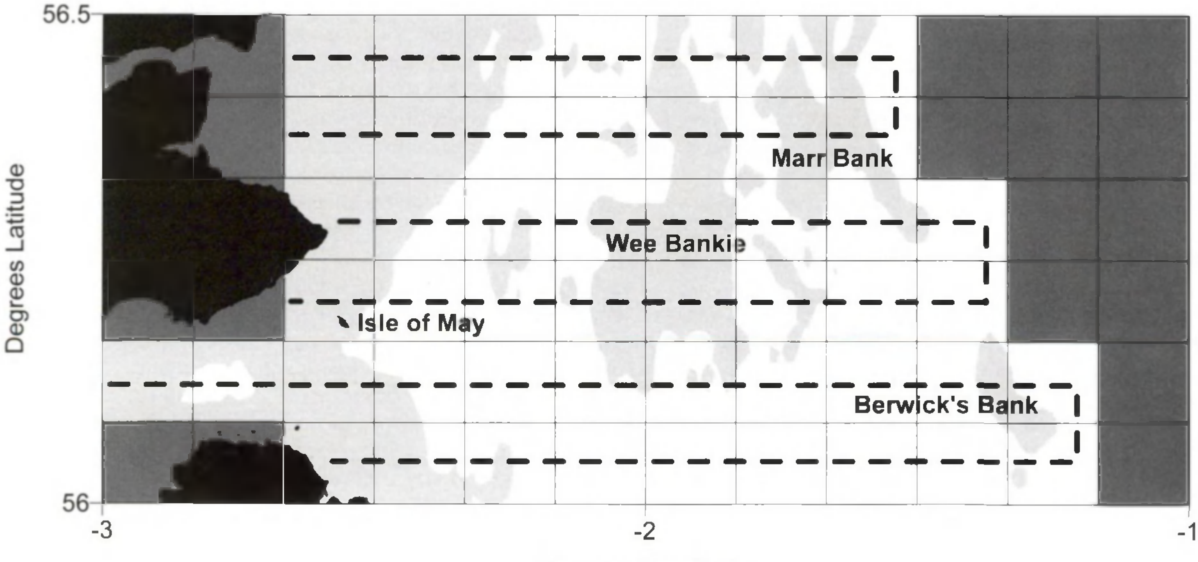


Figure 1.5.1. Chart of the study area showing 5' latitude by 10'longitude rectangles and six main acoustic survey transects. Areas outside the main study area are indicated by dark shading, while light shading indicates areas with a sea depth of 50m or less. The main sand-banks are indicated, as is the Isle of May, the principal seabird colony in the area.

Major concentrations of fish encountered during the course of the survey were sampled using an International Young Gadoid pelagic trawl fitted with a 6mm codend. These samples were required to either confirm or determine species composition, to determine the size and age composition of the fish involved, and to determine length-weight relationships for each species. This information was necessary for the correct interpretation of the acoustic integration data. Locations where these pelagic trawl samples were obtained in each survey are shown in Appendix 4. Each catch was sub-sampled as necessary and the numbers of each species per ½ cm size class in the catch determined. Weight-at-length relationships were determined and otoliths were collected to determine age-at-length keys (Appendix 4). During the course of each cruise a grid of 19 stations were fished using demersal rock-hopper gear to sample the fish predators of sandeels and clupeids. On occasion, for example, in June 1998 when inclement weather seriously hampered pelagic trawl sampling, the clupeids and sandeels taken in this demersal trawling survey were used to supplement the data on length frequency distribution and age composition, sprat:herring ratios in clupeid shoals and length-weight relationships obtained from the pelagic trawling.

Two split beam transducers, one of 38kHz and the other of 120kHz, were mounted in a towed body deployed forward of the propeller from a boom mounted near the bow of the vessel. The towed body, towed at a speed of 18km.h^{-1} (10 knots) approximately 5m below the sea surface, provided a more stable platform in rough weather and avoided the problems of interference from air bubble formation under the hull often associated with hull mounted transducers. Acoustic data were integrated over 5min periods of passage along the transects. Between six and eight 5min "samples" were collected in each rectangle. Once the transects had been surveyed, the acoustic record was examined and the integral values obtained from the 38kHz transducer for each 5min run period were assigned to species. Only data from the 38kHz transducer were used in the biomass estimation process. This frequency provides the best discrimination of clupeid shoals and reliable target strength data are available for herring and sprat (see below). Although not ideal for sandeel discrimination, 38kHz is certainly still adequate, and the only sandeel target strength data available were obtained at this frequency (Armstrong 1986). Sandeels provide a better acoustic return at higher frequencies, so data collected from the 120kHz transducer were used to aid identification and discrimination of sandeel shoals. Where there was any doubt regarding the identity of the fish recorded in a particular mark, the species composition in the appropriate pelagic trawl sample was used to attribute the integral values to species. It was relatively easy to distinguish shoals of sandeel and larger herring, but sprat and smaller herring were usually in mixed shoals. Generally it was necessary to use the trawl sample data to attribute species composition in these types of marks.

The Echo-sounder and 38kHz transducer were calibrated using a tungsten carbide sphere suspended in the centre of the acoustic axis. This sphere provided a target of known target strength. The biomass of any particular group of fish targets could then be determined using the following equations:

Sandeel target strength (db kg^{-1}) = -50

Herring target strength (db fish^{-1}) = 20 Log L (cm) - 71.2

Sprat target strength (db kg^{-1}) = -8.71 Log L (cm) - 19.6

The target strength value available for sandeels is independent of fish length; 1kg of sandeels is assumed therefore to have a target strength of -50db at 38 kHz no matter what size the fish are (Armstrong 1986). However, the trawl length-frequency distribution data and length-weight relationships allow us to break these biomass estimates down into particular size categories. For both herring and sprat, target strength depends on fish length. In the case of herring the equation indicates the target strength of fish of a given length. Given the size composition data provided by the trawl samples, the numbers of fish at length can be determined from the acoustic data, and a length-weight relationship is used to convert this to fish biomass estimates. For sprats the target strength equation provides an estimate of fish weight directly, provided one knows the proportion of sprat biomass at each length class. The trawl length-frequency distribution data, together with a length-weight relationship, provide this information. Using a sequential Kolmogorov-Smirnov routine, therefore, the trawl size composition data for each species were used to group together rectangles into between two and five sub-regions that differed in their length-frequency distributions. Each species was considered individually in this respect. In any specific cruise therefore, the sub-region partitioning varied for the different species. Within a sub-region for a particular species, a single length frequency distribution was assumed. In this way, for any particular species in each cruise and study area, the mean target strength in any given 5' latitude by 10' longitude rectangle could be assessed. The length-weight relationships obtained for each species in each cruise and study area were used to convert the numbers at length frequency distributions to distributions based on the proportion of biomass at length.

Knowing the target strength and identity of fish targets in the swath of water column ensonified by the acoustic pulse, the biomass of fish present could be determined. After correcting for variation in size of the acoustic footprint arising through variation in water depth, these biomass estimates were converted to density estimates (g.m^{-2}). Thus for each 5' latitude by 10' longitude rectangle, six or eight mean density estimates, each obtained over 5min of passage, were obtained and an overall mean density estimate was derived for each species. Raising these by the area of sea in each rectangle provided biomass estimates of each species in each rectangle. Summing the results over all rectangles gave estimates of the total biomass of sandeels, herring and sprats for each cruise. The mean density estimates for each 5' latitude by 10' longitude rectangle were gridded in SURFER (Golden Software Inc., Colorado, USA) using a multiquadric radial basis interpolation function and contour distribution plots constructed. Knowing the biomass and the proportion of biomass at length of each species in each sub-region, the biomass of fish in any particular length stratum could be determined. When summed over all sub-regions, biomass at length distributions could be determined for each species for the entire study area. Age at length keys could then be used to convert these to biomass at age estimates.

Table 1.5.2. Dates of the demersal trawl surveys undertaken over a seven-year period 1997 to 2003.

Year	Dates	Median Julian Day	Year	Dates	Median Julian Day
1997	27th June to 3rd July	180	2001	30th May to 3rd June	152
1998	18th to 22nd June	171	2002	9th to 13th June	162
1999	7th to 11th July	190	2003	6th to 11th June	159
2000	20th to 24th June	173			

Demersal trawl survey

The area into the Firth of Forth was not included in the region covered by the demersal trawl survey (WP4). The demersal trawl survey therefore covered an area of approximately 4529.1km^2, constrained between latitude 56°'N to the south, latitude 56° 30'N to the north, longitude 02°40'W to the west, and with an eastern boundary staggered between longitudes 01° 30'W in the north and 01°10'W in the south (Figure 1.5.2). Between late May and early July (Table 1.5.2) in each year over the period 1997 to 2003, Sandeel and Clupeid populations were sampled at 19 evenly spaced sample stations by the Scottish Fisheries Research Vessel Clupea (Figure 1.5.2). A Jackson Rockhopper demersal trawl with a 10mm mesh-size codend was towed for 30min at a speed of approximately 4km.h^{-1} at each station. Net geometry monitoring equipment (SCANMAR, Norway) recorded the width and height of the trawl opening every 30sec. The ship's position, determined by Differential Global Positioning System (DGPS), was recorded simultaneously. Thus for each trawl sample, the area of seabed swept and the volume of water filtered by the gear could be calculated.

The total catch of sandeels, herring and sprats in each trawl sample was quantified (number caught per 0.5cm size class). Length-stratified sub-samples were weighed to determine length-weight relationships for each species on every cruise, and had otoliths extracted to determine age at length keys (Appendix 4). These were used to convert numbers-at-length to weight-at-length of each species in every trawl sample. Dividing the number-at-length and weight-at-length of fish in each catch by the area of seabed swept by the trawl on each occasion converted these to density-at-length estimates (no.km^{-2} and kg.km^{-2}). Summing these across all length classes provided estimates of the total density of each species caught at each trawl station in each cruise. Multiplying the density-at-length estimates by the area of seabed associated with each trawl station determined by simple nearest neighbour interpolation, or tesselation (Figure 1.5.3), provided estimates of the total number and weight of each species, at each 0.5cm length-category, in each trawl station sub-area. Summing these sub-area population-at-length estimates across all trawl station sub-areas provided estimates of the total numbers- and biomass-at-length of each species in the whole study area. Finally, summing these across all length categories provided estimates of the total number and total weight of each fish species in the study area at the time of each survey. This final summing could also be done for sub-groups of the population, for example, particular size ranges that predators might concentrate on.

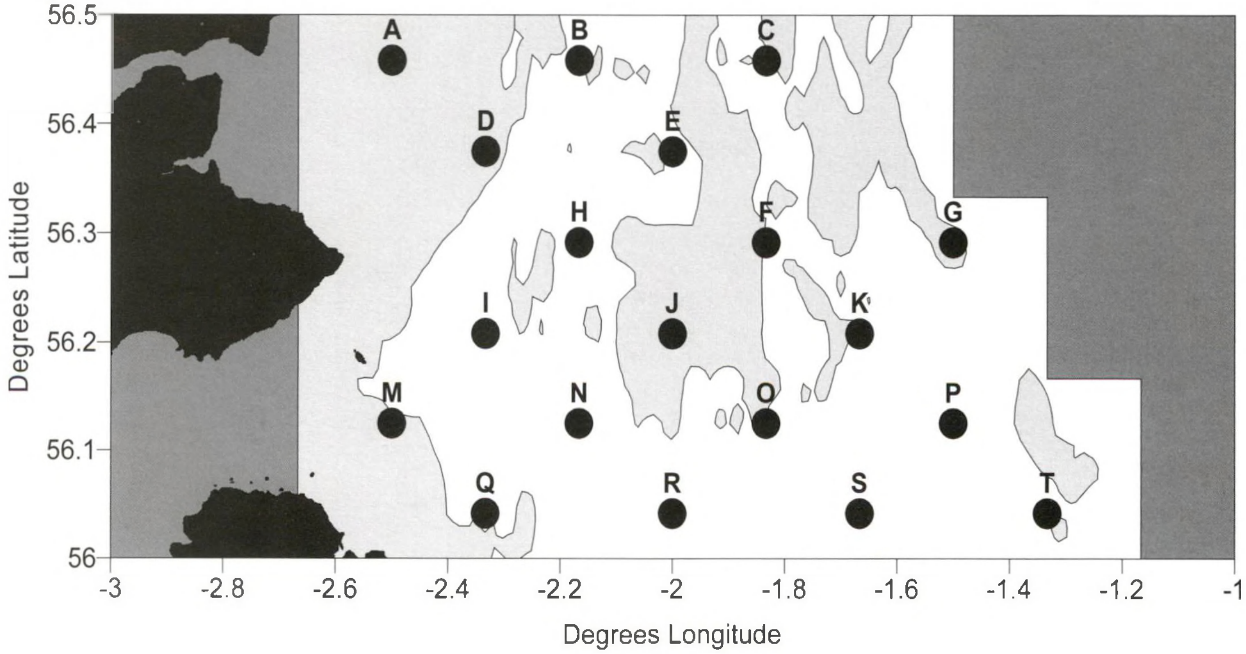


Figure 1.5.2. Location of 19 evenly spaced demersal fishing stations.

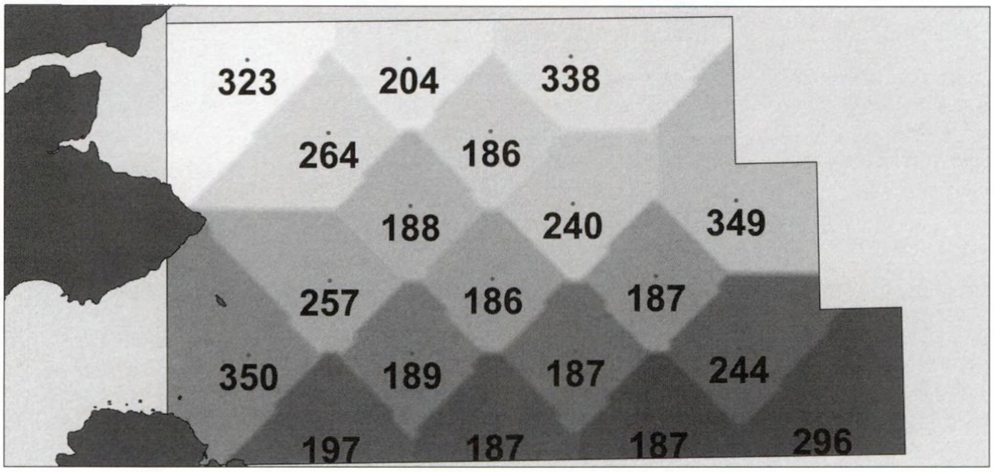


Figure 1.5.3. Chart showing the sea area associated with each demersal fishing station (figures show area in km^2.).

Table 1.5.3. Dates of each main grab survey

Survey	Dates	Median Julian Day	Survey	Median Julian Day	Dates
March 1998	9th to 18th March	72	October 2000	299	23rd to 30th October
June 1998	23rd to 27th June	176	March 2001	70	8th to 15th March
October 1998	2nd to 12th October	280	October 2001	286	10th to 17th October
July 1999	12th to 16th July	195	March 2002	85	23rd to 30th March
October 1999	13th to 19th October	289	October 2002	271	23rd Sept. to 4th Oct.
March 2000	21st to 28th March	83	March 2003	84	22nd to 29th March
June 2000	25th June to 1st July	179	October 2003	271	25th Sept. to 2nd Oct.

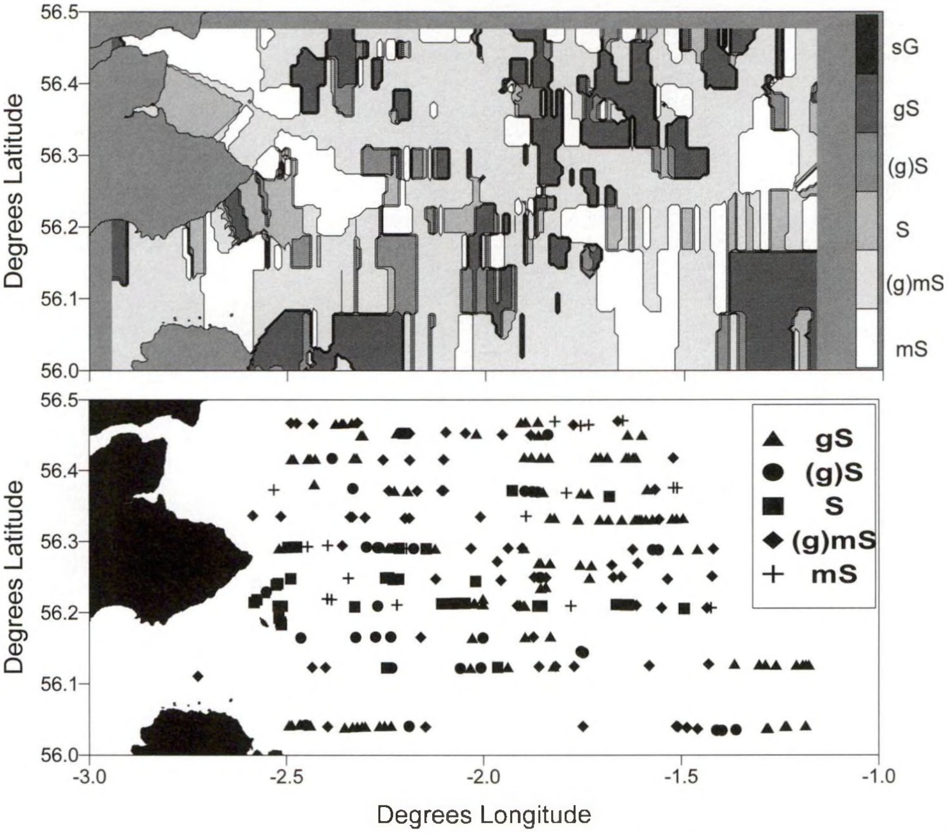


Figure 1.5.4. Top panel shows the preliminary habitat map derived from the Dana RoxAnn data using the Folk (1954) sediment classification scheme and original stratified random grab-sampling scheme (top panel). The positions of the initial 268 stations sampled in March 1998 are shown in the middle panel and the type of sediment on which they were targeted is indicated.

Otoliths were also removed from a further size-stratified sample of the fish processed for length-weight analysis. These were used to determine the age of the fish to construct age-at-length keys for each species in every cruise. These enabled the proportion of fish in each 0.5cm length-category belonging to each age group to be determined. Thus the catch numbers- and weights-at-length, trawl station density-at-length, and trawl station sub-area population- and biomass-at-length estimates could all be converted to numbers and weight-at-age, allowing the total abundance and distribution of each age-class of each species to be determined in each year. Too few older age-class fish were sampled so all fish 3 years old and older were combined into a single 3+ age-group.

Nocturnal Grab Survey

The study area was situated between latitudes 56°N and 56°30'N and longitudes 3°W and 1°10'W, east of the Firth of Forth, south-east Scotland. Fourteen grab surveys were carried out in spring, summer and autumn between March 1998 and October 2003 using the FRV *Clupea* (WP4; Table 1.5.3). The June grab survey was eventually considered unreliable because the short night-time period caused sandeels to emerge from the sediment while survey work was still in progress (for more details see Appendix 4). The summer grab surveys were therefore abandoned in 2001. However, data were collected in each year from 1998 to 2003 in the late autumn period and these provide an index of between year variation in the abundance of sandeels at the end of the sandeel growth, fishing and seabird breeding seasons.

In the first cruise a stratified random grab survey design was adopted based on a sediment map constructed for the area using the acoustic seabed classification system RoxAnn© (Marine Microsystems Ltd, Ireland). The Danish FRV *Dana* undertook the initial RoxAnn survey in April 1997 (ELIFONTS 1999). The acoustic classification data collected were analysed following recognised procedures (e.g. Greenstreet *et al.* 1997; Sotheran *et al.* 1997). Forty three Box Core sediment samples were used to calibrate the RoxAnn data, relating RoxAnn values to Folk (1954) sediment grades to produce a sediment map based on the same sediment categories as the British Geological Survey (BGS) North Sea sediment maps (Figure 1.5.4).

Individual RoxAnn observations were selected as grab stations so that each grab sample could be directly related to a specific RoxAnn datum. From the full RoxAnn data set of 60 979 values, records obtained only within the first 5 seconds of each minute were first extracted. This ensured that any two RoxAnn data that might be selected as grab stations were at least approximately 300m apart (the distance covered in one minute). Sections of duplicate RoxAnn track were then deleted, again to ensure that grab stations would not be too close to one another. For logistic reasons RoxAnn survey track not running in a west/east direction was also excluded. These exclusion processes reduced the number of "available" RoxAnn records to 2992 and had little effect on the proportion of RoxAnn data assigned to any particular Folk (1954) sediment category. These eventual proportions were therefore used to determine the number of grab stations that should be targeted at each sediment category.

On the basis of previous experimental studies (Reay 1970; Wright *et al.* 2000), two Folk (1954) sediment categories that together accounted for 67% of all the RoxAnn data, muddy sand (mS) and slightly gravely muddy sand ((g)mS), were considered *a priori* to be unsuitable sandeel habitat. Three sediment categories, sand (S), slightly gravely sand ((g)S) and gravely sand (gS), considered to be potentially suitable habitat for sandeels, accounted for the remaining 33% of the RoxAnn data. In designing the grab sample survey, the three potentially suitable sediment categories were targeted preferentially, such that the proportion of grab stations directed at these three sediment categories was double the proportion of RoxAnn values assigned to each category. Conversely, the proportion of grab stations directed at RoxAnn data assigned to the two unsuitable sediment categories was half the proportion of RoxAnn data assigned to each of these. Grab sampling density, in terms of stations per km^2, on suitable sediments was therefore approximately four times higher than on unsuitable sediments. A total of 87 grab stations were sited on RoxAnn data locations assigned to the two unsuitable sediment categories and 181 grab stations were sited on RoxAnn data locations assigned to potentially suitable sediment categories. The required number of grab sample stations on each sediment type was selected at random from the final extraction of 2992 RoxAnn records (Figure 1.5.4). In subsequent cruises time constraints required that the grab-sampling scheme be modified in order to concentrate sampling effort in areas thought to consist mainly of suitable sandeel habitat. Additional stations, selected at random from the RoxAnn data locations, were added in areas of S, (g)S and gS, and some stations, again selected at random, were deleted from mS and (g)mS areas. Depending upon variation in weather conditions, up to 240 grab stations, were sampled in each of the subsequent cruises using this modified stratified random design (shown in Appendix 4).

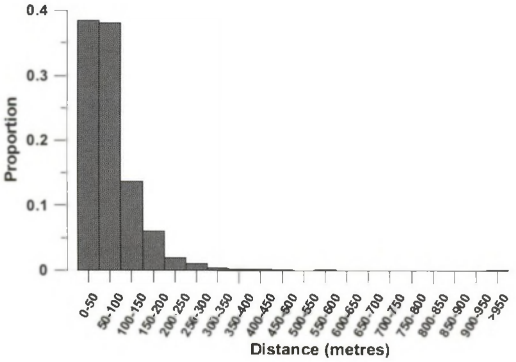


Figure 1.5.5. Distribution of "miss"-distances, the distance between the station target positions and the actual location where grab samples were taken.

Samples were collected at each station using a Day grab sampling an area of 0.0961m^2. Generally an adequate sample was obtained at each station with the first deployment of the grab. When this was not the case the grab was deployed between two and three times in an attempt to get a sample, dependent upon time constraints and how quickly the vessel was drifting off station. On occasion no sample could be obtained because the ground was too hard or the grab repeatedly misfired. When sampling each station, the vessel attempted to get as close as possible to the actual RoxAnn datum location. 76.3% of the grab samples were collected from within 100m of the actual station position and 97.8% were within 250m (Figure 1.5.5). The occasional need to deploy the grab more than once to obtain a sample accounted for many of the instances where "miss" distance exceeded 100m as the vessel tended to drift before the wind or with the tide during the extra time required. On recovery of the grab, a sample of the sediment was taken for analysis in the laboratory using a 32mm internal diameter 120mm long corer. Two cores were collected from different parts of each grab sample. To avoid losing the fine sediment material stirred loose from the main body of sediment in the grab, care was taken to include in the core samples the water lying over top of the sediment. The core samples were examined to check that no sandeels had been accidentally included. The remaining sediment was then washed through a 2mm sieve in which all the sandeels were retained. All sandeels caught were counted and measured to the ½cm below, weighed to the nearest 0.1g, and had their otoliths extracted for age determination back in the laboratory. The lengths of sandeels cut in two by the grab were estimated by comparing the available body part with whole sandeels of known length. Weights for such fish were then estimated from the length-weight relationships determined for each cruise. Ages for any sandeels from which no otoliths could be obtained were estimated from the age at length keys that were determined for each cruise.

In order to interpret the grab sample density data it was necessary to define "suitable" seabed sediment habitat for sandeels. This required particle analysis of the sediment material obtained in each grab sample. All sediment samples were stored frozen until analysed. Before analysis all water was removed from the samples by freeze-drying. The samples were then shaken through a sieve stack consisting of 8mm, 4mm, 2mm, 1.4mm, 1mm, 0.71mm and 0.5mm sieves. The material retained in each sieve was weighed in grams to two decimal places. Laser granulometry, using a Malvern particle sizer with 300µm and 45µm lenses, was used to determine the proportion of material retained in the 0.5mm sieve which belonged to finer particle size fractions. In effect, estimates of the quantity of material which would have been retained in sieves of 353.6µm, 250µm, 176.8µm, 125µm, 88.4µm, 63µm, 44.2µm, 31.3µm, 22.1µm, 15.6µm, 11µm, 7.8µm, 5.5µm, 3.9µm, 2.7µm, 2µm, 1.4µm, 1µm and 0.1µm were determined. Thus the proportion by weight of each sample belonging to 26 particle size fractions was estimated. Folk (1954) defined three broad sediment classes: gravel, sand and silt. These broad grades were split into two or three sub-categories with more restricted sediment particle size ranges (Table 1.5.4). For each sample, the percentage by weight belonging to these sediment categories was calculated.

Table 1.5.4. Particle size ranges for the eight sediment categories used in this study.

Sediment category	Particle size range
Coarse Gravel	≥ 8mm
Fine Gravel	≥ 2mm to < 8mm
Coarse Sand	≥ 710µm to < 2mm
Medium Sand	≥ 250µm to < 710:m
Fine sand	≥ 63µm to < 250µm
Coarse Silt	≥ 16µm to < 63µm
Medium Silt	≥ 3.9µm to < 16µm
Fine Silt	≥ 0.1µm to < 3.9µm

The detailed analysis by which seven grades of "suitable" seabed habitat for sandeels were identified, together with an eighth habitat type deemed "unsuitable" for sandeels, is presented in full in Appendix 4 (section 4.4). The preferences for these habitats by sandeels are also described in the Appendix. This analysis that habitats defined by terminal nodes 1 to 4 of a classification tree analysis had occupancy rates ranging from 80% to 45%. Occupancy rates in the remaining four habitats ranged from 2% to 19%. Only sandeel samples collected from the four most preferred habitats were used to determine an index of sandeel abundance in each cruise. Sample catches from each habitat type were log-transformed (Log x+1), and the mean (and SE of the mean) sample catch in each habitat in each cruise was determined. An overall density index was derived by calculating a weighted mean of these log transformed mean catch rates for each of the four preferred habitats. The relative proportion of all the samples assigned to each habitat was used as the "weighting" parameter, as given the original stratified random design of the survey, these would approximate to the relative area of each habitat. The overall mean log catch rate was then back-transformed and divided by the area of the grab (0.0961m^2) to covert the index to a density estimate (sandeels.m^{-2}) in the most preferred sandeel habitat.

Nocturnal Dredge Survey

Although some nocturnal dredging was carried out in June 2000 and March, June and October 2001, only in 2002 and 2003 were all eight dredge stations systematically sampled in each of the three cruises carried out in each year (WP4). Table 1.5.5 shows the stations sampled in each of the cruises when dredging was undertaken. Figure 1.5.6 shows the locations of the stations sampled and the general area each station represents. In 2000 and 2001 the dredging that was carried out was mainly done to collect additional sandeels to augment the samples for age at length analysis obtained by grab and trawl sampling. In 2002 and 2003 the same eight stations were sampled in each cruise with the specific intention of using these data to look at between year, within year and between area variation in the sandeel population. Only the data collected in these latter two years will be presented in this report. However, a detailed analysis of all dredge data collected is provided in section 5 of Appendix 4.

Table 1.5.5 Dredge stations sampled in the different cruises.

Cruise	St.1	St. 2	St. 3	St. 4	St. 5	St. 6	St. 7	St. 8	St. 9	St. 10
Jun 2000				*	*			*		
Mar 2001					*			*	*	
Jun 2001	*	*	*	*	*	*	*			
Oct 2001			*	*			*	*	*	*
Mar 2002	*	*	*	*			*	*	*	*
Jun 2002	*	*	*	*			*	*	*	*
Oct 2002	*	*	*	*			*	*	*	*
Mar 2003	*	*	*	*			*	*	*	*
Jun 2003	*	*	*	*			*	*	*	*
Oct 2003	*	*	*	*			*	*	*	*

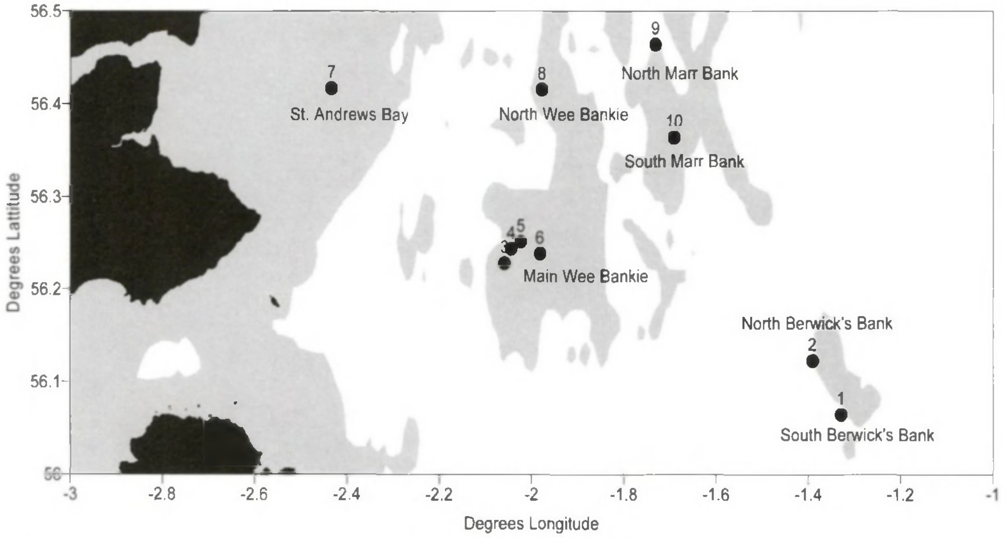


Figure 1.5.6. Map showing the positions of the dredge sampling stations.

Dredging was carried out at night when the sandeels were buried in the sediment; a 2-metre scallop dredge modified for sampling sandeels in the sediment with a net and codend mesh-size of 10mm was used. At each location the dredge was towed twice along the seabed for 10 minutes, towing down the line in both directions. A Scanmar depth unit was attached to the dredge so that the precise time and position of "touch down" onto, and "lift-off", from the seabed could be determined. The ships position was determined using a Differential Geographical Positioning System (DGPS). Dredge tows were always in a straight line thus the track length could be determined from the "touch down" and "lift off" positions.

When designing the dredge survey it was decided to conduct two 10-minute tows rather than one 20-minute tow. There were several reasons for this. Firstly, the sandeels caught would be in better condition for length and weight measurements and otolith extraction. Secondly, the dredge would be less likely to get clogged up with sediment and thus work more effectively and have more consistent sandeel catchabilty over the whole duration of each tow. Finally, smaller areas would sampled than had single 20-minute tows been used, thus the catches were more likely to be representative of a smaller number of sub-populations sampled from a smaller number of individual habitat patches within each sand-bank.

The total number of sandeels in each of the catches was counted and a sub-sample from each was measured to the half centimetre below. Normally, ten sandeels from each half-centimetre size class were weighed to determine length-weight relationships, but on rare occasions this was reduced to five if time constraints were pressing. Otoliths were removed from these fish to establish age-length keys. The length-weight relationships were used to convert catch numbers at length to weight at length. Summing over all length classes gave the total catch by both number and weight. Dividing these values by the area swept by the dredge during each tow (dredge width, 2m, multiplied by the tow track length), provided density estimates ($n.m^{-2}$ and $g.m^{-2}$) for each sample.

1.5.2 Collecting and analysing oceanographical data

Following the analysis of historical oceanographical data, a pilot sampling study was carried out during the June 2000 *Clupea* cruise, where the additional use of XBTs (eXpendable Batho-Thermographs) and the continuous deployment of a temperature mini-logger at 5 meters depth confirmed a high degree of spatial variability in vertical and horizontal water column temperature characteristics. Therefore the decision was made to double the number of CTD casts and deploy XBTs during the *Clupea* cruises for the duration of the IMPRESS project.

Onboard **FRV *Clupea*,** oceanographic information was collected via CTD casts and XBT deployments during the three seasonal cruises of the year (March, June and October; Fig 1.5.7 for locations of CTD casts) The data were used to produce an accurate quasi-synoptic 3-dimensional snapshot of the primary study area. Details of each cruise and annual comparisons for all the data collected have been compiled in the Appendix 3.

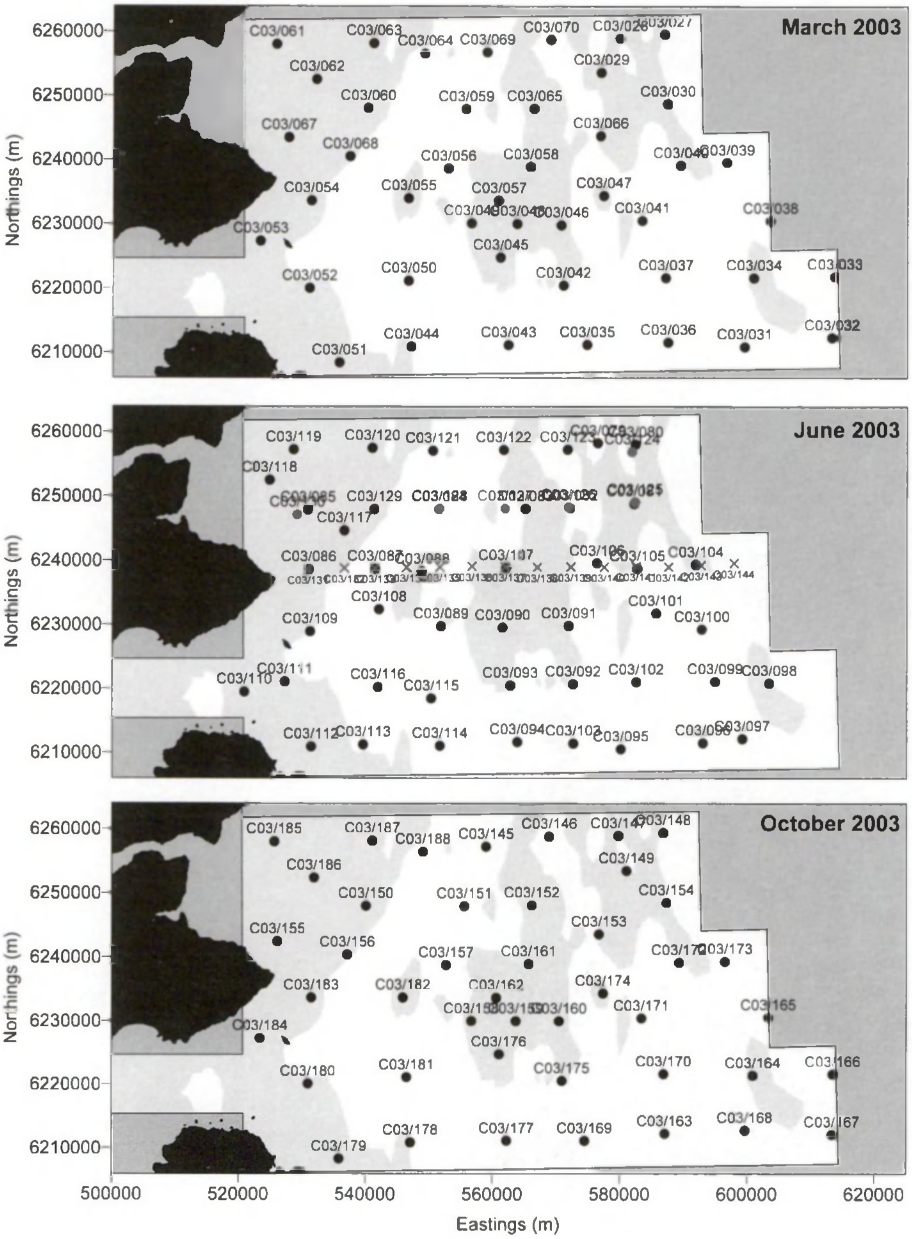


Figure 1.5.7. Location of the CTD and XBT (in red) sampling in 2003 on the Clupea cruise.

In 2001 and 2002 three **moorings** were deployed in the primary study area from March to October in what were assumed to be 3 contrasting water column characteristics: a bank region, a shallow sea region and a well mixed region (see Fig 1.5.8). The moorings were designed to provide very detailed temporal information within each region with recordings every 10 min on a series of temperature loggers placed at 5m to 10m intervals in the vertical. Recordings of current speeds where measured every 20 minutes and fluorometers (recording the level of chlorophyll present took readings once every hour. The moorings provided information on the changes in the vertical structure, including the depth of the surface mixed layer, the gradient of the thermocline and the abundance of chlorophyll (Chapter 3). The moorings provided detailed evidence of the annual timing of the stratification of the water and the initiation of the spring bloom.

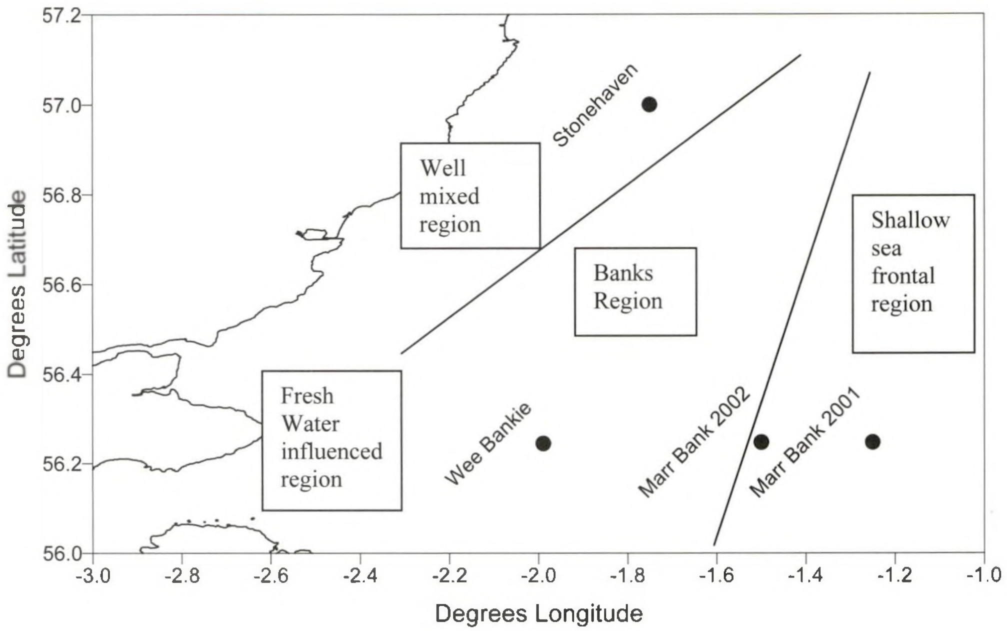


Fig. 1.5.8. Locations of the moorings deployed in the Firth of Forth 2001 and 2002 within the suspected regional boundaries.

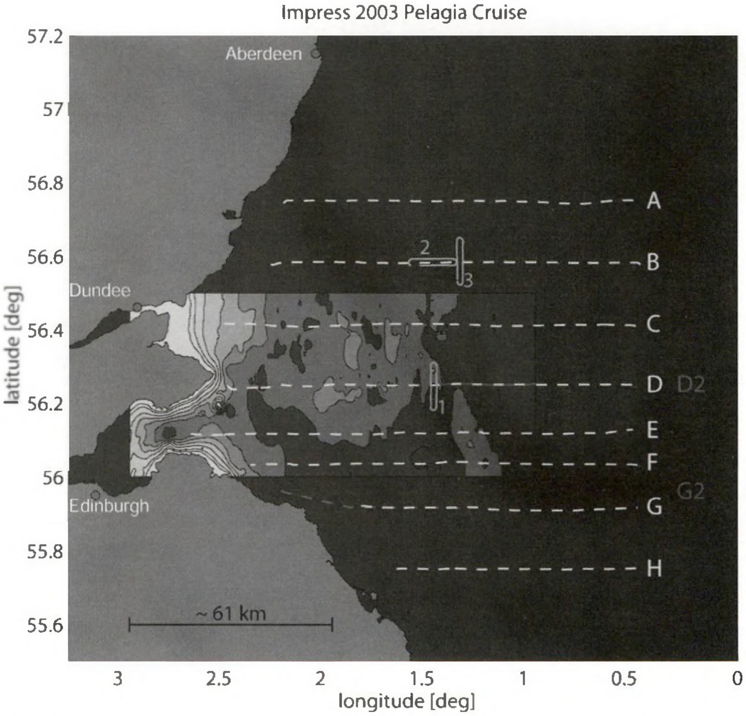


Fig. 1.5.9. Locations of transect tracks (A-H) and mini-surveys (1-3) for the Pelagia cruise, 6-19 June 2003. The bathymetry map covers the area of FRV Clupea during 2001 and 2002 field work.

During the IMPRESS project two weeks of dedicated surveys were scheduled to be performed in the third field season in a period chosen in response to research needs developed during the project (**RV *Pelagia* cruise 6-19 June 2003**). During the surveys, hydrographical observations would be combined with detailed behavioural and distributional studies of foraging seabirds and prey availability (acoustic signal). The surveys were to be designed to test predictions of foraging seabird behaviour, oceanographic characteristics and prey distribution that arouse from the previous 2 years of field work (both at colonies and at sea).

The oceanographic data collected from the 2 sets of moorings in the study over the previous years yielded very detailed temporal and vertical information. However, it was felt that the distance between the *Clupea* CTD stations (>10 km) has meant that detailed (non-interpolated) horizontal information for the entire study site was not available. Also, during the previous 2 years, the collection of the acoustic information was not performed at precisely the same time as the CTD stations were sampled. Therefore, it was a top priority to simultaneously collect physical properties, bird survey and acoustic (prey) information over the entire region at as fine a horizontal scale as possible. The accomplishment of this task would greatly increase the ability to define species-specific foraging habitat and to produce a predictive map of potential bird (single species and group) foraging habitats within the primary study area.

Covering the primary study area the *Pelagia* cruise completed 8 transects, with 2 of them repeated (Fig 1.5.9). The sampling was done with the use of a Scanfish (undulating CTD; Figure 1.5.10) such that continuous vertical and horizontal information on temperature, salinity, density and abundance of chlorophyll was collected at 1.0 second intervals and approximately 0.5 to 1.0 meters depth.

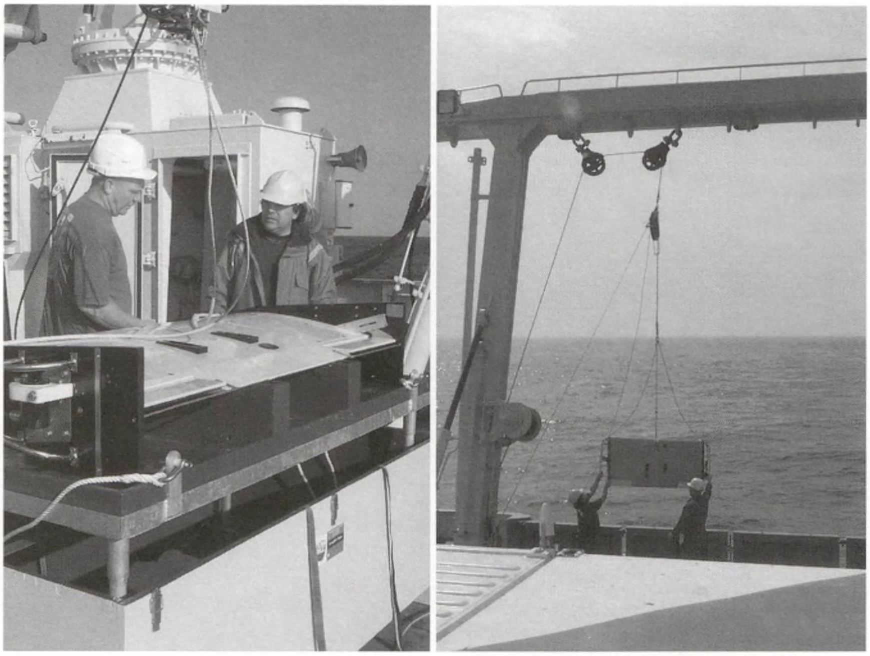


Figure 1.5.10. Scanfish deployment onboard RV Pelagia during the June 2003 cruise.

Logger data from tagged birds and observations of large inactive flocks of seabirds in the shallow frontal zone had suggested that there could be an influence of the speed of the tidal current on the timing and depth (of diving birds) of active foraging and that changes in tidal current strength might even influence the type of prey caught. It was decided therefore that the second priority of the RV *Pelagia* cruise would be to answer the question: Does the phase of the tide have any influence on the feeding behaviour and location of feeding of different bird species? To answer this question it would have been ideal to sample a set location such that we were sure to be observing only the changes in foraging behaviour due to the effects of tide and/or daylight. However a constraint of ship-based seabird surveys is that the ship has to be constantly moving so as to run the acoustics and scanfish equipment and not to become an attraction to wildlife. Therefore, **'mini-surveys'** were planned that were a compromise between a moving and a stationary ship. The track of the survey was an extended oval approximately 7 nautical miles in length and 1 nautical mile apart such that it takes 125 minutes to complete the circuit (Appendix 2). A tidal day (25 hours) was divided into 6 different phases (based on tidal speed) and the timing of the start and end of the circuits was such that each phase is measured twice (and in opposite directions of movement) during each Mini-survey. The series of Mini-surveys were designed to test all categories of the different types of feeding behaviour for each species with tidal phasing and to look for a repeat of similar locations for feeding activity for each species and for groups of species. The location for each Mini-survey was chosen on the basis of a combination of oceanographic information (e.g. scanfish data) and ornithological observations (intense feeding or particularly high densities of the target species during the transects performed in June 2003, compared with earlier data collected 2001-2002 in the same general area). The 3 different areas of the Mini-surveys were chosen so as to contrast the feeding areas of bank regions with those of Shallow sea fronts (Figs. 1.3.6, 1.5.9). Therefore the data available to explore the hypotheses stated above consisted of three 25h periods of continuous Scanfish data in 125 min blocks. As for the transect data, two types of data files were created. The predator– prey implications from the information gather in the mini-surveys will be discussed in detail in Chapter 7.

Due to indications that tides play an important role in the foraging of at least some seabird species, **tidal flag** information had to be provided (the speed of the tide at precise locations and time), to compare to tagged or observed bird foraging activity and acoustic information. A commercially available software (Polpred, Proudman Oceanographic Laboratories), was used to produce tidal predictions. The mooring data were used to validate the Polpred output for use in this region and found it to be accurate within ± 20 minutes in predicting the right time of maximum current. As our tidal phases are defined in 2 hourly bins this level of accuracy was deemed quite acceptable.

1.5.3 Studying seabirds in colonies: breeding success, diet and population trends

Whole colony counts of Shags, Kittiwakes and Guillemots were carried out each year (2001-2003) by Scottish Natural Heritage on the Isle of May as a continuation of data collected between 1997 and 2000, using standard methods (Walsh *et al.* 1995), and these data were made available to the IMPRESS project. Whole colony counts of gannets on the Bass Rock were carried out at ten-year intervals, most recently in 1994 (Murray & Wanless 1997) and these data were compared with the most recent census in 2004 (Wanless *et al.* 2004) and made available to the IMPRESS project. Breeding success was recorded for all species nesting on the Isle of May each year (2001-2003) by Scottish Natural Heritage on the Isle of May as a continuation of data collected between 1997 and 2000, using standard methods (Walsh *et al.* 1995). Breeding success of Gannets on the Bass Rock was assessed in 2002 and 2003.

Table 1.5.1. Observer effort (km² surveyed) per day, between 54°N and 59°N latitude, to the west of 3°E longitude, during herring acoustic surveys between 1991 and 2004.

Date	Month	1991	1993	1995	1997	1998	1999	2001	2002	2003	2004	Totals
24	Jun									125.1		125.1
25	Jun								106.3			106.3
26	Jun							74.8	63.0	83.0		220.9
27	Jun							53.2	55.6	66.1		174.8
28	Jun							70.2	27.5	2.1		99.8
29	Jun					2.9	107.8	70.5	8.1		127.6	316.9
30	Jun		53.9		3.3	88.8	81.5			31.5	32.9	291.9
1	Jul		59.4		91.1	15.1	80.5		79.0		69.9	394.9
2	Jul	34.7	74.5		85.6	72.2	76.5	73.0	80.6	58.6	80.4	636.1
3	Jul	65.9	45.1		81.5	38.0		79.7	75.3	77.4	51.2	514.1
4	Jul	54.5	46.3	18.6	70.0			67.0	81.6			337.9
5	Jul	67.9	67.1	62.0			77.7	82.3			74.3	431.2
6	Jul	76.7	24.9	90.0		78.5	85.6				75.9	431.6
7	Jul	8.9	49.3	79.8	99.9	58.6	73.1			8.4	75.2	453.3
8	Jul	70.1		59.7	86.9	72.0	108.6			78.8		476.1
9	Jul	7.4	55.8		54.3	82.7	83.3		65.1	65.9		414.6
10	Jul	68.6	51.5	104.1	105.6	85.8		81.1	77.3	75.0		649.0
11	Jul	56.8	79.6	95.7	84.9			65.2	72.7	50.2		504.9
12	Jul	81.2	57.0	89.1			81.0		69.9			378.3
13	Jul	46.9	82.4	77.8		32.8	92.6	71.1			56.5	460.2
14	Jul	59.0	57.4	95.0	88.3	26.8	44.7			77.9	72.6	521.7
15	Jul	69.7	71.8	22.0	100.9	73.4	80.9		74.4	70.1	70.4	633.6
16	Jul	79.5			86.8	72.4		83.4	75.7	57.4	91.0	546.3
17	Jul	71.8		90.3				76.5	83.8	32.4	33.2	388.0
18	Jul	37.3		98.2				0.7	46.9			183.1
19	Jul			78.4				52.3			80.6	211.3
20	Jul			68.3							57.4	125.7
21	Jul										84.2	84.2
		956.8	875.9	1128.9	1039.2	800.1	1073.9	1001.1	1142.7	959.9	1133.2	10111.7

More intensive sampling of diet was carried out throughout the breeding season in all four species between 2001 and 2003, so that within season patterns of diet composition could be examined in detail. Samples collected prior to the IMPRESS project were collected and analysed using standardised methods, similar to those used prior to the project (IMPRESS Report 2001.004).

1.5.4 Recording seabirds at sea

Ship-based seabird surveys in the study **area at large** (Fig. 1.3.4; WP3) were conducted using strip-transect counts, using line-transect technology (i.e. the distance of individual sightings estimated in distance strata to allow corrections for missed individuals at greater distances away from the observation platform; Camphuysen *et al.* 2004), which were developed as a standard for the North Sea in the late 1970s and early 1980s (Tasker *et al.* 1984). Counts were conducted outside, from the top-deck of the ship during steaming by two observers, operating a 300m wide transect on one side and ahead of the ship. Birds hitting the water or swimming were allocated to narrower bands: A= 0-50m to the side of the ship, B= 50-100m, C= 100-200m, D= 200-300m, and E (beyond transect) >300m. Birds were normally discovered with the naked eye and identified by using binoculars. Standard counting units were initially 10-minute, later 5-minute period bins and a mid-position was calculated for each bin (see Tasker *et al.* 1984 for details). The surveys started in The Netherlands and occasionally reached as far north as Shetland (2003), but the analysis was restricted to data collected between 54°and 59°N latitude, to the west of 2°E longitude. Surveys were discontinued during strong winds (6B or more headwind, 7B or more wind from behind) and during fog (<300m visibility). The resulting day-to-day observer effort is summarised in Table 1.5.1, showing some variation in timing between years. The amount of effort spent with distance to the UK coast is presented in Table 1.5.2.

It was important that feeding or foraging seabirds could be readily separated from (presumably) non-feeding individuals. Standard recording methods (Tasker *et al.* 1984) were therefore slightly modified, so that the behaviour of seabirds observed was recorded, coded and stored into the database (Camphuysen & Garthe 2004). Basically following the descriptions of Ashmole (1971), several types of feeding behaviour were recognised, including aerial pursuit, dipping or pattering, surface seizing or pecking at the surface, scooping, pursuit plunging, surface plunging, deep plunging, pursuit diving, scavenging at fishing vessels, and 'actively' searching for prey (head down and often circling). The information of feeding behaviour gained importance during later versions of the cruise (1995 and on), and older data needed to be re-processed, so that details of foraging behaviour in the observed seabirds, as they were scribbled on the margins of the original recording forms, could be entered into the database. All birds, whether swimming or flying, that operated 'together' or stayed tight in a particular area or in a particular movement were marked as 'flocks'. Flocks comprising more than one species were named 'multi-species (feeding) associations' (MSFAs; Camphuysen & Webb 1999). The behaviour of each of the participants within MSFAs was described upon encounter, using classifications listed by Camphuysen & Garthe (2004). Important roles were: producers (underwater predators driving prey towards the surface), initiators (surface feeders detecting the prey and actually starting the multi-species feeding frenzy), joiners (additional participants), scroungers (species joining the frenzy in an aggressive and dominant way, thereby excluding initiators from further access) and kleptoparasites (see Camphuysen & Webb 1999 for further details).

Table 1.5.2. Observer effort (km² surveyed) with distance (km) to the UK coast, between 54°N and 59°N latitude, to the west of 3°E longitude, during herring acoustic surveys between 1991 and 2004.

Distance	1991	1993	1995	1997	1998	1999	2001	2002	2003	2004	Totals	%
0-20km	92.0	54.2	90.2	32.8	30.2	94.4	67.8	115.8	24.2	84.8	686.3	6.8
20-40km	81.2	84.8	126.3	109.6	86.8	170.6	109.6	139.4	73.5	125.8	1107.6	11.0
40-60km	67.4	67.7	119.7	100.1	74.0	143.7	76.1	109.7	100.8	109.5	968.8	9.6
60-80km	69.3	63.2	87.1	90.5	58.6	103.1	74.3	87.8	83.6	101.1	818.7	8.1
80-100km	74.8	46.2	108.2	87.7	72.2	79.1	73.9	68.7	69.4	98.1	778.2	7.7
100-150km	205.3	178.0	241.1	214.0	134.2	168.2	180.3	186.3	232.7	223.9	1964.0	19.4
150-200km	210.7	218.0	187.1	198.1	132.7	161.3	173.0	248.7	211.5	173.2	1914.3	18.9
200-250km	151.9	146.2	150.8	206.5	169.7	117.0	161.7	127.8	147.8	139.5	1518.9	15.0
250-300km	4.3	17.6	15.9		41.7	36.4	84.3	58.5	16.3	75.9	350.8	3.5
>300km			2.7							1.4	4.1	0.0
	956.8	875.9	1128.9	1039.2	800.1	1073.9	1001.1	1142.7	959.9	1133.2	10111.7	

The **principal study area** was surveyed on board FRV *Clupea* (2001-2003) and RV *Pelagia* (2003) (WP3). Survey techniques onboard RV *Pelagia* was identical as that on board FRV *Tridens* in the study area at large, except that more observers were involved. To be able to cope with very long days of observation within high-density seabird areas, a rotating team of observers was established with two recorders and one 'writer' at anyone time, with one being replaced every hour to become refreshed in a rotating schedule.

Seabirds were surveyed at sea from the FRV *Clupea* using a slight modification of the standard shipboard transect survey methods proposed by Tasker *et al.* (1984) and Webb and Durink (1992). Instead of using a fixed transect width of 300m and determining 'correction factors' to adjust counts of seabirds on the water to account for birds missed at various distances out from the vessel's line of travel, a variable transect width was employed. Transect width was adjusted depending upon prevailing sea conditions to reduce as far as possible the chances of missing seabirds sitting on the water surface, yet at the same time attempting to maximise the area surveyed. This avoided the necessity of determining and using correction factors which would have been inappropriate in examining variation in the numbers and distribution of seabirds at the spatial resolution considered in this project. The maximum transect width employed was 300m as problems with species identification multiplied enormously beyond this distance. Generally a transect width of 300m could be used in sea states of up to two or three. Transect width was reduced in steps of 50m as sea states worsened, until in sea states of around five, the transect width was reduced to 150m. Transect width was never less than 150m and seabird survey was abandoned in sea states of six and above. Flying birds were surveyed using the same variable transect width, but with a fixed scan distance ahead of the ship of 300m. With the vessel travelling at 10 knots, this meant that one count of flying birds per minute was required to survey flying birds in the transect strip. Seabird behaviour was not recorded and coded with the same level of detail during these surveys as compared with surveys on board *Tridens* and *Pelagia* and this has therefore not been analysed.

1.6 The development of data loggers and methods of experimentation

1.6.1 Data logger development (WP7)

A vital component of the project was the development of new miniature electronic devices for attachment on seabirds. Four new loggers were developed and tested for the first time during this project. All loggers worked successfully in laboratory trials and in the field, producing data on 3D foraging distributions of the study species in unprecedented detail for the four study species (see Chapter 5). For instrument calibration and device performance as well as for further technical details of the devices, see Appendix 1.

Depth-Temperature-Recorder (PreciTD)
A new precision Depth-Temperature-Recorder (PreciTD) for monitoring diving activity and water temperature produced. Existing technology was further developed and optimized for application in flying birds. The task was to provide a small device that could be attached to small seabirds with a high wing loading (e.g. common guillemot), thus the total mass of the device had to be kept below 25g. High precision of the instrument and rapid response time in the temperature signal were required to allow functional relationships between hydrographic conditions and foraging performance. The main challenge involved, was to keep total mass at the absolute necessary minimum while still providing a high level of accuracy in the parameters to be monitored. For the external temperature sensor, incorporated in the PreciTD, an optimum had to be found between mechanical stability (device has to withstand smashing on rocks in the colonies etc.) and a short response time. The sensor had a response time T0.9 (time to reach 90% of ΔT, following a sudden temperature change) of *c.* 2s (Appendix 1), allowing profiling measurements of the water column to be done by diving seabirds with a very low time lag in the temperature signal.

- operational mass 23 g.
- dimensions: length 80, diamm. 19-22 mm
- temperature resolution 5 mK
- temperature uncertainty 0.03°C
- pressure resolution 5-6mbar
- pressure uncertainty <40mbar
- 2 MB capacity
- external fast-responding temp.-sensor
- non-volatile memory
- depth-rating 160 m

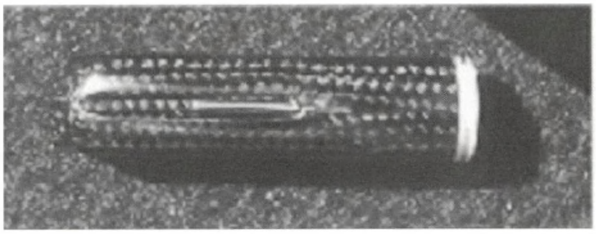


Figure 1.6.1. Specifications and picture of Depth-temperature (PreciTD) loggers developed under IMPRESS.

Our efforts at designing this device (in collaboration with IDE GmbH Kiel) resulted in an unparalleled precision for an instrument of this size and rigidity and with this device we were able to facilitate profiling temperature measurements of the water column with a precision that is otherwise only achieved with much bulkier ship-based equipment (e.g. CTD-probes, 'Scanfish', etc.). Logger specifications are summarised in Fig. 1.6.1.

Compass logger
The compass logger recorded horizontal bearings, mostly at 1s intervals. After retrieval of the data, the flight paths can be reconstructed by dead reckoning. For this method, to be accurate, the timing of flight phases and phases on the water (or on the nest) is a crucial prerequisite. Therefore, the logger contained a small temperature sensor on a cable stalk that allowed these phases to be accurately determined from changes in the temperature signal. A long sensor stalk (see Fig. 1.6.2) attached to the tail of the birds is mounted in a manner that it dips into the water each time a bird alights on the water. A summary of specifications is given in Fig. 1.6.2.

GPS logger- Mark I
The development of the GPS recorder was one of the key achievements of IMPRESS. The idea of developing this device was that it could be used to replace satellite transmitters, in species that were large enough to carry a GPS logger. This would provide better spatial accuracy, increase the number of fixes per unit time, and thus vastly improve spatial resolution. This higher resolution would reveal much more about the particular foraging behaviour and feeding locations of animals under study, than does satellite telemetry. While Argos-based systems only provide broadly spaced positions, with GPS, the small-scale sinuosity of the flight path can be assessed. The GPS technology should also remedy the problem of high and difficult to control running costs for the Argos service. Finally, the lack of any external antennas in this system would further help to reduce device effects in diving animals.

The logger is housed watertight in a lightweight epoxy-aramid-fiber composite casing. The casing is streamlined and tapers off at the front end with maximum outer dimensions being 48 x 24 x 100 mm. Although, the strong streamlining adds to the total length, the benefits from reduced hydrodynamic drag greatly outweigh this, especially with gannets, where there is a strong hydrodynamic impact on the device during plunge diving). The total operational mass of the present device is 65g (technical specifications see Fig. 1.6.3).

The GPS-logger could be run in two different modes: While in continuous mode, the receiver was permanently working, calculating positional updates at 1 s^{-1}. In intermittent mode, the receiver is set 'asleep' for certain intervals between fixes in order to save energy. In this latter case, the device receives satellite signals until a fix can be calculated, and thereafter the receiver is immediately switched off again. The logger is run with a standard 3V lithium battery (CR 123A) which allows the device to work continuously for up to 6 hours, providing up to 21 600 fixes. With the new receiver, due to a reduced power consumption, the operating time is up to 20h and >70 000 fixes with this battery type.

Six of the mark-1 devices were deployed in summer 2002 on Gannets. Two devices were additionally equipped with temperature and pressure sensors to test the feasibility of sampling additional data on external temperature and dive behaviour. All devices worked, but initially there was still some enhanced power consumption during the sleep mode in intermittent applications, so that batteries were exhausted much earlier than we had anticipated.

- operational mass 14.5 g.
- dimensions: length 65, diamm. 16 mm
- directional resolution < 0.1 °
- temperature resolution 5 mK
- temperature uncertainty 0.03°C
- 2 MB capacity
- external fast-responding temp.-sensor
- non-volatile memory
- depth-rating 160 m

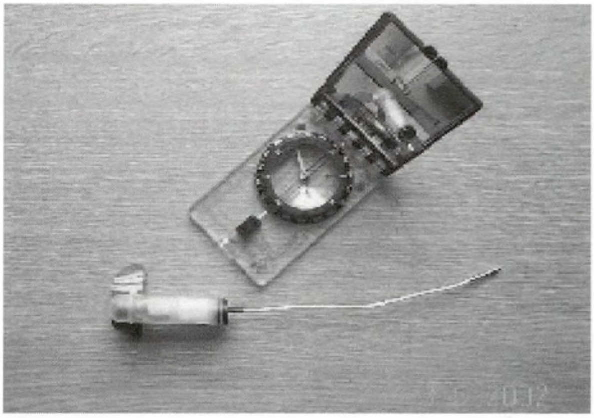


Figure 1.6.2. Compass/Activity logger with temperature sensor stalk. A saddle-shaped piece of darvic plastic (red) at the front end, fitting the shape of the bird's back, considerably reduced the tilting of the device.

- operational mass 65/70 g
- rigid aramid-fiber epoxy casing
- low power receiver
- locational error:
  - 3 - 5 m in continuous mode
  - 9 - 19 m in intermittent mode
- time to fix 16 s on average
- hot start < 3 s
- Additional analogue channels as in the PreciTD: pressure and temperature

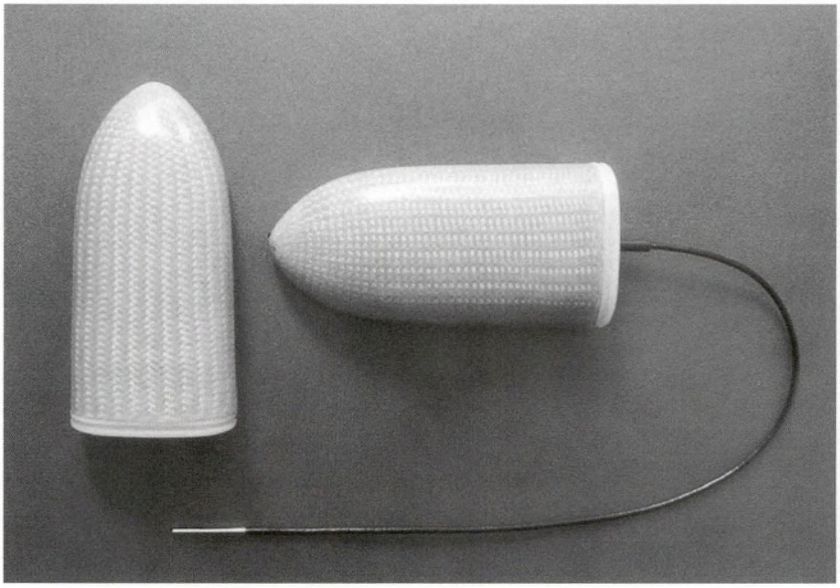


Fig. 1.6.3. Specifications and picture of the GPS logger (left) and GPS logger with temperature-depth probe (right).

GPS logger- Mark II

The unexpected quiescent power drain of the GPS electronics during deployments in 2002, resulting in a limited operating period in these devices (see above) was solved subsequently. Five of the 2002-GPS-recorders were modified, so that they finally stored up to ca 800 fixes in intermittent mode (continuously 5 to 5.5h, >19 000 fixes) with one single CR 123A battery. Depending on actual conditions and interval chosen this resulted in an operating period of about 1.5 days when set at 3-min intervals, 2.5 days for 5-min intervals and about 5 days for 10-min intervals. Compared to the currently used ARGOS-PTTs, this means an extreme improvement in terms of data density and spatial accuracy. Due to continued technical development and to use of a new GPS receiver with a considerably reduced power consumption (which became available toward the end of 2002), the total operating period of the GPS recorder could be considerably extended. Two of the new-type GPS recorders were delivered for use on gannets. In addition, one of the GPS recorders from the previous year was upgraded to this standard. With this configuration, the devices were now able to work continuously for up to 20 hours, thereby providing more than 70 000 fixes at high temporal resolution (1 fix per second). In intermittent mode, more than 4000 fixes were obtained (at *c.* 15°C, reduced to about 2300 fixes for environmental temperatures slightly below 0°C), and about 3400 fixes for GPS recorders that included additional temperature and pressure sensors.

With the GPS update rate set at e.g. 3-min intervals and the sensor's update rate set at one per second, the current device worked for 6 days, providing 2600 locational fixes and an additional 514 000 data pairs on water temperature and dive depth in the foraging areas. At such high sampling rate for environmental data, however, the memory becomes limiting and the obtained 2600 fixes is the maximum possible for this configuration, otherwise higher numbers of fixes could be obtained A summary of the effect of the sampling interval on time-to-fix for the new GPS-recorder is given in Table 1.6.1. For longer intervals, the total number of fixes obtained tends to decrease, due to the receiver remaining active for longer periods per single fix. By choosing longer intervals, operating periods of up to several weeks can now be achieved at a still comparatively high temporal resolution (compared e.g. with Argos-based systems) and high spatial accuracy.

Table 1.6.1 Effect of the GPS sampling interval on time-to-fix (stationary test). n meaning number of intervals tested during trials, not total number obtained with a single battery.

Interval (min)	Time-to-fix (s)		
	Average	Median	*n*
1	17	18	96
5	16	17	222
15	20	17	92
30	23	18	48
60	27	27	55
120	31	30	11

1.6.2 Experiments with (foot-propelled) pursuit diving European Shags in captivity (WP10)

Three adult **European Shags**, one male, two females, with a mean mass of 1.66 ± 0.32 kg (mean ± S.D., range 1.27 – 2.12 kg) were used in this study. Birds were captured from the Runde colony off the west coast of central Norway in June 2001. They were housed in a sheltered outdoor pen (6m long x 4m wide x 2.5 m high) with water tank access, which was part of a larger facility we built alongside the Hopavågen lagoon, Agdenes community, on the west coast of central Norway. Birds were fed approximately 10 – 20% of their body mass daily with a mixed diet consisting of Atlantic Herring *Clupea harengus* and Saithe *Pollachius virens*, supplemented with vitamins and minerals ('Sea Tabs', Pacific Research Laboratories, El Cajon, CA, USA). Body mass was determined to the nearest 25 g when birds were post-absorptive and dry, if possible every morning, using a spring balance (Salter Abbey, West Bromwich, UK). Birds maintained a fairly stable body mass throughout our study until daily food intake and body mass increased in mid October, coinciding with a decline in ambient temperature. Bird capture and all experimental procedures were conducted under permission of the Norwegian Animal Research Authority (permit reference numbers 7/01 and 1997/09618/432.41/ME).

Within the first week of capture, the shags were introduced into a v-shaped shallow dive trench (17.5 m long x 2 m wide x 1 m deep) that had been dug, lined with thick PVC sheeting and filled with seawater. Two submersible water pumps (ITT Flygt, Oslo, Norway) provided a continuous exchange with seawater from the adjacent lagoon (approx. 200 l min-1). Over the course of 4 weeks of training the surface of this trench was progressively covered with transparent PVC sheets until only a small section remained open at one end of the trench. Birds submerged here, swam to the opposite end of the trench where a small fish had been placed, swallowed the fish underwater and returned to the uncovered section. Eventually this last open section was covered by a floating platform with a metal frame in its centre which allowed the placement of a plexiglass dome, serving as respirometry chamber of an open flow-through respirometry system. Starting 2 weeks before data collection birds were captured on a daily basis, weighed and placed inside the respirometry chamber from which they dived continuously, while the respirometry system was running. Training trials lasted between 10 and 30 min and ended when a bird stopped diving voluntarily for more than 5 min. At the end of a trial the bird was released from the chamber.

Oxygen consumption rates ($\dot{V}o_2$) were measured using an open flow-through respirometry system (Sable Systems, Henderson, NV, USA). To measure the metabolic rate during shallow diving, we used a transparent plexiglass dome in the shape of a truncated pyramid as respirometry chamber (0.6 m long x 0.6 m wide x 0.4 m high; volume: 50 l) which was partially immersed and received outside air through small holes on its 4 sides just above the waterline. Similarly, to measure resting metabolic rate we used a 55 litre bucket (0.35 m diameter x 0.65 m height) with an airtight plexiglass lid where air was drawn in via 4 small side holes near its bottom. Air from the respirometry chambers was fed directly into the laboratory, which was set up inside a hut adjacent to the dive trench (Fig. 1.6.4). The main airflow from the respirometry chamber was dried using silica gel before being led into a mass-flowmeter (Sierra Instruments Inc., Monterrey, CA, USA) which automatically corrected the measured flow to STPD (273 K and 101.3 kPa). A sub-sample of 10 l min^{-1} was bled into a manifold from which an oxygen (paramagnetic O_2-analyser PA-1B, Sable Systems; resolution: 0.0001%) and CO_2 analyser (Beckman LB2 Medical CO_2-analyser, Schiller Park, IL, USA; resolution: 0.01%) sampled in parallel. All connections between the various components of the respirometry system were made with gas-impermeable tubing (Tygon, Norton, USA).

Air flow through the respirometry chamber was maintained at about 10 l min^{-1} during the resting in air trials and at about 80 l min^{-1} during the dive trials (Piston pump, GAST Corp., USA). Oxygen concentration inside the metabolic chamber was kept above 20.5% and CO_2 concentration was kept below 0.4% during all trials. The gas analysers were calibrated before each trial using 99.995% pure N_2, 1.03% CO_2 (AGA, Trondheim, Norway) and outside air (set to 20.95% O_2 and 0.03% CO_2). Analyser drift was minimal and corrected for. Absorption of CO_2 by seawater was assumed to be negligible. Before a trial the entire system was tested for leaks by infusing pure N_2 gas. Because of the high flow rate during the dive trials the drying capacity of the silica gel became exhausted rapidly and was replaced after every second run. Time delay between air leaving the metabolic chamber and arriving at the gas-analysers was calculated by dividing the total volume of the tubing and drying columns by the corresponding flow rate. The delay was found to be 27.0s (resting in air) and 16.8s (diving) for the oxygen analyser and 17.8s (resting in air) and 7.65s (diving) for the CO_2 analyser respectively. These delay times were taken into account when calculating $\dot{V}o_2$ and $\dot{V}co_2$ and relating them to diving events. The time constant of the metabolic chambers were calculated to be 5.5 min for resting in air and 37.5s for diving, respectively.

Data from the flowmeter and the gas analysers were fed into a universal interface (16 bits resolution, Sable Systems) and average values were recorded every 1s (dive measurements) or 5s (BMR measurements) onto a desktop computer using Datacan (Sable Systems).

Basal metabolic rate (BMR) was measured during the inactive (22 – 6h) and active period (8 – 18h) while birds were resting, post-absorptive and presumably within their thermo-neutral zone (measurement between 12 and 19°C air temperature; lower critical temperature for our birds calculated after the equation given by Kendeigh *et al.* 1977 for non-passerines should be 12°C). Birds were fasted overnight or for at least 7h before being placed inside the metabolic chamber. After the initial disturbance birds calmed down quickly and sat quietly in the darkened chamber for the remainder of the trial. A stable $\dot{V}o_2$ was typically reached within the first hour of these 3 to 5h long trials. Air temperature in the respirometry chamber was monitored using a digital thermometer (Oregon Scientific, Portland, OR, USA) and usually did not differ from outside air temperature by more than ± 2°C. Birds were familiarized with the procedure on at least two occasions before data collection began. BMR was determined from at least three trials per bird during September.

Diving metabolic rate was measured in all birds during September and October in water temperatures ranging from 4.9 to 12.6°C. Water temperature was measured after each set of trials 10 cm below the surface. During a trial a bird was captured, weighed and placed inside the respirometry chamber from which it dived continuously. Through the window in the laboratory hut (Fig. 1.6.4) it was possible to observe the bird without any disturbance. All relevant behaviour of the bird was marked onto the respirometry traces, so that behaviour as well as dive and surface events could be related to the respirometry recordings. In a subset of trials swim speed was recorded. For this an observer with a digital stopwatch was placed on a ladder 2 m above ground at the 10 m mark of the dive trench. Swim speed (m s^{-1}) was calculated by dividing the distance swam (10 m) by the time taken to swim 10 m. Only dives in which birds swam in a straight line were included in the analysis. The majority of trials lasted about 20 min (range: 10 – 50 min) during which birds dived voluntarily and without any interference. A trial was terminated when a bird remained at the surface for more than 10 min. Trials were conducted in the mornings and afternoons with a maximum of 2 dive trials per bird per day.

To investigate the effect that feeding might have on diving metabolic rate birds were diving in both the post-absorptive and absorptive state. For the post-absorptive trials birds were fasted overnight for at least 15h. For the absorptive trials birds were fed various amounts of herring (40 – 160g) at various times before a trial (0.5 – 5h) and/or ingested herring during a trial.

During some trials birds would dive very little or not at all but rest at the surface, resulting in fairly stable respirometry traces. Similarly, one bird often rested for extended periods on the water surface at the end of a dive trial, while $\dot{V}o_2$ declined to a stable level. Stable resting periods from these trials were selected to calculate the metabolic rate during resting on water for both the post-absorptive and the absorptive state.

In parallel with the respirometry measurements, temperature loggers (MiniTemp-xl, 25 g, resolution: 0.03°K; earth&OCEAN Technologies, Kiel, Germany) were employed with all birds to measure stomach temperature during the dive trials. Stomach temperature will reflect abdominal body temperature during post-absorptive dive trials if no food is ingested. Temperature loggers were programmed to record stomach temperature every 5 s and were fed to the birds hidden inside a herring. The loggers were retrieved when the memory was filled (after about 5 days). After retrieval the data were downloaded onto a laptop computer, the logger was cleaned, re-programmed and re-fed to cover the entire period of dive experimentation.

Data analysis and statistics: Oxygen consumption rates ($\dot{V}o_2$) were calculated using equation 3b given by Withers (1977). BMR was calculated from the lowest 15-min running average value of $\dot{V}o_2$. Although our respirometry system was sufficiently fast to allow separation of individual dive and surface events, we decided to calculate diving metabolic rate (MRd) as the average value of $\dot{V}o_2$ during a dive bout from its start until 30s after the last dive in a bout (i.e. MRd = oxygen consumption during the entire dive bout divided by the sum of all dive and surface durations within that bout). A dive bout was characterised by continuous diving activity and ended by definition when the bird started other activities (e.g. wing-flapping, see Fig. 1.6.5) or remained at the surface for longer than 2 min (using a log-survivorship plot as bout ending criterion; Slater and Lester, 1982). Birds typically started to dive from the moment they were introduced into the respirometry chamber. Because of the intrinsic time constant of our system, however, it took approximately 1 min before our system stabilised at an equilibrium point (see Fig. 1.6.5). Dives performed during this time were excluded from analysis. Oxygen consumption rates (ml O2·min-1·kg-1) were transformed to kJ using the caloric equivalent corresponding to the respiratory exchange ratio (RE) of the birds. The RE was calculated by dividing CO2 production rates ($\dot{V}o_2$) by $\dot{V}o_2$ and averaged 0.72 ± 0.09 (mean ± S.D.) during resting in air, 0.74 ± 0.07 during post-absorptive diving and 0.76 ± 0.03 during absorptive diving. Hence, a conversion factor of 19.7 kJ·l-1O2 (Schmidt-Nielsen, 1997) was used to transform these values to Watts (W). Metabolic rate (MR, in W·kg^{-1}) is given by:

$$\frac{19.7 \cdot \dot{V}o_2}{60 \cdot M_b},$$

where M_b is body mass in kg.

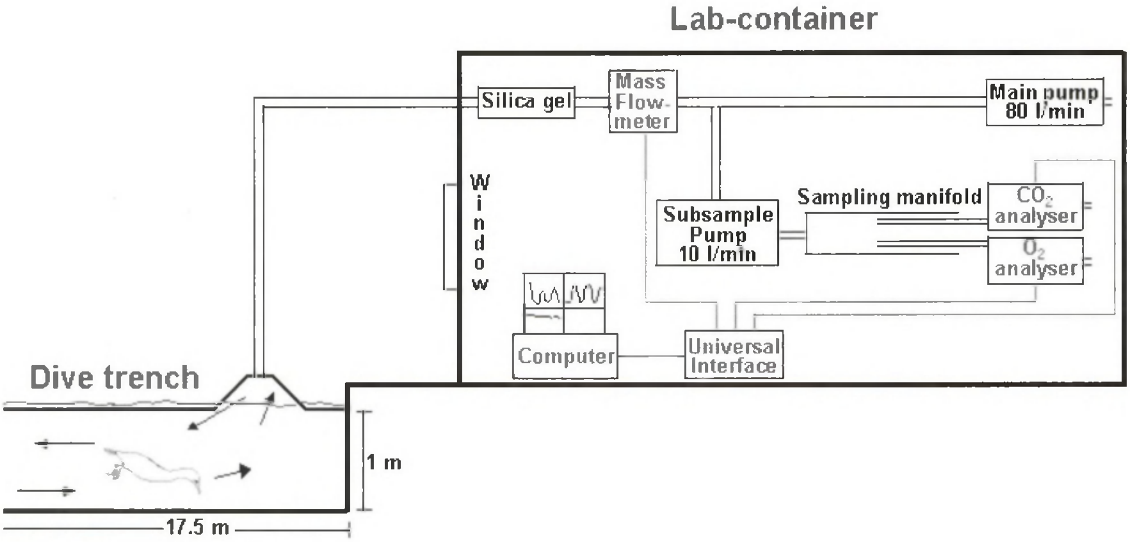


Fig. 1.6.4. Side view and dimensions of the shallow dive trench and the set-up of the respirometry system within the laboratory container. The approximate underwater routes taken by the birds are indicated by the arrows, with arrowheads indicating the direction of locomotion.

Stomach temperatures were analysed using Multitrace (Jochim Lage, Kiel, Germany). Resting values during the night and day were established from periods when birds were calm. Temperature recordings were averaged over a period of 6h during the night (between 23h and 5h) and over periods of at least 2h during the day (between 8h and 18h). Temperature recordings from the entire experimental period were included in the analysis.

Stomach temperatures during the various phases of a dive trial were taken as averages from the first and last minute of a trial ('diving start' and 'diving end' respectively), and as the single highest value during a trial ('diving peak'). Only stomach temperature recordings from birds which had not ingested food for at least 3h were included in the analysis to exclude periods of decreased stomach temperature after food ingestion.

One-way repeated measures analysis of variance (ANOVA) with Tuckey test pairwise multiple comparisons was used for comparison of metabolic rate during different activities and feeding status and for comparing stomach temperatures during various phases. When single comparisons were made, as in comparing BMR measured during the day and during the night, Student's paired t-test was used. Significance was accepted at $P < 0.05$. The relationship between energy expenditure and water temperature that takes into account variability between subjects was determined using repeated-measures multiple linear regression, with each bird being assigned a unique index variable (Glantz & Slinker 1990). All mean values are presented with standard deviation (± 1 S.D.).

1.6.3 Experiments with (foot-propelled) pursuit diving Double-crested Cormorants in captivity (WP10)

Twelve adult or sub-adult Double-crested Cormorants (minimum age 2 years) with a mean body mass of 2.10 ± 0.16kg (mean ± S.D., range 1.81 – 2.47kg) were used in this study. Ten of the birds had been captured as chicks (5-6 weeks of age) from the Mandarte Island breeding colony. Two birds had been bred in our captive setting. All birds were well established in captivity and were housed communally in sheltered outdoor pens (8 m long x 4 m wide x 5 m high) with water tank access at the South Campus Animal Care Facility of the University of British Columbia (UBC), Vancouver, Canada. Birds were fed approximately 10% of their body mass daily with a mixed diet consisting of Pacific Herring *Clupea pallasi* and Rainbow Smelt *Osmerus mordax*, supplemented with vitamin B1 tablets (thiamine hydrochloride, Stanley Pharmaceuticals Ltd., North

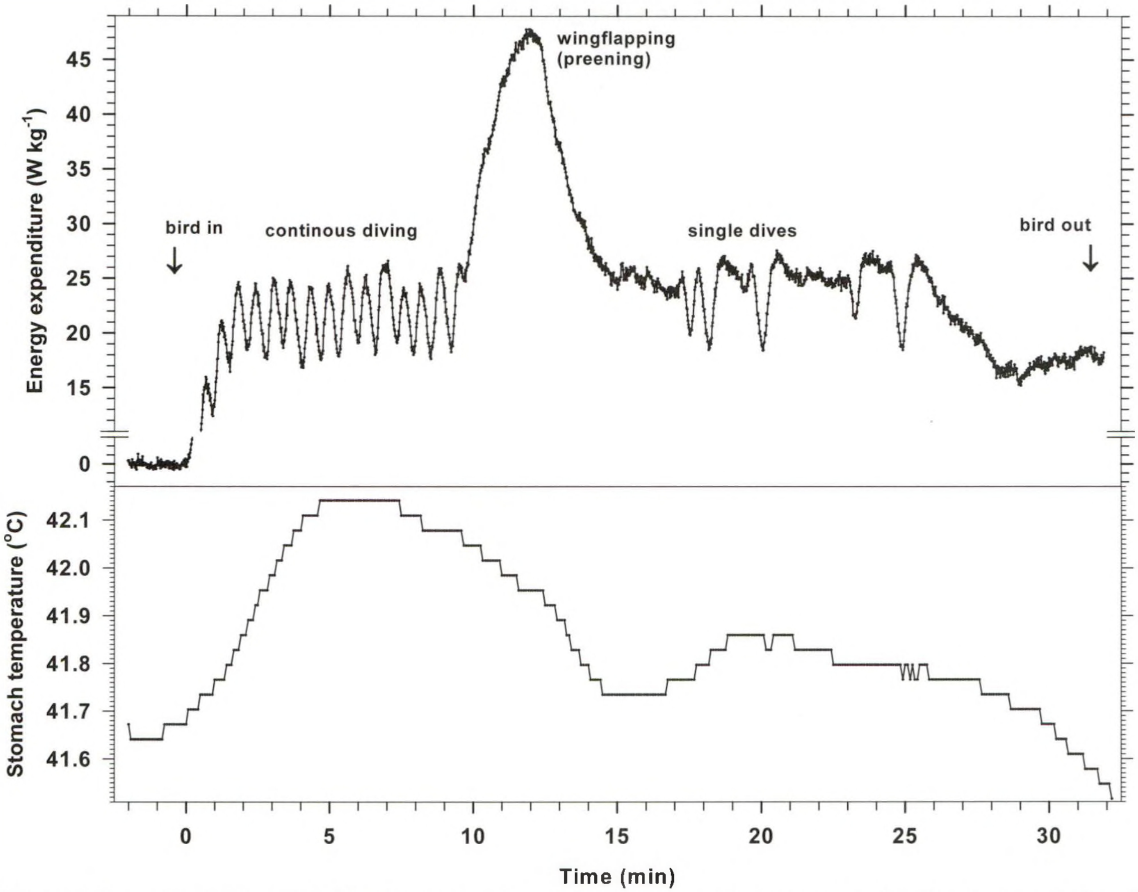


Fig. 1.6.5. Energy expenditure (W·kg^{-1}; upper trace) and stomach temperature (°C; lower trace) of a Shag during a shallow dive trial (post-absorptive). Arrows indicate when the bird entered and left the respirometry chamber. The trial lasted 32 min in water of 10.1°C.

Vancouver, Canada). Body mass was determined to the nearest 10 g when birds were post-absorptive and dry, if possible every morning, using a digital spring balance (UWE, HS-15K). All birds maintained a fairly stable body mass throughout our study. All experimental procedures were approved by the UBC Animal Care Committee (Animal Care Certificate # A02-0122) and were in compliance with the principles promulgated by the Canadian Council on Animal Care.

All birds had taken part in earlier studies on diving physiology, where they had been trained to dive within a shallow and a deep dive tank (see Enstipp *et al.* 2001). Birds were split up into groups of 4 individuals, which were housed either within the shallow dive setting, the deep dive setting or in their outdoor pen. In the shallow dive setting the entire surface of the tank (16.5 m long, 2 m wide, 1.5 m deep) was covered with flexible PVC mesh with the exception of a small area at the one end of the tank that held a plexiglass dome inside a frame, which served as a respirometry chamber. Birds were trained to submerge from within this plexiglass dome, swam to the opposite end of the tank to pick up a chopped herring piece and returned to the dome to swallow their prey ('shallow horizontal dives'). Similarly, in the deep dive setting the surface of the tank (5 m in diameter, 10 m water depth) was covered and birds were trained to dive from within the same dome. Birds dived to the bottom of the tank where they picked up chopped herring pieces from a suspended feeding platform ('deep vertical dives') before surfacing into the respirometry dome. Birds were rotated between the various settings throughout the experimental period, so that they were constantly trained for the tasks they had to perform. Birds were trained for a period of at least 2 weeks in a particular setting before data collection started. Both tanks were filled with freshwater which was continuously replaced at a water turnover rate of approximately 30 l min^{-1} for the shallow dive tank and 100 l min^{-1} for the deep dive tank. Because of this continuous mixing water temperature in both tanks was fairly homogenous (no stratification) and this was checked by running temperature profiles for both tanks throughout the seasons (max temperature difference between top and bottom in the deep dive tank was ± 2 °C).

Oxygen consumption rates ($\dot{V}o_2$) were measured using an open flow-through respirometry system (Sable Systems, Henderson, NV, USA). To measure the metabolic rate during diving, we used a transparent plexiglass dome in the shape of a truncated pyramid as respirometry chamber (0.6 m long x 0.6 m wide x 0.4 m high; volume: 50 l) which was partially immersed and received outside air through small holes on its 4 sides just above the waterline. Similarly, to measure resting metabolic rate we used a 55 litre bucket (0.35 m diameter x 0.65 m height) with an airtight plexiglass lid where air was

drawn in via 4 small side holes near its bottom. Air from the respirometry chambers was fed directly into the laboratory, which was set up inside a hut adjacent to the dive tanks. The main airflow from the respirometry chamber was dried using silica gel before being led into a mass-flowmeter (Sierra Instruments Inc., Monterrey, CA, USA) which automatically corrected the measured flow to STPD (273 K and 101.3 kPa). A sub-sample of 10 l min^{-1} was bled into a manifold from which an oxygen (paramagnetic O_2-analyser PA-1B, Sable Systems; resolution: 0.0001%) and CO_2 analyser (Beckman LB2 Medical CO_2-analyser, Schiller Park, IL, USA; resolution: 0.01%) sampled in parallel. All connections between the various components of the respirometry system were made with gas-impermeable tubing (Tygon, Norton, USA).
Air flow through the respirometry chamber was maintained at about 10 l min^{-1} during the resting in air trials, at about 45 l min^{-1} during the resting in water trials and at about 80 l min^{-1} during the dive trials (Piston pump, GAST Corp., USA). Oxygen concentration inside the metabolic chamber was kept above 20.5% and CO_2 concentration was kept below 0.4% during all trials. The gas analysers were calibrated before each trial using 99.995% pure N_2, 1.03% CO_2 (PraxAir, Richmond, Canada) and outside air (set to 20.95% O_2 and 0.03% CO_2). Analyser drift was minimal and corrected for. Before a trial the entire system was tested for leaks by infusing pure N_2 gas. Because of the high flow rate during the dive trials the drying capacity of the silica gel became exhausted rapidly and was replaced after every second run. Time delay between air leaving the metabolic chamber and arriving at the gas-analysers was calculated by dividing the total volume of the tubing and drying columns by the corresponding flow rate. The delay was found to be 18 s ('resting in air') and 11 s ('resting in water' and 'diving') for the oxygen analyser and 21 s ('resting in air') and 11 s ('resting in water' and 'diving') for the CO_2 analyser respectively. These delay times were taken into account when calculating $\dot{V}o_2$ and $\dot{V}co_2$ and relating them to diving events. The time constant of the metabolic chambers were calculated to be 5.5 min for resting in air, 67 s for resting in water, and 37.5 s for diving. Data from the flowmeter and the gas analysers were fed into a universal interface (16 bits resolution, Sable Systems) and average values were recorded every 1 s ('resting in water' and 'diving') or 5 s ('resting in air') onto a desktop computer using Datacan (Sable Systems).

Basal metabolic rate (BMR) was measured during the active period (8 – 18 hrs) while birds were resting, post-absorptive and presumably within their thermo-neutral zone (mean air temperature was 22.1 ± 1.7°C; range: 18.3 – 25.4°C; lower critical temperature for our birds calculated after the equation given by Kendeigh *et al.* (1977) for non-passerines should be 12°C). Birds were fasted overnight (for at least 15 hrs) before being placed inside the metabolic chamber. After the initial disturbance birds calmed down quickly and sat quietly in the darkened chamber for the remainder of the trial. A stable $\dot{V}o_2$ was typically reached within the first hour of these 3 to 5 hrs long trials. Air temperature in the respirometry chamber was monitored using a digital thermometer (Oregon Scientific, Portland, OR, USA) and usually did not differ from outside air temperature by more than ± 2°C. Birds were familiarized with the procedure on at least three occasions before data collection began. BMR was determined from at least three trials per bird. To investigate the effect of air temperature on resting metabolism and to determine the lower critical temperature (below which thermoregulatory costs will increase) measurements were conducted at various temperatures, ranging from 5 to 25°C.

The **metabolic costs associated with resting** in water were measured in separate trials during which birds floated calmly inside the dome, on the water surface of the shallow dive tank. A metal grid mounted about 30 cm below the base of the respirometry chamber prevented birds from submerging. After the initial disturbance, when introduced into the chamber, birds calmed down quickly and a stable $\dot{V}o_2$ was typically established within 10 min. In a few cases some birds became agitated during a trial and these trials were consequently discarded. Trials lasted 30 min during which birds were observed from inside a hut through a stained glass window, which allowed undisturbed observation of the birds. Birds were familiarized with the procedure on at least three occasions before data collection started. To investigate the effect of water temperature on metabolic rate when resting in water, we conducted trials in water temperatures ranging from 8 to 16°C. The effect of feeding (heat increment of feeding, HIF) on the metabolic rate during resting in water was investigated in specific trials when birds were fed a known amount of food (60 g of herring) at various times (30 – 120 min) before a trial. Mean water temperature during the later trials was 14.6 °C (range: 13.5 – 15.8°C).

Diving metabolic rate was measured in all birds during shallow and deep diving in water temperatures ranging from 6.1 to 17.5 °C. Water temperature was measured after each set of trials 10 cm below the surface. During a trial a bird was captured, weighed and placed inside the respirometry chamber. A trap door at the bottom of the dome prevented the bird from submerging directly. When the bird floated calmly and a stable $\dot{V}o_2$ was established (usually within 5 – 10 min) the trap door was opened through a remote pulley system and the dive trial began. During a trial birds dived continuously to the opposite end of the shallow dive tank or to the bottom of the deep dive tank. Through a stained glass window in the laboratory hut it was possible to observe the surface behaviour of the birds without any disturbance. To monitor the behaviour of birds underwater a submersible camera (Mariscope, Kiel, Germany) was positioned within the tanks and connected to a video monitor inside the hut. This was especially important in the deep dive setting where dives were classified as deep (diving to the bottom) or shallow (diving to less than 3 m of depth). Here birds typically started a dive bout with an exploratory shallow dive before performing a series of deep dives to the bottom of the tank. Similarly, they terminated a deep diving bout by either remaining at the surface or by switching back to shallow diving. To avoid the mixing of shallow and deep dives within a deep dive trial as much as possible, the trap door was closed, preventing birds from submerging, as soon as it became apparent that birds had no intention to return to depth. Deep dive trials during which birds spent more than 30% of the overall time spent submerged at shallow depth were excluded from the analysis. All relevant behaviour of the birds was marked onto the respirometry traces, so that behaviour as well as dive and surface events could be related to the respirometry recordings. The majority of shallow dive trials lasted about 20 – 30 min during which birds dived voluntarily and without any interference. Here a trial was terminated by remotely closing the trap door when a bird remained at the surface for more than 10 min. In the deep dive setting birds were not motivated to dive to the bottom of the tank unless food was placed there. Hence, birds ingested small herring pieces during all deep dive trials. Preliminary results from experiments during which cormorants were fed a similar amount of herring while resting in air, showed that metabolic rate was not increased during the first 10 min after ingestion (Enstipp unpubl.). Consequently the duration of deep dive trials were kept within this time frame. Therefore, 'post-absorptive deep dive trials' refers to trials where birds had been fasted overnight (at least 15 hrs) beforehand but ingested small amounts of herring during the trial.

To investigate the effect that feeding (HIF) might have on diving metabolic rate birds were diving in both the post-absorptive and absorptive state. For the post-absorptive trials birds were fasted overnight for at least 15 hrs. For the absorptive trials birds were fed a known amount of food (60 g of herring) at various times (30 – 240 min) before a trial. Trials were conducted in the mornings and afternoons with a maximum of 2 dive trials per bird per day.

In a preliminary analysis oxygen consumption rates ($\dot{V}o_2$) were calculated using equation 3b given by Withers (1977), which indicated a respiratory exchange ratio (R_E) of 0.73 in post-absorptive birds resting in air. However, during some of the dive trials these values seemed unreasonably low, probably because CO_2 was absorbed by the water or because of non-pulmonary CO_2 loss by our birds (Walsberg and Wolf, 1995). Hence, for our analysis we assumed a R_E of 0.71 for all post-absorptive and 0.8 for all absorptive trials and used equation 3a from Withers (1977) to calculate oxygen consumption rates ($\dot{V}o_2$). Metabolic rate during resting in air was calculated from the lowest 15-min running average value of $\dot{V}o_2$. Similarly, metabolic rate during resting in water was taken as the average from the lowest and stable 10 min section of $\dot{V}o_2$ from each 30 min trial. Although our respirometry system was sufficiently fast to allow separation of individual dive and surface events, we decided to calculate diving metabolic rate (MR_d) as the average value of $\dot{V}o_2$ during a dive bout from its start until 30 s after the last dive in a bout (i.e. MR_d = oxygen consumption during the entire dive bout divided by the sum of all dive and surface durations within that bout). A dive bout was characterised by continuous diving activity and ended by definition when birds remained at the surface for longer than 100 s (using a log-survivorship plot as bout ending criterion; Slater and Lester, 1982) or when the trap door was closed (deep diving). Birds typically started to dive from the moment the trap door was opened. Because of the intrinsic time constant of our system, however, it took approximately 1 min before our system stabilised at an equilibrium point. Dives performed during this time were excluded from analysis. Oxygen consumption rates ($ml\ O_2 \cdot min^{-1} \cdot kg^{-1}$) were transformed to kJ using the caloric equivalent corresponding to the assumed respiratory exchange ratio (R_E). We used a conversion factor of $19.7\ kJ \cdot l^{-1} O_2$ for post-absorptive trials ($R_E = 0.71$) and $20.1\ kJ \cdot l^{-1} O_2$ for absorptive trials ($R_E = 0.8$; Schmidt-Nielsen, 1997) to transform these values to Watts (W).
Metabolic rate (MR, in $W \cdot kg^{-1}$) is given by: $\frac{19.7 \cdot \dot{V}o_2}{60 \cdot M_b}$ for post-absorptive and by $\frac{20.1 \cdot \dot{V}o_2}{60 \cdot M_b}$ for absorptive trials respectively, where M_b is body mass in kg.

One-way repeated measures analysis of variance (ANOVA) with Tuckey test pairwise multiple comparisons was used for comparison of metabolic rate during different activities at various temperatures and feeding status. When single comparisons were made, Student's paired t-test was used. Significance was accepted at $p < 0.05$. The relationship between energy expenditure and air or water temperature that takes into account variability between subjects was determined using repeated-measures multiple linear regression, with each bird being assigned a unique index variable (Glantz and Slinker, 1990). All mean values are presented with standard deviation (± 1 S.D.).

Studying foraging behaviour under controlled conditions

Nine adult or sub-adult double-crested cormorants (minimum age 2 years) with a mean body mass of 2.10 ± 0.16 kg (mean ± S.D., range 1.81 – 2.47 kg) were used in this study. Eight of the birds had been captured as chicks (5-6 weeks of age) from the Mandarte Island breeding colony. One bird had been bred in our captive setting. All birds were well established in captivity and were housed communally in sheltered outdoor pens (8 m long x 4 m wide x 5 m high) with water tank access at the South Campus Animal Care Facility of the University of British Columbia (UBC), Vancouver, Canada. Birds were fed approximately 10% of their body mass daily with a mixed diet consisting of Pacific Herring and Rainbow Smelt, supplemented with vitamin B1 tablets (thiamine hydrochloride, Stanley Pharmaceuticals Ltd., North Vancouver, Canada). Body mass was determined regularly to the nearest 10 g when birds were post-absorptive and dry, using a digital spring balance (UWE, HS-15K). All birds maintained a fairly stable body mass throughout our study (June – Nov 2003). All experimental procedures were approved by the UBC Animal Care Committee (Animal Care Certificate # A02-0122) and were in compliance with the principles promulgated by the Canadian Council on Animal Care.

An **underwater video** array was set-up within a deep dive tank (5 m in diameter, 10 m water depth), consisting of 8 b/w video cameras (Model CVC6990, a light sensitive, submersible camera with a 3.6 mm wide angle lens; minimum illumination 0.01 lux; Lorex), 2 multiplexer (EverFocus Electronics Corp., Taipei, Taiwan), a video date time generator (RCA), 2 video recorders (Sony) and 2 video monitors (Citizen). The cameras were mounted at various positions within the deep dive tank, which allowed for a complete visual coverage. Depending on light conditions observation was hampered at a few small spots within the tank (e.g. the upper 1 m zone) but overall coverage was excellent. The visual field of most cameras was overlapped, so that foraging activity could be observed from different positions. Three cameras were mounted on tripods outside the tank, while the underwater cameras were suspended from a rope, positioned in the centre of the tank. The video signal of the cameras was fed into 2 multiplexer, which projected the images onto 2 video monitors (4 cameras per monitor). One multiplexer was equipped with an internal clock (resolution: 1 s) which was projected onto the monitor. The signal of the other multiplexer was fed into a video date time generator (resolution: 0.1 s) which projected the time onto the other monitor. Both clocks were synchronized before a series of trials started and were recorded together with the images on VHS tape. All recording equipment was kept inside a small observation hut on top of the dive tank, from which additional observations were carried out during the trials.

Juvenile Rainbow Trout *Oncorhynchus mykiss* (total length 15–22 cm; body mass 24–92 g) were obtained from the Fraser Valley Trout Hatchery (British Columbia Ministry of Water, Land and Air Protection) in June 2002 and kept in dechlorinated, fully aerated Vancouver city tapwater. Upon arrival fish were caught, weighed (to the nearest g), measured (to the nearest 0.5 cm) and sorted into 2 weight/size classes ('small fish' with a mass < 50 g and a total length < 18.5 cm, and 'large fish' with a mass ≥ 50 g and a total length ≥ 18.5 cm) which were kept in separate holding tanks. A linear relationship was found between fish body mass and total body length and was best described by 'length (cm) = 0.11 (mass, g) + 12.93' ($r^2 = 0.85$). Water temperature in the tanks varied according to season and ranged between 6 °C in winter and 15 °C in summer. Fish were fed commercial trout food daily (Jamiesons Feed, Richmond, Canada) until used in experimentation.

At least 3 days before any trials began, the deep dive tank was filled with chlorinated Vancouver city tapwater. To eliminate the chlorine, air was bubbled through the tank for at least 2 days before any fish were introduced into the tank. Chlorine levels were checked before fish introduction and were always less than 0.05 mg l^{-1}, well below a level that might have affected our fish and no adverse effects were observed. Because water inside the dive tank was standing, water temperature inside the dive tank fluctuated more widely than the water temperature inside the fish holding tanks, where water ran through at a constant rate. However, the temperature difference between the fish holding tanks and the deep dive tank rarely exceeded 5 °C. Every morning, before a set of trials, 15 – 20 'small' or 'large' trout were caught, weighed (to ensure proper classification and to calculate the mean fish mass/size inside the dive tank) and introduced to the bottom of the dive tank by means of a PVC tube and a plunger. To allow fish to accommodate to the new environment, they were introduced at least 2 hrs before the start of the trials. A variety of structures (concrete blocks, PVC tubes, etc.) had been placed at the bottom of the tank to provide hiding places for the fish. While fish made use of these structures, they were generally very mobile and roamed throughout the tank after initial introduction to the bottom.

All birds had taken part in earlier studies on diving physiology and energetics and were familiar with diving to the bottom of the deep dive tank, where they picked up chopped herring pieces. Birds were split into two groups of four and five individuals. While the first group participated in this foraging behaviour study, the second group participated in a foraging energetics study. When data collection with the first group was complete, groups were switched around. Hence, all birds were maintained in an active state throughout the study and had to dive for their food. Birds were trained to dive for live juvenile rainbow trout of varying size and density within this set-up for at least 3 weeks before data collection began. Each bird participated in one trial per day. At the beginning of a trial a bird was caught in its holding pen and introduced into the dive tank. Here the bird usually started to dive immediately. All underwater and surface activity during the trial was filmed with the video set-up. After the capture of a number of fish the bird usually left the water and wingspread for some time, often starting another foraging bout towards the end of the 30 min trial. At the end of a trial the bird was caught and returned to its holding pen.

One important factor to consider when conducting foraging behaviour experiments with captive animals is motivation. If the motivation of an animal to forage and capture prey fluctuates too much between trials, this might obscure results. In an attempt to keep bird motivation during the trials similar over the course of data collection, we kept the daily amount of food ingested by a bird constant. The amount needed for each bird to maintain motivation was established during the training trials. When the daily trials were completed, birds were handfed their remaining daily allotment. Birds were then kept post-absorptive for at least 17 hrs before a new set of trials started. Consequently, all birds cooperated well during the period of data collection and seemed highly motivated to capture live fish.

Concurrent with filming we recorded the following parameters for each trial: air temperature, water temperature, illumination, fish density in tank, mean mass/size of fish in tank. Air temperature was measured at the start of each trial, while water temperature was measured at the end of a set of trials just below the water surface and at the bottom. A light attenuation profile (at 1 m, 5 m, and 10 m water depth) was taken at the end of every single foraging trial using the GeoLT data logger (earth&OCEAN Technologies, Kiel, Germany). Fish density (g m^{-3} or number of fish m^{-3}) was calculated as the overall fish mass (or number of fish) inside the dive tank at the start of a trial divided by water volume (196 m^3). Mean fish mass/size for each trial day was calculated as the mean mass/size of the trout introduced into the dive tank in the morning. Occasionally birds did not eat all the fish that had been introduced into the dive tank in the morning. The exact number of fish left over was counted via the video set-up the following morning and checked against our records. Fish density in the dive tank was then balanced by introducing relatively fewer fish of the same weight/size class for that day. Weight/size of the individuals left over was taken as the mean weight/size from the day before.

Videotapes were viewed and all dive and surface times within a 30 min trial were marked down to the nearest second. Each dive cycle (dive and subsequent surface interval) was split into the following behavioural categories: searching, prey pursuit, prey handling, rest at surface. For each behavioural category observed, start and end time as well as duration was noted to the nearest second. By definition a bird was 'searching' during a dive until it started a 'prey pursuit' or surfaced. 'Prey pursuit' was taken as an interaction between a bird and a fish (or shoal of fish) and its initiation was typically accompanied by a change in swim direction or speed (as indicated by an increase in stroke frequency) on the birds side, with the clear intention of attacking the fish. 'Prey pursuit' ended either when the bird caught a fish or when it 'gave up', as indicated by a change in swim direction or speed (slowing of stroke frequency). After an unsuccessful 'prey pursuit' the bird, by definition, continued 'searching' until it either initiated a new 'prey pursuit' or surfaced. 'Prey handling' was taken as the time between prey capture and prey ingestion. 'Rest at surface' marked the time spent at the surface between consecutive dives. Additionally, we noted a variety of observations regarding fish and bird behaviour (e.g. fish distribution within the dive tank; are fish shoaling? do single fish remain stationary or move away from an approaching bird? do birds pursue individuals or a shoal? number of fish caught, etc.).

We investigated the effect of the following parameters on **cormorant prey capture behaviour**

Prey availability (fish density)

Fish density at the beginning of a series of trials was kept relatively constant (about 7 g m^{-3}). The fish density that a bird encountered during a trial, however, was altered by randomly changing the birds position within the daily trial order. Fish density was highest at the beginning of the first trial of the day and declined as successive birds caught and ingested fish, so that fish density was lowest during the last trial of the day.

Prey size

It would have been interesting to additionally use another fish species that is typically taken by cormorants and whose behaviour contrasts with that of the rainbow trout used in our experiments (e.g. benthic fish). For practical reasons, however, this was not possible (i.e. no commercial availability of live specimen). In the absence of this possibility we investigated the effect that fish size might have of predator performance. To this end we systematically altered the size/mass of trout introduced into the dive tank, while choosing trial days with 'small' or 'large' fish at random. Two size classes were distinguished: 'small fish' with a mass < 50 g and a total length < 18.5 cm, and 'large fish' with a mass ≥ 50 g and a total length ≥ 18.5 cm. Predatory performance was assessed by computing CPUE values ('catch per unit effort' in g fish caught s^{-1} submerged) for trials of both size classes with similar fish densities. We also computed the success rate of initiated prey pursuits and the duration of successful pursuits (as an indication of foraging effort) for both fish size classes.

Light conditions

To investigate if the predatory performance of cormorants might be limited by the available light, we altered light conditions encountered by the birds underwater. This was achieved by conducting trials either around midday, when light conditions were best, or in the late afternoon, when light conditions deteriorated.

Fish behaviour (shoaling versus non-shoaling fish)

During the training trials we became aware that fish behaviour might greatly affect predatory performance. We observed that fish often started to form shoals inside the dive tank and this appeared to affect predator behaviour and success. Hence, together with bird behaviour we also noted down fish behaviour (of attacked individuals and of the group), distinguishing between a 'shoaling' and a 'non-shoaling' situation. Video analysis of bird behaviour was performed accordingly. By definition, in a non-shoaling situation the bird targeted an individual fish that was not part of a shoal (although a shoal might have existed elsewhere within the dive tank). In contrast, in a shoaling situation the bird targeted the shoal or an individual that was part of the shoal. Predatory performance was assessed by computing the duration of successful pursuits as an indication of foraging effort, and success rate of pursuits, contrasting a shoaling and non-shoaling situation.

Bird condition (body mass)

To assess the effect that bird condition (body mass) might have on foraging success, we computed for each bird the 'catch per unit effort' achieved under the various fish densities encountered. A linear regression best described the observed relationship for all birds. The effect of body mass on foraging success was assessed by plotting the CPUE achieved by each bird at a medium fish density (4 g m^{-3}) against bird body mass.

Water temperature

The effect that water temperature might have on cormorant foraging behaviour was investigated by conducting trials at various water temperatures ranging from about 5 to 22°C.

Dive depth

We compared predator-prey interactions occurring at shallow depth (≤ 3 m) with interactions occurring at greater depth (> 3 m) to assess the effect of depth on cormorant foraging behaviour. In our analysis we included dive and surface durations as well as the success rate of prey pursuits initiated at shallow and greater depth.

All statistical analysis was performed using SigmaStat software (Jandel Scientific). When single comparisons were made, as in comparing the success rate of pursuits attacking shoaling or non-shoaling fish, Student's paired t-test was used. Significance was accepted at $P < 0.05$. The relationship between fish density and prey capture rate (CPUE) that takes into account variability between subjects was determined using repeated-measures multiple linear regression, with each bird being assigned a unique index variable (Glantz and Slinker, 1990). All mean values are presented with standard deviation (± 1 S.D.).

1.6.4 Establishing time-energy budgets (WP 7)

Shags and guillemots were equipped with compass loggers and/or precision temperature/depth recorders (PreciTD; both from Earth&Ocean Technologies, Kiel, Germany; Appendix 1). These provided very fine scale activity data that distinguished between phases of rest on land or at sea from flight and diving. A flight activity sensor combined with a saltwater switch was deployed on kittiwakes (Instituto di Elaborazione dell'Informazione, C.N.R., Pisa, Italy) and this allowed us to distinguish between periods of flight associated with travelling or foraging, periods of rest on land and at sea. Satellite tags (PTT; Microwave Telemetry, Inc., Columbia, MD, USA) on gannets enabled us to distinguish between periods spent at the colony from periods at sea and PreciTD loggers allowed to distinguish between flight, time spent submerged and resting at sea. All field data for kittiwakes, shags and guillemots were collected during the early chick-rearing period (June to July) from 1999-2003 on the Isle of May, Firth of Forth, southeast Scotland. Field data for the gannets were collected from the nearby Bass Rock breeding colony during early to mid chick-rearing in 2003. Input values for our algorithm were generated from yearly mean values for the time that birds spent in various activities per day, weighted according to sample size.

Activity-specific metabolic rates for shags were measured directly via respirometry. This included measurement of BMR, metabolic rate during resting on water and during diving, incorporating the effect of water temperature. All other values were compiled from the literature. For kittiwakes all metabolic rates except for flight were taken from Humphreys (2002). BMR for gannets was taken from Bryant and Furness (1995) and metabolic rate during resting at sea was taken from Birt-Friesen *et al.* (1989). For guillemots we used the BMR value given by Hilton *et al.* (2000a) who established a regression equation from all published BMR values. Metabolic rate during resting at sea and during diving (incorporating the effect of water temperature) was taken from Croll and McLaren (1993). To account for activities at the nest such as chick feeding and preening, which will increase metabolic rate above BMR, we assumed a metabolic rate at the nest that was twice the BMR for all species except for the kittiwake where we used the measured value from Humphreys (2002). To incorporate the effect of water temperature on metabolic rate during resting at sea for kittiwakes and gannets we used the slope given by Croll and McLaren (1993) for guillemots. In the absence of data we assumed that metabolic costs of travel-flight and forage-flight for the kittiwake are identical and the same assumption was made for flying and plunge-diving for the gannet. All estimates of energetic costs during flight were calculated using the aerodynamic model of Pennycuick (1989), using the latest version ‘Flight 1.13’. Wing morphology values were taken from Pennycuick (1987). We accounted for the presumably higher flight costs during the return trip, after birds have ingested food and carry food for their chicks. Estimates of the daily energy expenditure of chicks were based on those provided by Visser (2002) for all species except the guillemot, which was taken from Harris and Wanless (1985), corrected for assimilation efficiency.

Diet samples were collected as regurgitations, observations of prey delivered to chicks or from food dropped at the ledge. A mean calorific value for prey taken was established for each species based on the biomass proportions of prey and its size. Calorific values of the various prey items were taken from the literature (Hislop *et al.* 1991; Pedersen and Hislop, 2001; Bennet and Hart, 1993), accounting for seasonal effects. We took assimilation efficiencies for the gannet from Cooper (1978) and for all other species from Hilton *et al.* (2000b). Assimilation efficiency for chicks was assumed to be the same as in adults except in kittiwakes, for which we took the value from Gabrielsen *et al.* (1992).

Body masses were obtained from birds during routine handling associated with ringing. Breeding success was determined as the number of chicks fledged from surveyed nests where eggs had been laid. We took water temperatures from Daunt *et al.* (2003) who measured water temperatures in the same area directly from foraging shags and guillemots during chick-rearing. The algorithm used to compile the time-energy budgets (‘baseline situation’, see Table 1.6.2 for key input values) and to investigate the different scenarios was based on Grémillet *et al.* (2003) but incorporated the energetic requirements of chicks. CPUE values are based on the time spent underwater for shags and guillemots, the time spent in forage-flight for kittiwakes and the total time spent at sea for gannets (a CPUE value based on the active time spent at sea is included in brackets to allow comparison across species).

Table 1.6.2. Some of the input values (means ± SD) used to compile a time-energy budget (‘baseline situation’) for 4 North Sea seabirds during chick rearing (BMR = basal metabolic rate; DEE = daily energy expenditure).

	Kittiwake	Shag	Gannet	Guillemot
Body mass (g)	361.64 ± 36.14	1780.43 ± 97.63	2998 ± 234	920.34 ± 57.44
Assimilation efficiency for chick (%)	80.00 ± 1.25			
Calorific value of fish (kJ/g wet)	5.0 ± 0.5	5.4 ± 0.5	5.8 ± 0.6	5.1 ± 0.5
Water temperature at surface (°C)	11.1 ± 0.5	11.1 ± 0.5	11.1 ± 0.5	12.0 ± 0.5
Water temperature at bottom (°C)		10.3 ± 0.4		8.8 ± 0.5
BMR (kJ day^{-1})	267.28	726.07 ± 46.15	1256.28 ± 227.94	584.48
Energy costs, resting at colony (W kg^{-1})	13.69 ± 1.20	9.44 ± 0.6	9.70 ± 1.76	14.70 ± 1.47
Energy costs, resting at sea (W kg^{-1})	12.82 ± 2.56	17.18 ± 2.02	12.46 ± 2.16	10.19 ± 1.02
Energy costs, flying (W kg^{-1})	44.83 ± 4.48	98.07 ± 9.81	43.69 ± 4.37	92.58 ± 9.26
Energy costs, foraging (W kg^{-1})	44.83 ± 4.48	20.58 ± 2.8	43.69 ± 4.37	23.83 ± 2.38
DEE of chick (kJ day^{-1})	525.71 ± 52.57	1203.98 ± 120.40	1593.30 ± 159.33	221.71 ± 22.17

To identify hotspot feeding areas in terms of energy acquired at sea, generalized distribution maps were produced for the study area at large for each of the study species as well as for all 4 species combined. Densities of foraging seabirds (i.e. densities of swimming Guillemots and Shags, and densities of actively foraging Gannets and Kittiwakes) were multiplied with the energy acquired at sea (kJ) and mapped in 5' latitude x10' longitude or 10' latitude x 20' longitude rectangles. Hotspots were rectangles where >25 000 kJ km^{-2} day^{-1} were obtained.

1.6.5 Effects of device attachment on seabird behaviour

A number of studies have demonstrated an impact of devices on the behaviour of birds (reviewed in Withey *et al.* 2001). In all four species, we detected no negative response to the deployment procedure, with all birds returning to the nest immediately or soon after deployment. On retrieval, there was no evidence of physical impairment caused by the loggers, and birds returned to normal behaviour at the nest soon after release. We also examined the effect of loggers on foraging behaviour.

The largest loggers carried by Kittiwakes were the activity loggers described in section 1.6.1 (also in Appendix 1). These loggers were 4-6% of the mass of the birds. Although near the limit generally regarded as acceptable for a flying bird (Cochran 1980), Kittiwakes have a relatively low wing loading (Pennycuick 1997) that should mitigate against the impact of the devices. Potential impacts of the loggers on activity patterns and feeding trip durations were examined by observing the nest attendance of chick-rearing adults at a sample of nests in the same part of the colony as the instrumented birds. Two series of watches were carried out, each series spread across six days. Daily observations were carried out for three hours per day, timed to ensure that all hours from 04:00-22:00 were covered in each watch series. In each observation period, we recorded the number of changeovers that occurred during each hour. Changeovers only took a few minutes to complete, so the average trip duration could be estimated from the changeover frequency (Hamer *et al.* 1993) and compared with that of the instrumented birds. We found that neither instrumented nor uninstrumented birds left chicks unattended, and trip durations were comparable (instrumented birds: 5.9 ± 2.5 SD h, n = 24; uninstrumented birds: 7.8h, n = 113). Thus, we have no reason to believe that the birds were not foraging normally. However, it is possible that behaviour or time activity on trips were different among the two groups, although we were not able to assess this.

In Guillemots, we were able to examine the effects of devices on behaviour at sea, by comparing birds carrying PreciTD loggers (the largest device carried by this species: 23g, dimensions 80 mm x 19 mm x max 22 mm, ca. 2.5% of body mass; a lower percentage of body mass is generally regarded as acceptable among birds with high wing loading, such as Guillemots) simultaneously with another sample of birds carrying much smaller temperature-depth loggers (LTD1110, Lotek, St Johns, Newfoundland; weight 5g with dimensions 32mm x 11mm). The LTD1110 does not have a rapid response temperature probe, which is why the larger PreciTD logger was the main device employed to study ocean physics/seabird interactions described in – see Chapter 7. We found no significant differences in foraging behaviour between the two samples of birds (Table 1.6.3). Whilst this result was encouraging, given the large difference in mass between the two logger types, we cannot exclude the possibility that both sets of birds were foraging differently from uninstrumented birds.

Table 1.6.3. Comparison of foraging behaviour between Guillemots carrying PreciTD loggers and Guillemots carrying Lotek LTD1110 loggers.

Parameter	PreciTD	Lotek	test	*P*
Number of dives per bout	9.7	7.7	GLMM	0.37
Dive duration (s)	97.0 ± 10.0	100.1 ± 6.6	REML	0.79
Vertical descent speed (m s-1)	1.28 ± 0.05	1.24 ± 0.03	REML	0.43
Vertical ascent speed (m s-1)	1.20 ± 0.07	1.22 ± 0.03	REML	0.79
Maximum foraging depth (m)	41.1 ± 5.6	41.3 ± 3.0	REML	1.00
Mean foraging depth (m)	41.0 ± 5.9	40.2 ± 3.0	REML	0.89
Sample size (birds)	8	6		
Sample size (dives)	1291	868		

For Shags, we used a similar approach to the logger comparison carried out in Guillemots by comparing birds carrying the instruments of different weight at the same time. We were able to compare number of trips carried out per day and trip durations between birds carrying PreciTD loggers (23g, <1.5% of body mass) and GPS loggers (70g, the largest loggers carried by Shags in this study, ca. 4% of body mass) in 2003. We found no difference in these two measures between the two groups (trips per day: GPS, mean = 3.20 ± 0.36, n = 10; PreciTD: mean = 3.25 ± 0.41; GLM with poisson errors: $F_{1,16}$ = 0.00, ns; trip duration: GPS, mean = 1.49 ± 0.31, n = 27 trips; PreciTD: mean = 1.38 ± 0.10, n = 26 trips; REML: W = 0.01, ns). This also suggests that the differences in foraging location observed between years (Chapter 5) were due to environmental differences between years, rather than the different masses of devices carried.

Previous studies have shown that attachment of PTTs had no impact on the trip durations of gannets (Hamer *et al.* 2000; Hamer *et al.* 2001). In this study, the maximum mass of devices deployed in combination on gannets (PreciTD + GPSlog + Minitemp-xl) was 113 g (3.6 - 4.0 % of body mass). This was well within the 5% limit recommended by Cochran (1980). More recently, Kenward (2001) suggested that the standard should be lowered to 2-3% for birds that depend greatly upon continuous flight, for instance during migration. However whilst gannets rely upon flapping flight for foraging, their requirements are some way below those of a migrating bird. Nonetheless, in 2003 we compared the trip durations of instrumented birds (deployed with a PreciTD, GPSlog and Minitemp-xl or with a GPS-TDlog and Minitemp-xl) with a control group in which one of the partners at each nest had been marked with a spot of coloured dye on the plumage but was not carrying any devices. Nests were checked hourly from 04:00-22:00h over three days to record which adult was present, and trip durations were calculated as the time elapsed between a bird leaving the nest and returning to relieve its partner. There was no difference in trip durations of instrumented birds and controls (instrumented birds; 23.2 SD ± 9.3 h, n = 22: controls; 18.6 ± 9.6 h, n = 62: REML; W = 2.0, ns). In addition, the trip durations of instrumented birds were similar to those of birds equipped with PTTs only (24.6 ± 1.7h). We are therefore satisfied that deployment of devices had no discernible effects on foraging behaviour.

1.7 Consultation

Apart from normal international contacts, two phases of presentation and consultation were organised as part of the project. Stake-holders, end-users and colleagues from other institutes were invited to participate in two international conferences, one organised in Hamburg when the project began, one organised jointly with University of St Andrews, (UK) at the Zoological Society in London.

Affiliations of invited speakers and delegates at the IMPRESS conference in Hamburg, 22-21 November 2001 included the Bundesforschungsanstallt für Fischerei, Germany; BirdLife/RSPB,UK; Centre for Environment Fisheries and Aquaculture Science (CEFAS), UK; Danish Fishermen's Association (DFA), Denmark; Danish Institute for Fisheries Research (DIFRES), Denmark; FRCF, Germany; Glasgow University, UK; IFM, Germany; IHFS, UK; Joint Nature Conservation Committee, UK; Marine Laboratory (Fisheries Research Services), UK; NINA, Norway; and SNTA, Norway.

Delegate affiliations registered for the conference at the Zoological Society in London, 2004 included Alterra Texel, The Netherlands; Atlantic Salmon Trust, UK; Australian Antarctic Division, Australia; Barrister, Fenners Chamber, UK; Bedford Institute of Oceanography, Canada; British Antarctic Survey, UK; Bureau Waardenburg, The Netherlands; Cambridge University Press, UK; CEH Banchory, UK; Centre d'Ecologie et Physiologie Energetiques, France; Conservation Programmes, ZSL, UK; Countryside Council for Wales, UK; Dalhousie University, Canada; DIFRES, DK; English Nature, UK; Federal Agency for Nature Conservation, Germany; Fisheries Research Services, UK; Fundacao Universidade Federal do Rio Grande, Brasil; Glasgow University, UK; Hadlow College, UK; IMAREST, UK; Imperial College London, UK; Institute for Baltic Sea Fisheries, Germany; Institute of Marine Research, Norway; JNCC, UK; Marine Conservation Society, UK; Memorial University of Newfoundland, Canada; MRAG, UK; Museum of Natural History, Farøe Islands; NERC Centre for Ecology and Hydrology, UK; Royal Netherlands Institute for Sea Research, The Netherlands; Open University, UK; RSPCA, UK; Scottish Fishermen's Federation, UK; Scottish Natural Heritage, UK; The Scottish White Fish Producers Ass. Ltd., UK; Tromsø University Museum, Norway; UC Santa Cruz, USA; University of Aberdeen, UK; University of British Columbia, Canada; University of California, Santa Cruz, USA; University of Cork, Ireland; University of East Anglia, UK; University of Hamburg, Germany; University of Hull, UK; University of Kiel, Germany; University of Leeds, UK; University of Manitoba, Canada; University of Newcastle, UK; University of Oslo, Norway; University of St Andrews, UK; Zoological Society London, UK.

The London presentations were peer-reviewed by independent referees. selected by the co-organiser of that conference Prof. Ian Boyd and the work has benefited considerably from both these reviews and the discussions on each of the conferences.

The project was consulted by the ICES working group on Seabird Ecology in 2004 and preliminary results were provided on request (Anon. 2004).

Chapter 2 Setting the scene (1): Sandeels and the Sandeel fishery in the North Sea and off the east coast of Scotland

Simon Greenstreet and Kees Camphuysen

2.1 Introduction

This chapter provides a short description of sandeel natural history and a brief summary of the sandeel's role within the marine foodweb of the North Sea. The main trends in the sandeel fishery in the North Sea, and in the area immediately to the east of southeast Scotland where much of the IMPRESS fieldwork was carried out, are then presented.

2.2 Sandeel Natural History

During the summer period sandeels form large schools that feed on zooplankton in the water column during part of the daytime period. During the remainder of the time, particularly at night, they bury in the sediment (Reay 1970; Winslade 1974a-c; Freeman *et al.* 2004). Sandeels stay buried in the sediment through the late summer to early spring period, emerging briefly in winter to spawn (Macer 1966; Gauld & Hutcheon 1990). The fraction of the population that is buried varies in response to variation in water temperature, zooplankton abundance and risk from predation (Reay 1970). Different components of a sandeel population, for example 0 group fish compared with older aged fish, may also spend different fractions of the available time feeding in the water column and buried in the seabed.

Several studies have reported on sandeel sediment habitat preferences using observations made "in the field", but generally these have not provided much in the way of detail. For example, Macer (1966) and Scott (1973) both reported that sandeels occurred in areas of coarse sand, although no information on particle size was provided. Reay (1970) provided a little more detail suggesting that sandeels showed a preference for sediments with a particle range of 0.35 to 1.35mm. Other studies have presented the results of laboratory-based choice experiments. For example Pinto *et al.* (1984) suggested that sandeels preferred sand habitat over gravel habitat while Wright *et al.* (2000) demonstrated that sandeels showed a strong preference for medium to very coarse sands, sediment habitats with a median particle size of 0.25 to 2.0mm. The ease of penetration into the sediment has been considered to be an important factor in determining sediment habitat choice (Macer 1966; Reay 1970; Meyer *et al.* 1979; Pinto *et al.* 1984), and this may be associated with coarser sand and finer gravel sediments. Sandeels are known to prefer depths of 30-70m, although they occur between depths of 15-120m (Wright *et al.* 1998).

Since sandeels require the presence of oxygen to survive in the sediment and the oxic layer in the seabed sediment of the North Sea is rarely more than 8cm deep (Lohse *et al.* 1996), sandeels will normally be buried at relatively shallow depths (Girsa & Danilov 1976). The avoidance of silt rich sediments by sandeels has previously been reported both in the field (Macer 1966; Reay 1970; Meyer *et al.* 1979; Wright *et al.* 2000) and experimentally (Pinto *et al.* 1984; Wright *et al.* 2000). Wright *et al.* (2000) reported that sandeels were not found in field samples where the silt content in the sediment was greater than 10%. They also noted that sandeel densities decreased as the silt fraction increased from 0 to 10%. The fact that sandeels do not maintain permanent burrow openings, and therefore have to ventilate their gills with interstitial water probably explains why they do not occupy silt rich sediments. The fine particles would tend to clog their gills inhibiting respiration (Scott 1973; Meyer *et al.* 1979; Pinto *et al.* 1984). If the interstitial spaces between sand and gravel particles are occupied by silt particles space for water is reduced and there is therefore less oxygen in the sediment. The presence of silt within the interstitial spaces would also tend to slow the rate of interstitial water exchange. Oxygen would be used up more quickly and replenished at a lower rate. Lohse *et al.* (1996) found that oxygen concentrations differed greatly between sandy sediments and those with a high silt content. In the sandy sediment the oxygen concentration in the top 16mm was almost identical to the values found in the overlying water, and the oxic zone extended down to 45mm. The depth of the oxic zone in the siltiest sediments was only 0.5mm. In a closely related species, *Ammodytes hexapterus*, oxygen tensions lower than 30 μmol dm^{-3} at summer temperatures (12°C), or 16 μmol dm^{-3} at winter temperatures (5°C), could not be tolerated (Quinn & Schneider, 1991). Many studies have also shown that sandeels require well flushed, tidally active areas (Macer 1966; Meyer *et al.* 1979; Pinto *et al.* 1984; Wright *et al.* 2000). Wright *et al.* (1998) reported that the areas where most *A. marinus* occur in sediments have current flows of >0.6ms^{-1}.

2.3 The role of sandeels in the foodweb of the North Sea

Sandeels constitute important prey for many marine top predators, including marine mammals such as grey *Halichoerus grypus* and harbour seals *Phoca vitulina* (Pierce *et al.* 1989, 1991; Tollit *et al.* 1997) and Harbour Porpoise *Phocoena phocoena* (Santos & Pierce 2003), important commercial fish species, such as Whiting *Merlangius merlangus*, Cod *Gadus morhua*, Haddock *Melanogrammus aeglefinus* and Mackerel *Scomber scombrus* (Daan 1989) (Hislop *et al.* 1997; Pedersen

1999), and many seabird species (ICES 1998; Furness 1990; Furness 1996; Tasker & Furness 1996; Wanless *et al.* 1998). Of 1016 seabird and marine mammal diet studies in the North Sea and northwest Scotland, 342 studies (34%) reported sandeels as common prey (ICES diet database, unpublished material). Of 30 species occasionally consuming sandeels, 76.7% had these fish as principal prey during at least part of the year (Table 2.3.1). For the breeding season, when 172 studies out of 392 (44%) reported sandeels as principal prey, the IMPRESS study species were all represented in the top ten of main sandeel consumers (Table 2.3.2).

Table 2.3.1. Diet studies in the North Sea and around Scotland reporting sandeels as common food (i.e. sandeels present in >25% of the studied samples, or comprising >25% of consumed prey mass; ICES diet database).

		n	%	studies
Red-throated Diver	*Gavia stellata*	1	8%	12
Northern Fulmar	*Fulmarus glacialis*	6	12%	51
Northern Gannet	*Morus bassanus*	6	16%	38
Great Cormorant	*Phalacrocorax carbo*	7	5%	155
European Shag	*Phalacrocorax aristotelis*	19	79%	24
Red-breasted Merganser	*Mergus serrator*	1	17%	6
Arctic Skua	*Stercorarius parasiticus*	3	50%	6
Great Skua	*Stercorarius skua*	19	23%	83
Common Gull	*Larus canus*		0%	32
Lesser Black-backed Gull	*Larus fuscus*	1	4%	28
Herring Gull	*Larus argentatus*		0%	37
Great Black-backed Gull	*Larus marinus*	3	8%	38
Black-legged Kittiwake	*Rissa tridactyla*	19	38%	50
Sandwich Tern	*Sterna sandvicensis*	20	71%	28
Common Tern	*Sterna hirundo*	5	18%	28
Arctic Tern	*Sterna paradisaea*	21	57%	37
Common Guillemot	*Uria aalge*	32	56%	57
Razorbill	*Alca torda*	10	43%	23
Black Guillemot	*Cepphus grylle*	4	18%	22
Atlantic Puffin	*Fratercula arctica*	68	80%	85
Harbour Porpoise	*Phocoena phocoena*	2	22%	9
Grey Seal	*Halichoerus grypus*	45	62%	73
Common Seal	*Phoca vitulina*	50	53%	94
		342	34%	1016

Table 2.3.2. Diet studies in the North Sea and around Scotland in the breeding season reporting sandeels as common or staple food (i.e. present in >25% of the studied samples, or comprising >25% of consumed prey mass; ICES diet database). Top-10 species only.

		n	%	studies
Shag	*Phalacrocorax aristotelis*	14	87.5%	16
Puffin	*Fratercula arctica*	65	81.3%	80
Guillemot	*Uria aalge*	12	80.0%	15
Kittiwake	*Rissa tridactyla*	17	70.8%	24
Sandwich Tern	*Sterna sandvicensis*	12	70.6%	17
Arctic Tern	*Sterna paradisaea*	13	48.1%	27
Gannet	*Morus bassanus*	4	25.0%	16
Great Skua	*Stercorarius skua*	15	21.7%	69
Fulmar	*Fulmarus glacialis*	4	20.0%	20
Common Tern	*Sterna hirundo*	1	5.3%	19

From diet studies in a wide range around the principal study area, Gannets were found to have the most variable diets, while Shags, Guillemots and Kittiwakes were focussing largely on sandeels (when available). Very few reports provide information as how and where piscivorous seabirds obtain different prey items, because most studies are colony observations, either based on pellets (regurgitated indigestible matter), regurgitated prey (either by the chick or by the adult), or visual observations (display fish handled in the colony, fish fed to the chick) or on stomach contents from birds killed or found dead along the shore. The species selected within the IMPRESS project are known to have highly contrasting at-sea distributions, and different feeding techniques (Ashmole 1971; Stone *et al.* 1995).

With so many marine predators dependent on sandeels, the level of exploitation of sandeels by the industrial fishery has raised concerns regarding the impact of this fishery on marine food webs. Annual North Sea sandeel stock assessments suggest that current levels of fishing mortality are not excessive (ICES 2004), however, sandeels in the North Sea may consist of several discrete meta-populations rather than a single homogenous stock (Proctor *et al.* 1998; Pedersen *et al.* 1999). While the population might appear "healthy" at a North Sea spatial scale, because of the patchy distribution of sandeel fishing, it is possible that at a more "local" scale, individual sandeel meta-populations may have been over-exploited. Many sandeel fishing grounds are close to seabird colonies and overlap between post-settlement sandeels, seabirds at sea, and industrial fishing activity distributions is considerable (Jensen *et al.* 1994; Wright & Begg 1997). Consequently, most concern has focused on the potential impact of sandeel fishing on seabirds (Monaghan 1992; Furness & Tasker 2000; Furness 2002; Furness 2003). On two occasions, in the mid 1980s at the Shetland Isles and in the late 1990s at the Firth of Forth, declines in seabird breeding success appeared to be associated with increased sandeel fishing activity nearby (Monaghan *et al.* 1989; Hamer *et al.* 1991; Hamer *et al.* 1993; Furness 1996; Wright 1996; Harris & Wanless 1997). In both instances a precautionary approach was taken and the sandeel fishery in question was closed.

2.4 The fishery for sandeels in the North Sea and off the Scottish east coast

Fishing for sandeels for industrial purposes in the North Sea started in the early 1950s. However, annual landings never exceeded 200,000t until the early 1970s. During the 1970s, annual landings increased markedly so that by 1977 and 1978 nearly 800,000t was being landed each year. Since the late 1970s, annual landings have fluctuated considerably, but an increasing trend has remained apparent, with the highest annual catch of 1,149,000t being recorded in 1997 (ICES 2002; ICES 2004; ICES 2005; Figure 2.4.1). Based on the most recent estimates of SSB, ICES classifies the stock as having reduced reproductive capacity (ICES 2004). SSB in 2004 is estimated to be at a historic low value (325 000 t). SSB in 2003 was above B_{lim}, but has in 2004 decreased to below B_{lim} due to a historic low recruitment in 2002. In absence of a defined F reference point, the state of the stock cannot be evaluated with regard to sustainable harvest. The fishing mortality in 2003 was slightly below the time-series mean. There are no explicit management objectives for this stock.

The high natural mortality of sandeel and the few year classes in the fishery make stock size and catch opportunities largely dependent on the size of the incoming year classes (ICES 2004). Age-0 CPUE is a poor predictor of recruitment, and deterministic forecasts are not generally considered appropriate. The European Community has decided to apply the precautionary approach in taking measures to protect and conserve living aquatic resources, to provide for their sustainable exploitation and to minimise the impact of fishing on marine ecosystems. A precautionary approach should be taken if a full year effort or TAC is decided.

The fishery for sandeels is now the largest single species fishery in the North Sea. It would appear that part of the explanation for the continued upward trend in annual sandeel landings over the last 25 years has been the opening up of new sandeel grounds. One such fishing ground was on the Wee Bankie/Marr Bank sandbank complex of the Firth of Forth in south east Scotland, where a significant fishery took off in the early 1990s. Figure 2.4.1 also shows landings data for 9 ICES statistical rectangles off the east coast of Scotland. These data supplied to the STECF study group set up to examine the impact of this sandeel fishery on local marine top predators and asses the potential of an area closure as a management response to mitigate against such impacts. Figure 2.4.2 shows the location of these rectangles, which ultimately constituted that extent of the area that was closed to fishing. Although potentially of great consequence to local seabird, marine mammal and fish predators, sandeel landings from this area off the Scottish coast rarely constituted more than 10% of the total North Sea landings.

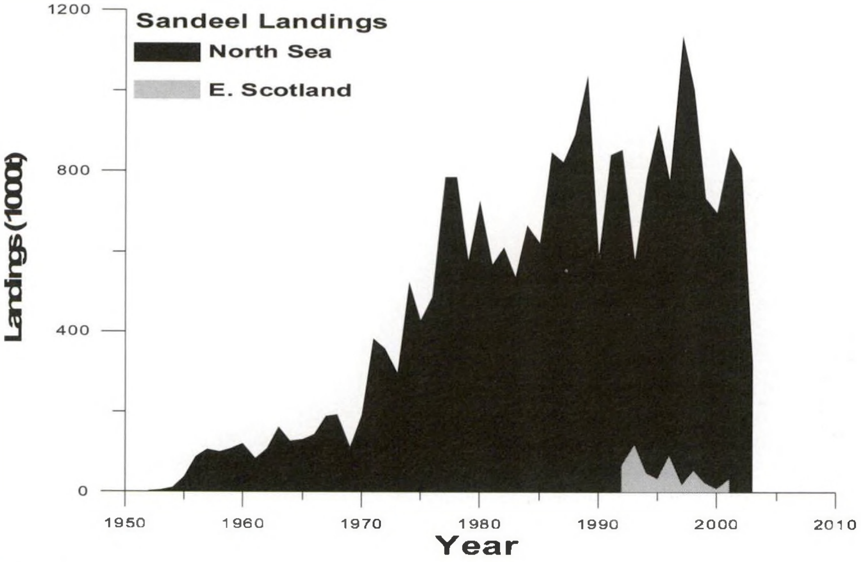


Figure 2.4.1. Trends in landings of sandeels taken from the whole North Sea (black) and from 18 ICES statistical rectangles east of Scotland (grey) (see Figure 2.4.2 for location of these 18 rectangles).

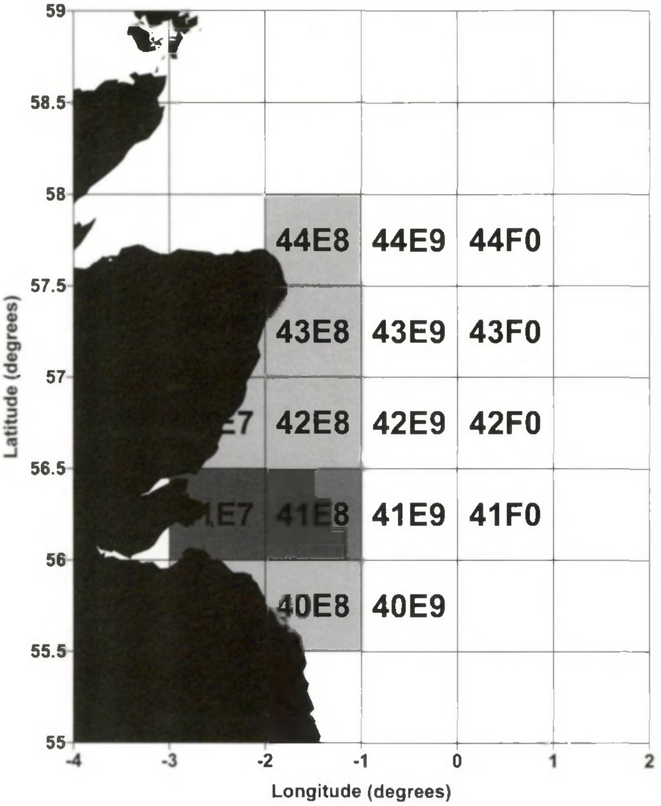


Figure 2.4.2. Chart showing the location of the nine rectangles immediately adjacent to the coast that were closed to sandeel fishermen in 2000 (light shading). The two rectangles that included the main sand-banks that were principally targeted by fishermen are also shown (intermediate shading) together with the extent of the study area covered by FRS surveys (see chapter four) (dark shading). The IMPRESS principal study area encompasses squares 41E7 and 41E8.

Coincident with the increase in the removal of sandeels from areas close to the Scottish east coast, seabird breeding success at colonies along the coast started to decline. Concerned that the sandeel fishery, by reducing feeding potential in waters close to the colonies, might be the cause of the decline in seabird breeding performance, fisheries managers adopted a precautionary stance and prohibited fishing for sandeels in nine ICES statistical rectangles close to the coast. This closed area extended from the Farne Islands in the south to north of Rattray Head in the north, and eastwards out to longitude 1°E (Figure 2.4.2). Landings data from these nine rectangles suggest that, in most years, nearly all the sandeels caught from within the closed area were in fact taken from just two ICES statistical rectangles east of the Firth of Tay and Firth of Forth (Figure 2.4.3). The area covered by intensive fisheries independent assessment surveys covered most of these two rectangles, and included all the main sand banks in these rectangles.

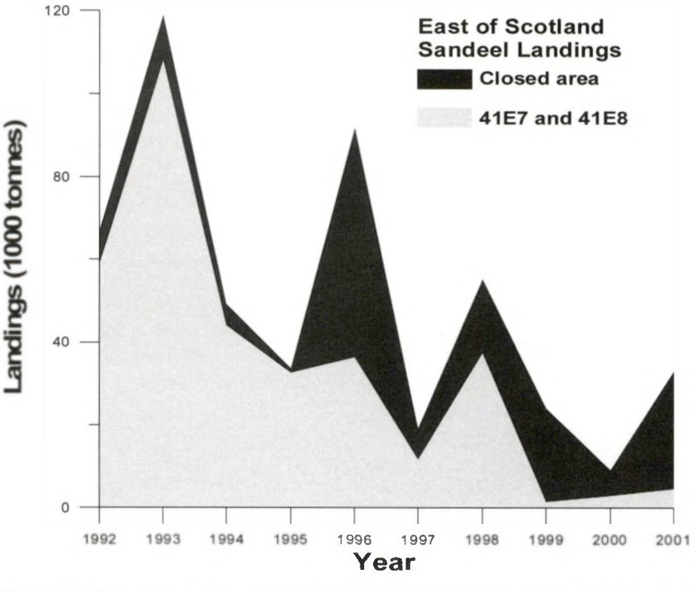


Figure 2.4.3. Landings data for the 9 ICES statistical rectangles closed to sandeel fisheries, and for the two rectangles within which FRS fisheries independent surveys were carried out.

The critical state of the North Sea sandeel stock indicated by the current assessment made the Council of the EU to agree during the December 2003 meeting that the Commission should implement a fishing effort regulation for vessels fishing for sandeel in the North Sea and the Skagerrak (ICES 2004). Effort for the 2004 fishery was not allowed to exceed the 2003 level. This maximum effort level was to be revised as early as possible based on the strength of the 2003 year class.

2.5 Management plan evaluations (from ICES 2004)

There are no management objectives set for this stock, but a need has been identified to develop management objectives that ensure that the stock remains high enough to provide food for a variety of predator species. Mortality has considered to be determined mostly by natural causes rather than by fishing. Similarly, the recruitment of sandeels is considered more linked to environmental factors than to the size of the spawning stock biomass. In the light of studies linking low sandeel availability to poor breeding success of Kittiwakes, all commercial fishing in the Firth of Forth area has been prohibited since 2000 (see above), except for a maximum of 10 boat days in each of May and June for stock monitoring purposes. The closure has been extended until 2006, with an increase in the effort of the monitoring fishery to 20 days, after which the effect of the closure will be evaluated. The direct effects of industrial fishing that have been identified on other species fished for human consumption, e.g. haddock and whiting, are relatively small in comparison to the effects of directed fisheries for human consumption species. However, there is still relatively scant information on the effects of fisheries targeting these stocks (sand eel, Norway pout, sprat), and further analysis of the ecological impacts of these fisheries is required. The effects of variation in the sizes of most industrial stocks on their predators are also poorly known.

Sandeel trawler homeward bound (C.J. Camphuysen)

Chapter 3 Setting the scene (2): Oceanography

B. Scott, J. Sharples and O. Ross

3.1 Introduction

The oceans are the medium in which the (seabird) predator – prey (sandeel) interactions occur. The objective of including detailed sampling and modelling of the primary study area was to determine how oceanographic features could be used to define seabird foraging habitats, and whether variability in any of these features could be causative in controlling variability in prey availability. We approached this objective using two very different temporal and spatial scales as the variability of the 3-dimensional structure of the study area is driven by the variability of tidal currents, wind stress, solar heating and freshwater input on time scales ranging from minutes to years. The competition between the mixing and buoyancy inputs is particularly important in determining the strength of vertical stratification, and the depth of the surface mixed layer. The extent to which a water column is mixed or stratified is pivotal in setting the environmental conditions for primary production. There are correlative links between inter-annual changes in the success of higher predators and their prey and the basic physical oceanography as it forces the primary production of the region. Understanding the causes of inter-annual variability in the timing of the onset of stratification and the spring bloom is thus a key requirement in developing a broader understanding of annual predator-prey interactions. However, the combination of currents, stratification and primary production can also play an immediate role in the horizontal and vertical aggregation of planktonic organisms, which, in turn, attracts larger predators such as fish, birds and cetaceans to a particular foraging location where physical predator-prey interactions occur on an hourly / daily bases. Thus the collation of old (Chapter 1.4) and collection of new meteorological and oceanographic information (Chapter 1.5) gathered in this project was structured to improve our understanding of both the annual/seasonal cycle of primary production and the location specific, hourly/daily variation in vertical characteristics of the water column.

3.2 Collected data

Summary of available pre 2001 oceanographic / meteorological data

The data up to and including 2000 provided a basic understanding of the seasonal dynamics of the study area. Typical of a shallow sea, the water column for the entire study area was well mixed for most of the year (especially during the winter months of October to March). The onset of stratification was usually observed in April and reached a maximum in late July/ early August. Summer data showed a variable picture in terms of how strongly or weakly stratified the water column could be and also indicated that there was great spatial variability in the stratification of the water column. The western and/or eastern extremes of the primary study area generally being the more strongly stratified regions. The western region, close to the coast, is influenced by fresh water while the eastern region away from the coast is deep enough for surface thermal stratification not to be mixed by tidal friction.

Recent surveys and moorings data

The oceanographic information collected via CTD casts and XBT deployments during three seasonal cruises of FRS *Clupea* (March, June and October, 1997-2003) were used to produce an accurate quasi-synoptic 3-dimensional snapshot of the primary study area (Fig 3.2.1-2). With the use of the CTD and XBT data from 1997 to 2003 and compared to the historical meteorological data mentioned above and the output of the moorings and 1-D bio-physical model (described below) the differences in the water column characteristics between years are found to be explained by the differences in previous weeks weather (in particular the degree of wind mixing and irradiance) and the timing of each June cruise in relation to the timing of when stratification first occurred.

It has become clear over the course of this study that the apparent spatial and annual variability in the degree of mixing across the study area is not so much spatial variability but the time at which the location was sampled relative to the timing of the seasonal progression of stratification within that region. The seasonal progression of stratification and primary production within a given region (see below) follows a roughly similar pattern each year. However the summer cruises have sampled the water column anywhere from 25 to 77 d after the water column has stratified. This difference in the seasonal timing of sampling needs to be taken into consideration when interpreting not only the physical data, but the collected fish and bird data as well. The water column characteristics of the spring and autumn surveys are most effected by the previous week's weather.

The combination of meteorological and CTD (and 1-D model output) data therefore provides a reference within which the interpretation of fish size, abundance and bird abundance and distribution can more accurately proceed. The collaborative use of this data will be presented in detail in Chapter 8.

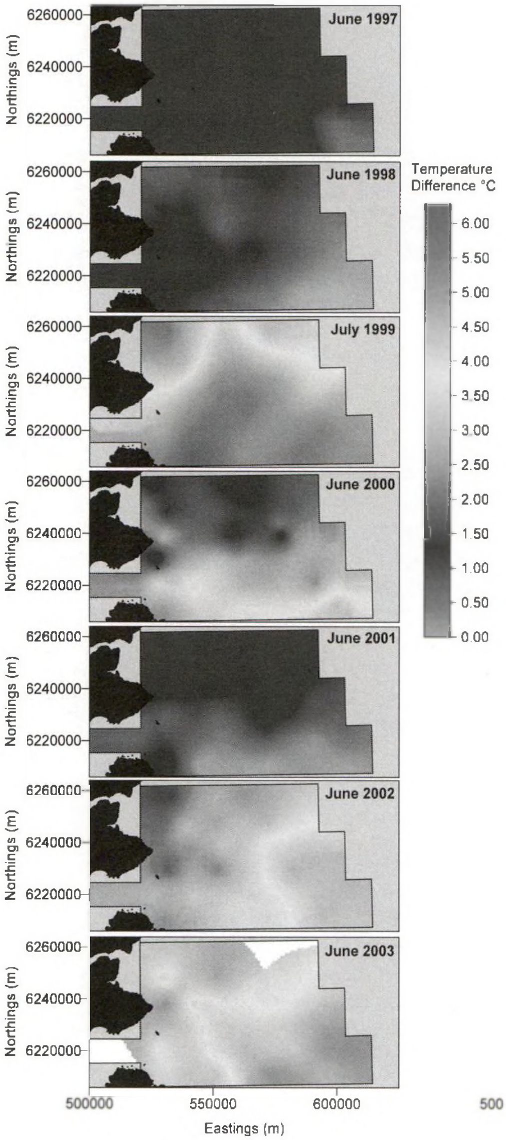


Fig 3.2.1. The difference between surface and bottom temperature in each of the June Clupea cruises from 1997 to 2003.

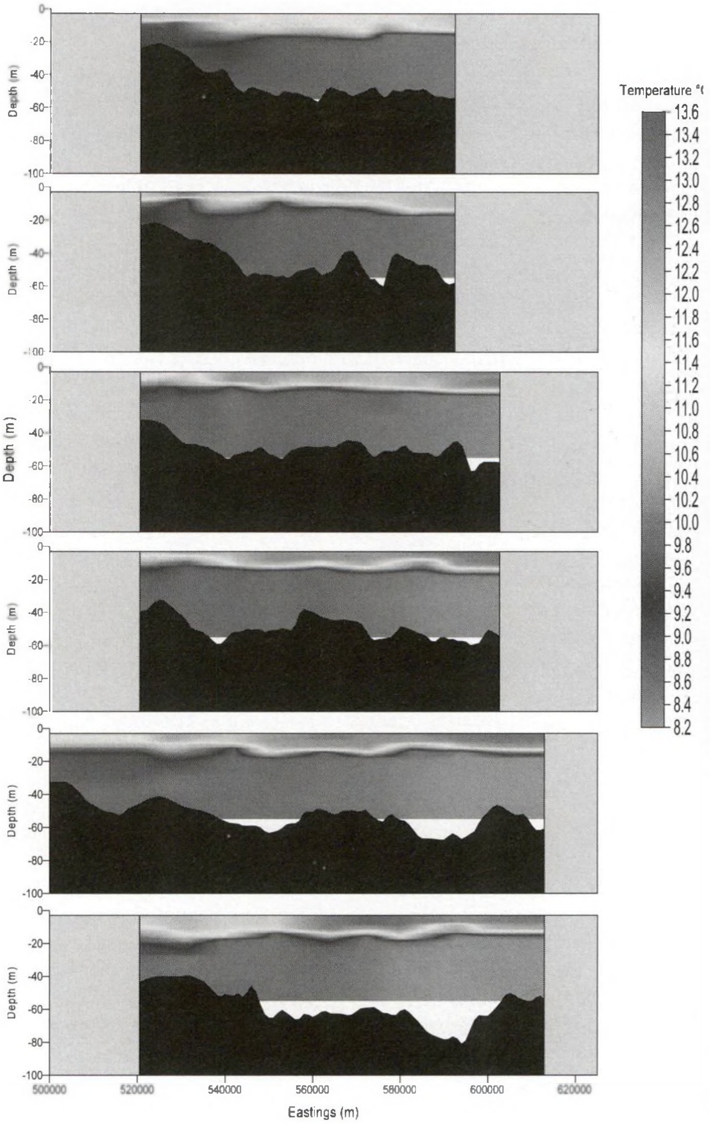


Fig 3.2.2 West - east variation in seawater temperature through the water column at different northings in the Firth of Forth study area form theClupea cruise, June 2003

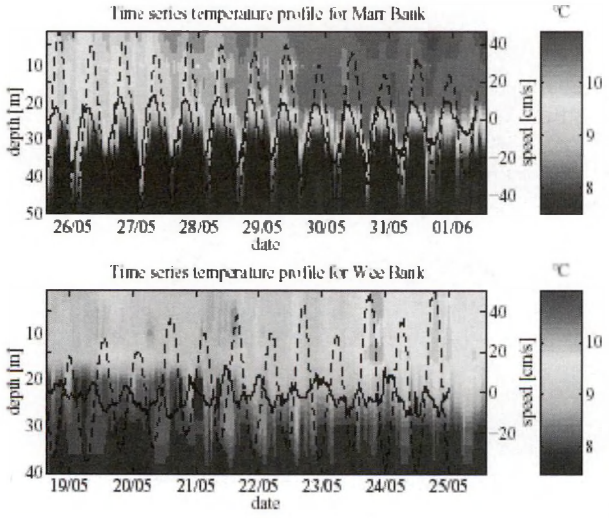


Fig 3.2.3. The temperature data (every 10 minutes) over a one week period from mini-loggers on the Marr and Wee Bank mooring at set depths (1, 5, 10, 15, 20, 30, 35 and 50m). The N-S currents are plotted as a dashed line (positive is to the North), the E-W currents as a solid line (positive to the East). The data show evidence of both advection events occurring with the flood and ebb of the tide and of internal waves occurring with a period of approximately 40-50 minutes.

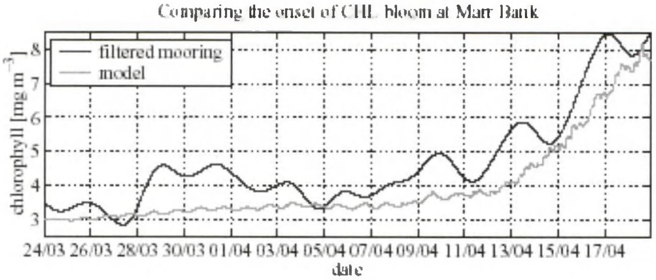


Fig. 3.2.4. A comparison between the 1-D model output of hourly chlorophyll abundance and the empirical hourly data collected on chlorophyll abundance from the moorings at the Marr Bank site.

The **moorings** provided information on the changes in the vertical structure, including the depth of the surface mixed layer, the gradient of the thermocline (Fig 3.2.3) and the abundance of chlorophyll (Fig 3.2.4). The moorings provided detailed evidence of the annual timing of the stratification of the water and the initiation of the spring bloom. The mooring data were used to parameterise site-specific 1-dimensional coupled bio-physical models (see *1-D modelling* below). The data indicated the presence of internal wave activity and the scale of advection events occurring with the flood and ebb of the tide. The level of detail provided a comprehensive understanding of the hourly and daily dynamics of the water column behaviour over the entire productive season in three different regions. These detailed data were used to compare directly to tagged birds and the timing and depth of their foraging activity (see details of use in Chapter 7 and 8). The mooring data was also used to test and validate the output of Polpred (Proudman Oceanographic Laboratories, tidal prediction software), that was later used to produce a tidal flag for those times and areas when and where we did not have mooring data (see more detail below under the heading *Tidal Flags*).

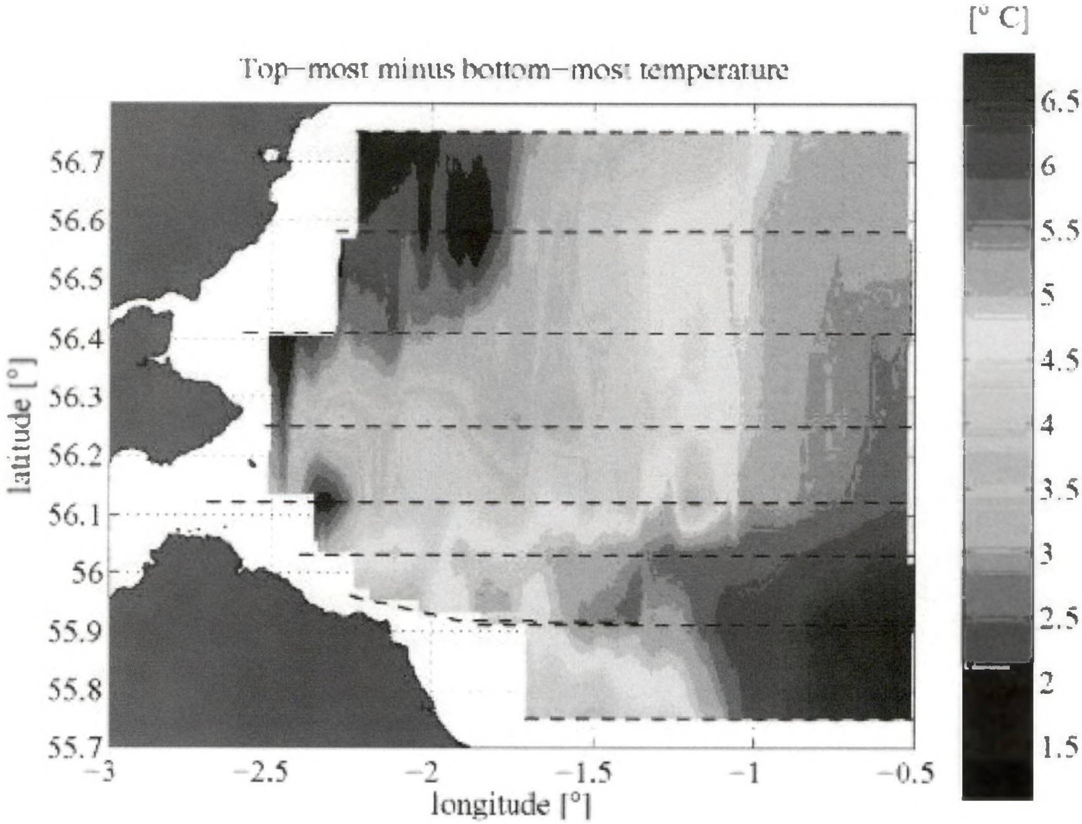


Fig. 3.2.5. The degree of thermal stratification across the June 6-19 Pelagia Cruise produced with data collected by the Scanfish.

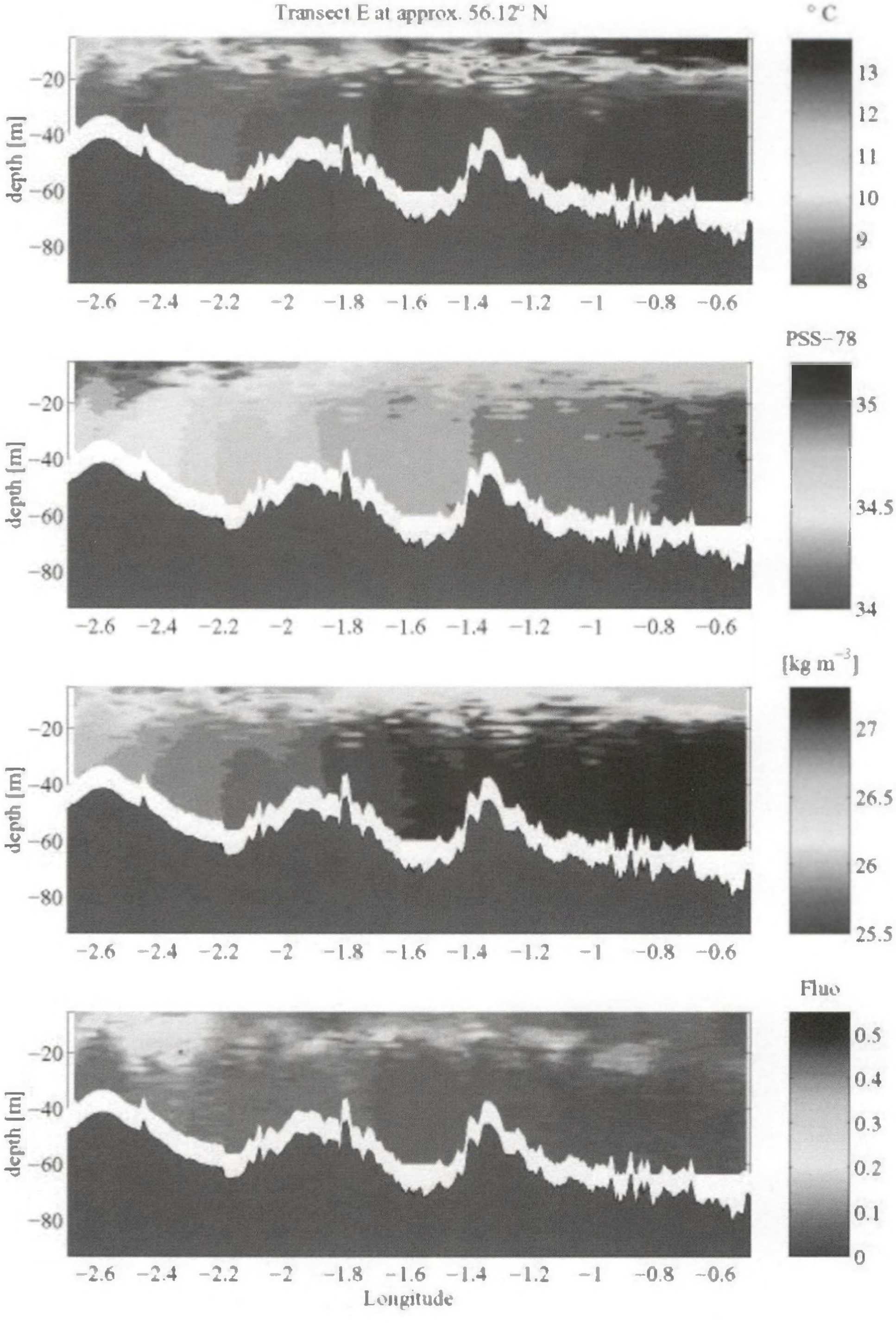


Fig. 3.2.6 The "E" transect in detail for temperature, salinity, density and fluorescence data collected by the undulating Scanfish. Interpolation in the horizontal direction is at most 300 m (the widest section of the 'V' shaped undulation of the instrument during either a decent or an accent) and there is no interpolation in the vertical direction.

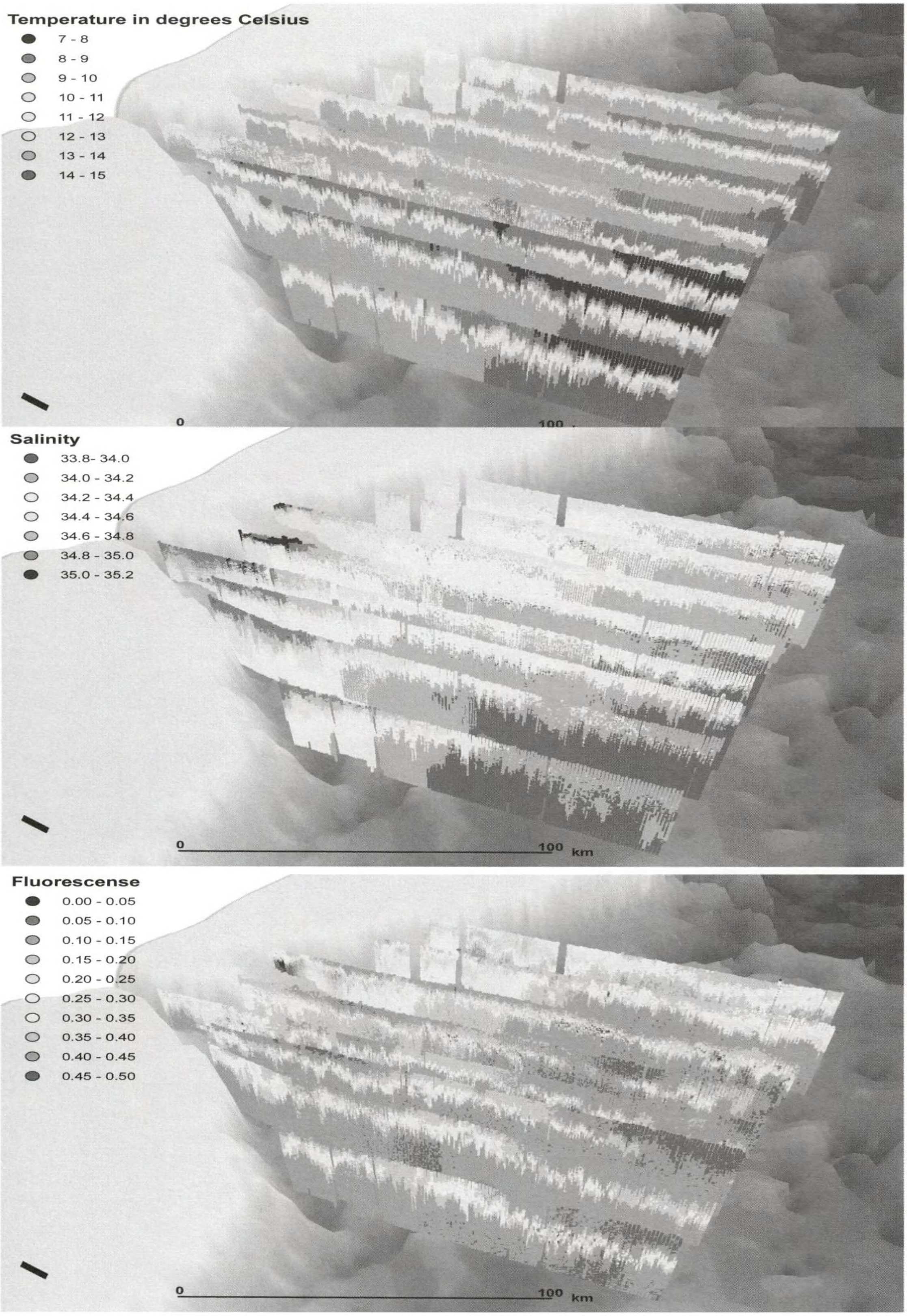


Fig 3.2.7 All of the scanfish data of temperature, salinity and fluorescence at depth and x, y location is presented in the figures below. The data is presented over the bathymetery of the primary study area.

Shallow sea front and bank regions

During the IMPRESS project two weeks of dedicated surveys were scheduled to be performed in the third field season in a period chosen in response to research needs developed during the project (RV *Pelagia* cruise). During the surveys, hydrographical observations were combined with detailed behavioural and distributional studies of foraging seabirds and prey availability (acoustic signal). The surveys were to be designed to test predictions of foraging seabird behaviour, oceanographic characteristics and prey distribution that arouse from the previous 2 years of field work (both at colonies and at sea).

The sampling was done with the use of a Scanfish (undulating CTD) such that continuous vertical and horizontal information on temperature, salinity, density and abundance of chlorophyll was collected at 1 sec intervals and approximately 0.5 to 1.0m depth. Rich spatial detail is obvious (Fig 3.2.5-6) with multiple locations displaying different degrees of mixing. Comparing this data with the 2003 CTD *Clupea* cruise results (Fig 3.2.1-2) indicates that the sparse interpolated data, which suggests that a rather uniform pattern of stratification of the water column is misleading. The *Pelagia* data set provides the true east-west spatial variability of the water column with an accurate picture of the mosaic pattern of the differences in vertical mixing and stratification within the primary study area (Fig 3.2.7) and was therefore used in subsequent analysis of characterising predatory and prey foraging habitat.

These observations allowed the defining of separate regions with different mixing and/or productivity characteristics such that analysis of longer term, but spatial sparse, data could be categorised by the region in which it was collected. The detail available suggested that what we considered as the former Banks region at the beginning of the project (Fig 1.5.8) could be more accurately viewed as 2 types of regions (Inner and Outer Banks) due to proximity and interaction with the Shallow sea front and the stratified region seaward of the front (the Offshore stratified region) and what we now call the Outer Bank region (Figure 3.2.8.)

Offshore stratified: A region which begins with the location of the Shallow sea front and continues eastward into deeper waters. This region contains the strongest gradient in density at the pycnocline and has the coolest bottom temperatures, both of which are characteristics of the combination of greater depths and lack of mixing of bottom water with surface layers.

Outer Bank: Evidence of greater mixing than in the offshore stratified region but less mixing than inner banks area or the well mixed regions. This region can become strongly stratified and is influenced by the presence of the Shallow sea front and so has access to nutrient rich cool bottom water, which leads to a difference in the seasonal productive regime as compared with the Inner Bank region.

Inner Bank: Greater mixing (mostly due to shallower depth) than outer banks and no access to nutrient rich cool bottom water, however the region can stratify.

Well mixed regions (shallow and deep): Regions of strong tides with the near shore region of consistent shallow depth (< 40 m) defined as the shallow region. This shallow region also is influenced by fresh water. Both the shallow and deep well-mixed regions show the greatest amount of primary production throughout the vertical water column relative to the other regions and generally lack strong vertical structure that would aggregate prey.

Fresh water influenced region: This region has a strong influence of fresh water that follows the coastline in the southern portion of the primary study area. It also has deeper topography than either of the bank regions. The influence of fresh water does not allow the separation of the region via the mixing properties as the influence on density more easily creates stratification of the water column.

However, in order to compare the continuous physical water column characteristics measure by the Scanfish with the locations of continuously measured foraging animals, the data were prepared in several different approaches. (1) Sections of the continuous data are comparable to tagged foraging birds found in the same locations, and (2) creating 5 min summaries of important physical and biological characteristics of the water column such as stratification of water column, depth and gradient of pycncoline, depth of maximum chlorophyll abundance, sum of water column chlorophyll and bottom depth (etc.) was the only way to compare the data the to the at-sea 5 min bin observations of top-predators and 5 min bin acoustic observations of prey species. The results of the collaborative analysis they have generated will be presented in detail in Chapter 7.

Mini-surveys

Logger data from tagged birds and observations of large inactive flocks of seabirds in the shallow frontal zone had suggested that there could be an influence of the speed of the tidal current on the timing and depth (of diving birds) of active foraging and that changes in tidal current strength might for example even influence the type of prey caught. The mini-surveys (Chapter 1.5.2) were designed to test all categories of the different types of feeding behaviour for each species with tidal phasing and to look for a repeat of similar locations for feeding activity for each species and for groups of species. The location for each Mini-survey was chosen on the basis of a combination of oceanographic information (scanfish data) and ornithological observations (intense feeding or particularly high densities of the target species during the transects performed in June 2003, compared with earlier data collected 2001-2002 in the same general area). Figure 3.2.9 is an example of the results obtained. The predator–prey implications from the information gather in the mini-surveys will be discussed in detail in Chapter 7.

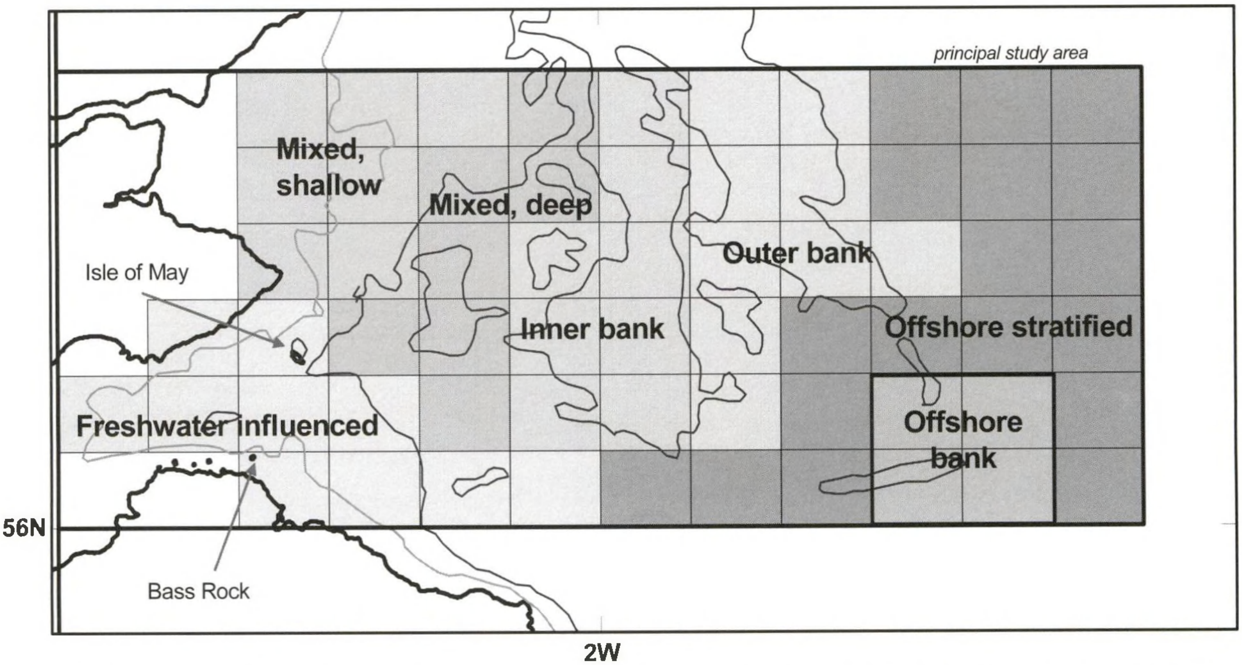


Figure 3.2.8. Partitioning of the principal study area into seven broad regions based on the topographic features, the degree of tidal mixing and the influence of freshwater .

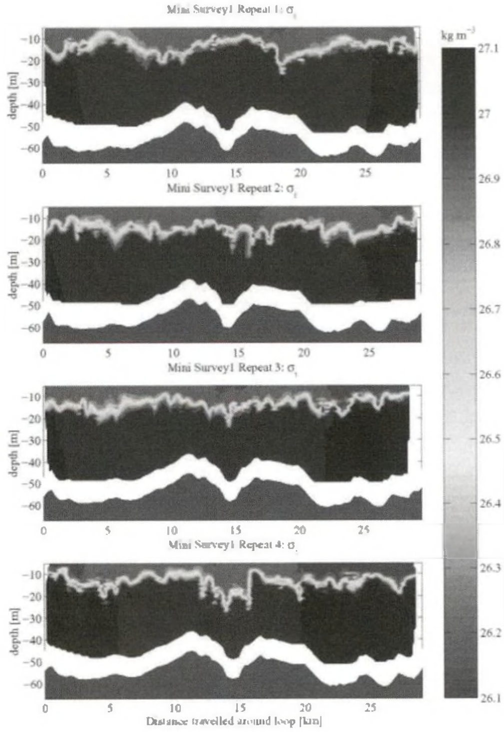


Fig. 3.2.9. The first four repeats of mini-survey 1 showing the dynamics of the vertical density profiles. The interpolation in the horizontal direction is 300 m or less.

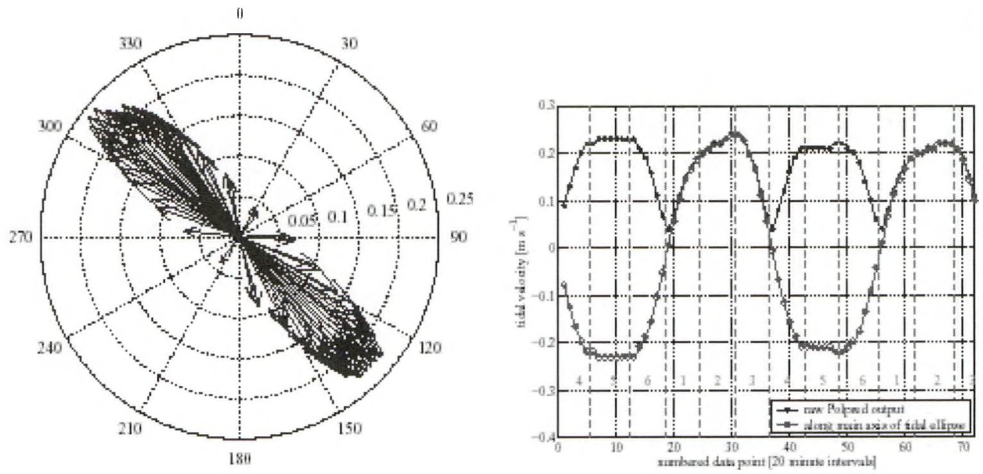


Fig. 3.2.10 An example of how the flagging corresponds to the tidal phase for 6 June 2001 at 56.05 N and 2.583 W. The left panel shows the raw Polpred data plotted on a polar plot which makes it easy to see the shape of the tidal ellipse. The concentric circles with numbers next to them indicate the current amplitude in ms^{-1}. The graph on the right shows the same data on an x-y-plane, where the abscissa shows the increasing time (20 minutes with every data point). The red curve has been obtained by projecting the current vector onto the major axis of the tidal ellipse and using the direction vector to distinguish between north-going (positive) and south-going (negative) currents. The dashed vertical lines show the segments of the tidal flags with the numbers indicating the value of the flag.

Tidal Flags

Since tides may play an important role in the foraging of seabirds, tidal flag information had to be provided (the speed of the tide at precise locations and time; see Chapter 1.5.2), to compare to tagged or observed bird foraging activity and acoustic information. The speed of tide was defined in six phases:

1. **increasing North** - tidal phase is starting to ebb and the velocity can be between 0 and 85% of daily maximum
2. **maximum North** - period of maximum north-going currents with amplitudes >85% of daily maximum
3. **decreasing North** - decaying ebb with velocities between 85%of the daily maximum and zero
4. **increasing South** - beginning flood
5. **maximum South** - maximum flood
6. **decreasing South** - decaying flood

Flagging the tidal segments for the above flags were not determined from the velocity amplitude but by using time (Fig 3.2.10). The mentioned 85% mark is therefore only approximate (corresponding to sin(π/3)). The use of time instead of velocity amplitude was made to ensure that the time intervals for the above flags have approximately the same length as the velocity signal can be rather irregular. On each day there are three to four occasions during which the tidal velocity is zero (or minimal). The first step was thus to locate these minima or nodes. The intervals between each node were then split into three evenly sized bins (regardless of the velocity). The three bins correspond to the increasing, maximum, and decreasing flags respectively. The direction (south or north) was determined from the Polpred direction vector. Due to the 20-min time interval and a sometimes odd number of data points between the nodes this can produce rounding errors and slight irregularities in the size of the bins. 'North' in the above descriptions means the general northward direction. Since the tidal ellipse is different throughout the study area, the maximum ebb current could be anywhere from a N-E to a N-W direction. Near the coasts, and in particular at the mouth of the Firths of Forth and Tay, this assumption breaks down as there is no predominant N-S current direction.

3.3 1-D modelling 1974- 2003

At the start of the project, a prototype 1-D coupled model available was available (Sharples 1999). Over the course of the project several modifications have been made aimed at improving the user interface, keeping the model up to date (specifically in its calculation of turbulent mixing), configuring the model to the IMPRESS study region, and providing appropriate model output.

In the first two years of the project the user-interface of the model was completely re-designed, and the model was set-up to accept meteorological data for the study region (acquired from the British Atmospheric Data Centre). The first mooring deployment was used to calibrate the model to the local oceanographic (i.e. the depths and tidal constituent current amplitudes and phases). An updated turbulence scheme was also incorporated. In 2004 the only additional changes made were incorporation of the latest meteorological information, and a re-write of the integration scheme used by the Coriolis term of the model (to a scheme that has been shown to conserve the energy of inertial oscillations correctly). Data from the second mooring deployment was used to validate the model (primarily in terms of the model prediction of the onset of spring stratification). Long term sea temperature data held by ICES was used to provide a means of assessing the model's capability of the full 30 years of available meteorological data.

Further data analysis of the mooring data in combination with at-sea data collected on water clarity on both the *Clupea* trips and the *Pelagia* trip highlighted the need to slightly alter the parameter values for PAR from a value of 0.12 to 0.10 for the Marr Bank mooring data and value of 0.13 for the Wee Bankie mooring. The value of 3.0 for the respiration rate was held constant for the model at both sites, as there is insufficient information available to assess any temporal or spatial changes in plankton physiology. This meant that while the model physical predictions of stratification timing were reliable, the biological predictions needed to be interpreted with caution. Running this new parameter for water clarity through the 1-D model for the Marr Bank site produced very a close match between the modelled timing of the bloom and the mooring data. The differences in water clarity offshore allowed the plankton bloom to proceed at a slightly greater rate than previously modelled, such that the difference in the modelled timing of the bloom between sites is never greater than 8 days. Therefore the deeper site with a lower likelihood of being influenced by fresh water was used to define the timing of stratification and the spring bloom over the 30 years we have all the necessary meteorological input data.

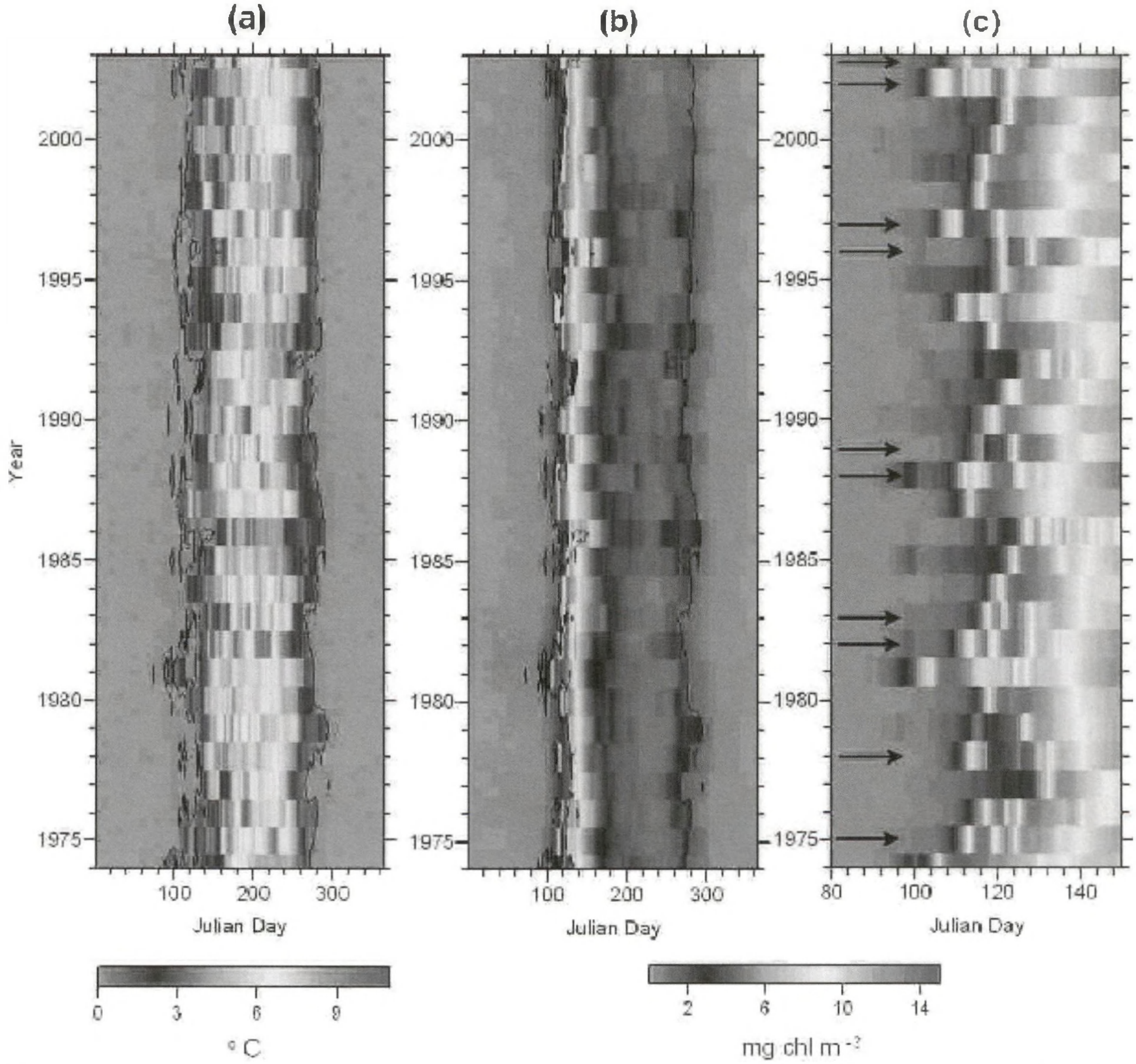


Fig. 3.3.1. 1-D Model results of stratification and chlorophyll patterns from 1974 to 2003. (a) Inter-annual variability of the seasonal stratification (surface – bottom temperature difference). The contour line is a surface – bottom temperature difference of 0.5 °C. (b) Inter-annual variability in the seasonal surface chlorophyll concentration. The contour line is a surface – bottom temperature difference of 0.5 °C. (c) As (b) but focused on the time of initiation of the spring bloom. The arrows highlight years when an apparently established spring bloom is sharply curtailed for a few days, and then re-establishes.

Several experiments were then conducted with the model, over the entire 1974-2003 meteorological series available, towards understanding the controls of the timing of spring stratification and the spring bloom (Sharples *et al.* submitted). The work used the 1-dimensional coupled physics-primary production model to investigate the processes that control inter-annual variability in the onset of spring stratification and the spring bloom, between 1974 and 2003 in the northwest North Sea (Fig 3.3.1). Validation of the model against available winter water temperatures showed that advection of warmer water from the Northeast Atlantic Ocean did not play a role in controlling water temperatures in the region; i.e. in regions where stratification is predominantly thermal, the development of stratification is controlled by local processes of meteorological forcing and vertical turbulent mixing. This finding is consistent with recent work that shows North Sea temperatures to be more closely correlated with temperatures in UK lakes than with the temperature of the NE Atlantic (D. Prandle *pers. comm.*). The main model findings were that over the 30 years, meteorological variability drove most of the inter-annual variability of both the onset of stratification (86% of the variance) and the spring bloom (70% of the variance), with variability in the spring solar irradiance being more important than variability in wind stress. Tidal variability, acting through the spring-neap cycle, seemed to have a marked effect by causing a double spring bloom. Correlation of the meteorological data with the North Atlantic Oscillation (NAO) suggests that the NAO plays a significant, but not dominant, role in generating inter-annual variability in the timing of spring stratification and the spring bloom.

Output from 1-D model to compare to predator and prey population variables

The output of the 1-D model provided accurate and long-term predictions on the annual timing of important seasonal events in the marine ecosystem. The modelling work provided an estimate of the annual timing of the spring bloom (modelled surface chlorophyll exceeded 5 mg m^{-3}), the onset of stratification (bottom-surface temperature difference exceeds 1°C and is sustained for at least one week) and the end of the surface bloom (chlorophyll drops below 5 mg m^{-3}; Table 3.1). The daily output of the model allowed relative annual estimates of the sum of primary production before the spring bloom, during the surface bloom and for the subsurface production after the spring bloom. All of these annual variables could be compared to both predator and prey population variables such as breeding success and growth. The result of a detailed collaborative analysis with these variables is presented in Chapter 8.

Table 3.1 Estimates of the timing of the onset of stratification (bottom-surface temperature difference >1°C and sustained for at least one week), of the spring bloom (when modelled surface chlorophyll exceeded 5 mg m^{-3}), and the end of the surface bloom (clorophyll <5 mg m^{-3}) between 1997 and 2003.

	Onset of stratification bottom-surface temp. difference >1°C	Start of the spring bloom chlorophyll >5 mg m^{-3}	End of the bloom chlorophyll <5 mg m^{-3}
1997	12 April	17 April	4 June
1998	21 April	25 April	9 June
1999	24 April	25 April	11 June
2000	28 April	29 April	20 June
2001	30 April	1 May	11 June
2002	7 April	14 April	28 May
2003	22 April*	19 April*	2 June

* bloom appears to occur before the stratification, but there was a lot of weak stratification up to 22 April, allowing the bloom to develop

3.4 Monthly composites of sea surface temperature (SST), summer 2001-2003

From a combination of observation techniques, our work has emphasised the importance of the Shallow Sea fronts for foraging seabirds and the results indicated that this also forms an outer 'barrier' for many birds breeding down the east coast of Britain (Camphuysen *et al.* 2006; see Chapter 5, Chapter 7). Top predators frequently congregate around these Shallow Sea fronts that are normally associated with increased abundances of fish, larvae and zooplankton (Pingree *et al.* 1975; 1978; Richardson *et al.* 1986). Closer to land, surface waters are cooler than over stratified waters further offshore and the outer boundary of the main (coastal) feeding zone (and the approximate location of the fronts separating the mixed waters along the coast and thermally stratified waters further offshore) could be visualised by using satellite images presenting sea surface temperatures (SST; Fig.3.4.1-3.4.3).

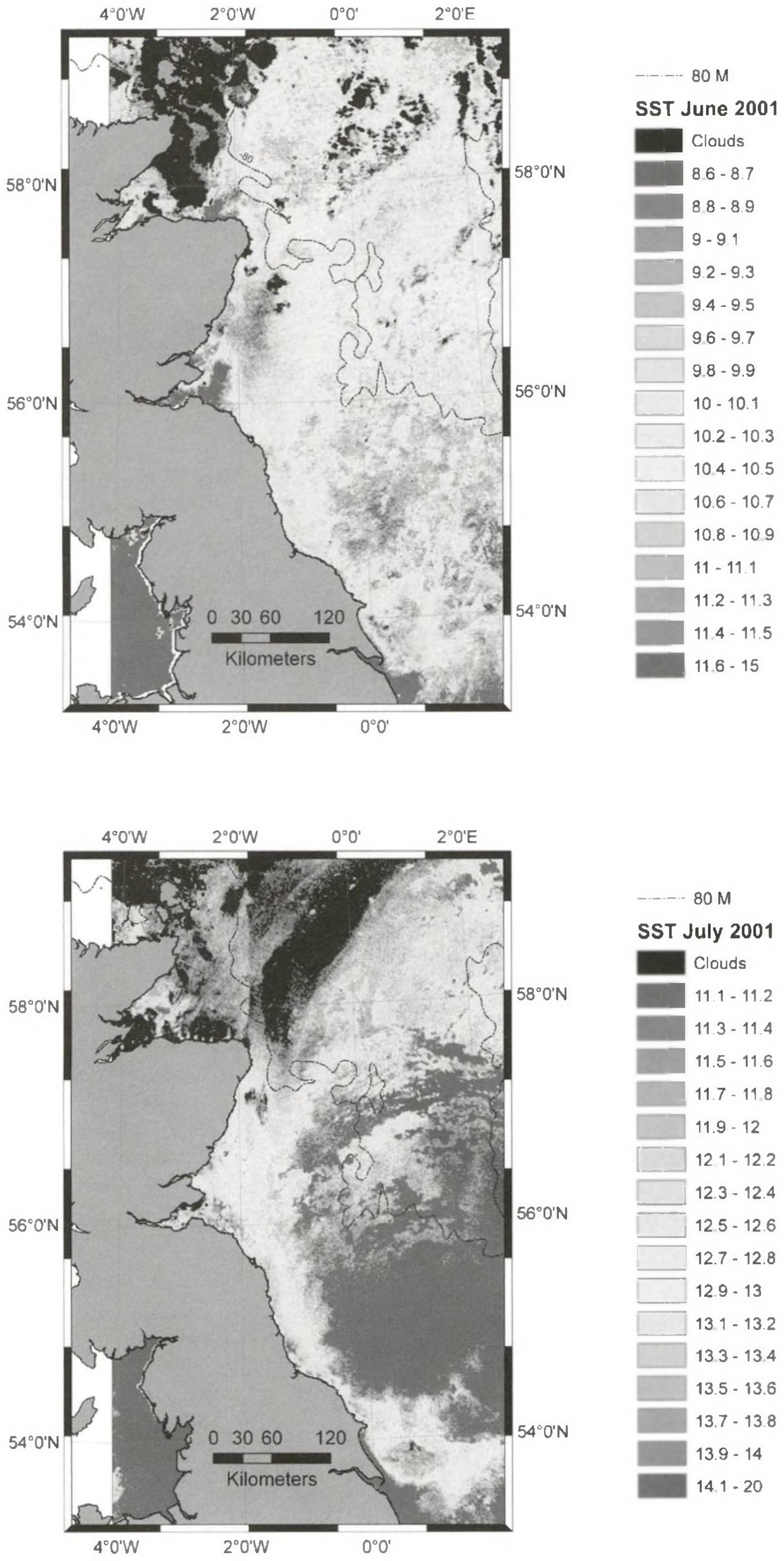


Figure 3.4.1. Sea surface temperature composite maps of the study area at large; June-July 2001.

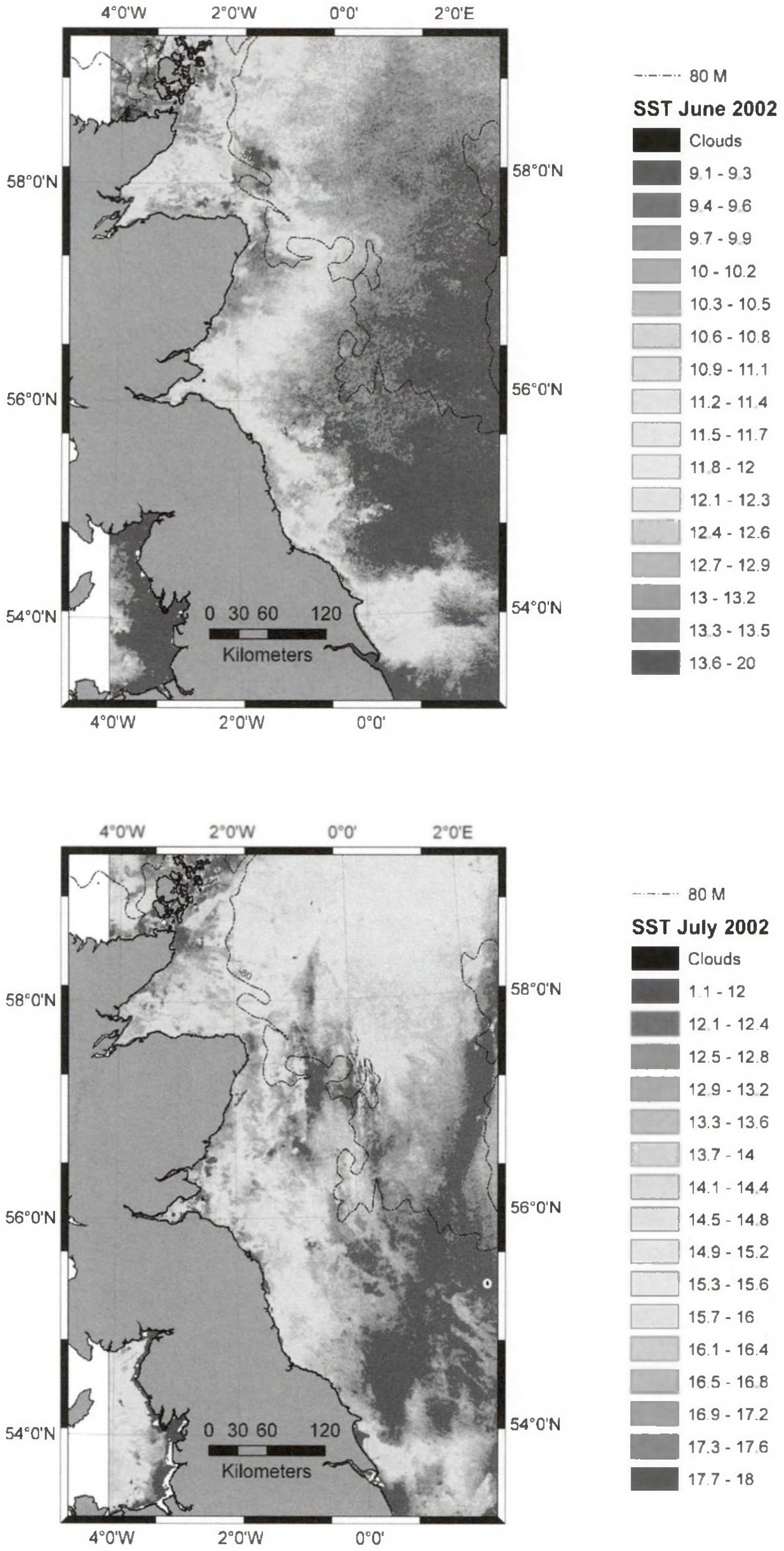


Figure 3.4.2. Sea surface temperature composite maps of the study area at large; June-July 2002.

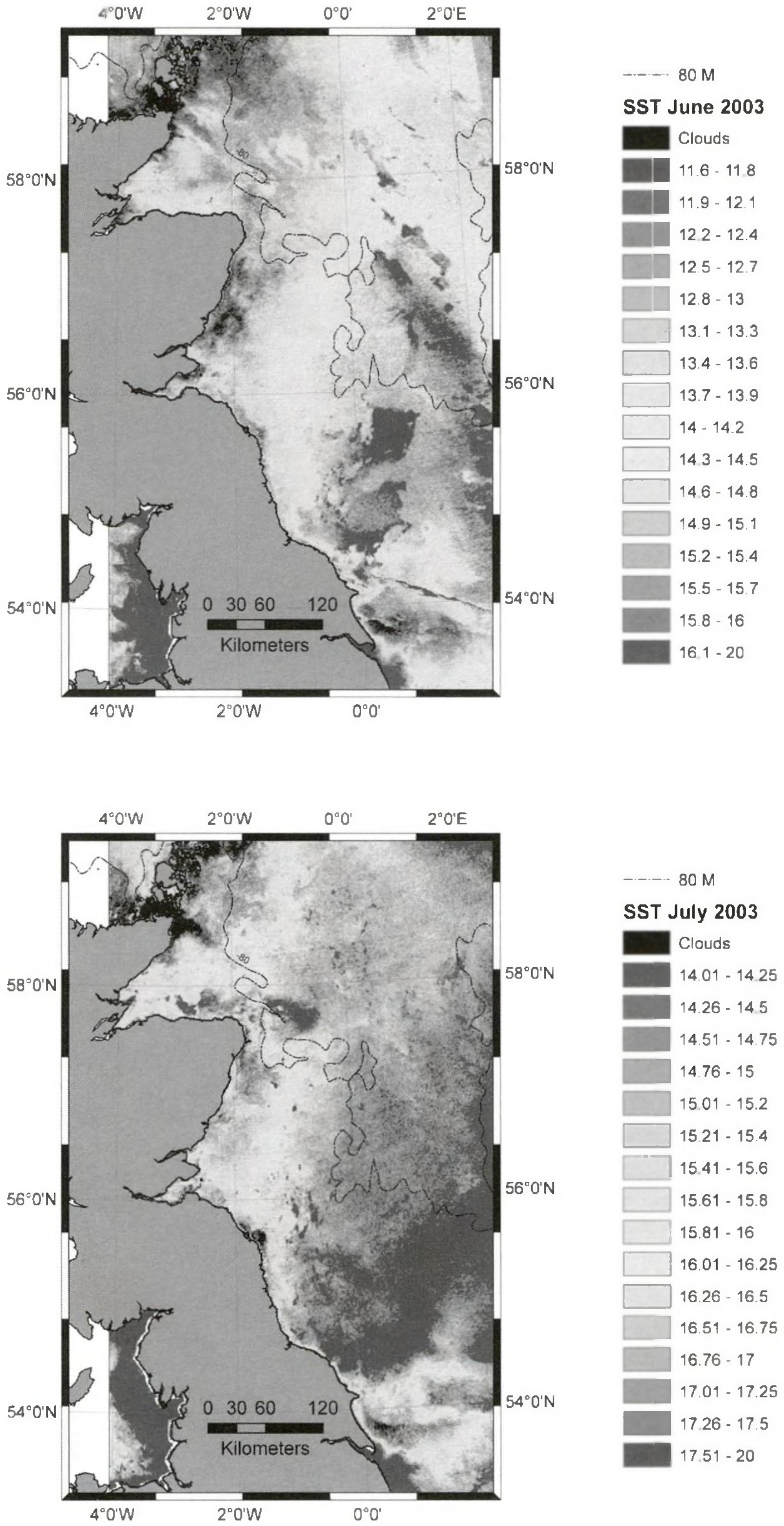


Figure 3.4.3. Sea surface temperature composite maps of the study area at large; June-July 2003.

Chapter 4 Setting the scene (3): Sandeels and clupeids in the Wee Bankie/Marr Bank region

Simon Greenstreet, Eric Armstrong, Helen Fraser, Gayle Holland & Iain Gibb

4.1 Introduction

There is an obvious requirement to monitor changes in the abundance of sandeels in areas where fisheries may be reducing their availability to marine predators. The catch data from the fisheries themselves can provide some indication of changes in the size of local sandeel populations. These data are relatively inexpensive to obtain, and have often been collected for an extensive period. Furthermore, if the mortality due to fishing is high, the reduction in the derived index from one time step to the next can be related to the effort employed in the area, and from this type of analyse, a biomass estimate can be derived (Hilborn & Walters 1992). However, fishery derived indices suffer from the disadvantage of not being randomly sampled from within the areas concerned, and this may lead to artificially high indices, through sampling from only the high-density areas (Hilborn & Walters 1992).

In 1996 a project involving research institutes in Scotland, England and Denmark was initiated with part funding from the European Commission. This *ELIFONTS* project analysed field data collected over two years, 1997 and 1998. Because of its short-term nature, the project was not conclusive, however, the results suggested that there was indeed serious cause for concern. The UK government adopted a strong stance on this issue and proposed that industrial fishing for sandeels be banned over a large area along the east coast of the UK. An ICES study group was set up to discuss this proposal and to recommend an appropriate course of action. The group concluded that a ban on industrial fishing should be imposed, however, it suggested that a much smaller area be considered. This was be centred around the Wee Bankie/Marr Bank/Berwick's Bank complex, where fishing intensity had been exceptionally high, and sandeel catches per unit effort among the highest of any industrial fishing ground in the North Sea. The need to assess variation in the abundance of sandeels, so as to monitor the effectiveness of the fishery closure, is an obvious requirement where such a management approach is adopted.

Over the period 2000 to 2003 a limited amount of sandeel fishing was permitted in the area to allow the maintenance of the scientific catch and population structure statistics data-base at the Danish Institute for Fisheries Research. Because of the stance adopted by the UK government, and the Scottish nature of this particular issue, Fisheries Research Services (FRS) Marine Laboratory in Aberdeen continued to undertake scientific research in the area for the Scottish Executive, effectively continuing, as far as possible, the earlier *ELIFONTS* programme. In 2000, *IMPRESS* gained EC funding and whilst this was a four-year project, FRS's commitment to the project only included the continuation of its field-data collection programme up to and including 2002. However, given the possibility that the fishery might have reopened in 2003, FRS' data collection programme was extended to include 2003, which was also the final year that field data were collected by partner institutes within the *IMPRESS* programme. Thus data have been collected over a seven-year period, from 1997-2003: three years when the industrial fishery was active, followed by four years when the fishery was closed.

Assessing prey fish stock abundance

Quantifying the abundance and distribution of prey is a major requirement of any predator-prey interaction study. Consequently, a principal objective of the FRS contributions to the programme of research carried out in the Wee Bankie/Marr Bank/Berwick's Bank area has been to assess changes in the sandeel population from year to year, and over the course of each year. Sandeels spend much of their time buried in the seabed sediment, moving out into the water column to feed during daylight hours, mainly in the months of May and June in the Wee Bankie area. Assessment methods based on fisheries catch statistics are presumed to provide estimates of the total population size in an area, as do assessment methods based on sampling sandeels in the sediment during the hours of darkness (see later sections). However, seabirds are dependent on finding their prey at various levels in the water column, and the entire population of sandeels is rarely, if ever, all up in the water column simultaneously. In order to estimate prey availability to seabird predators, estimates of the abundance of sandeels active in the water column are required. Acoustic surveys can provide such estimates. FRS has carried out acoustic surveys each year from 1997 to 2003, timed as far as possible to coincide with the seabird chick-rearing period. Acoustic surveys also provide estimates of the abundance of other pelagic fish in the water column, such as Herring and Sprats. In the event of a shortage of sandeel prey, these species could provide suitable alternative prey resources.

Sandeels are a particularly difficult species to assess using acoustic survey techniques. Their low target strength means that small errors in acoustic integral attributed to sandeels in the water column can lead to large errors in the density estimate (1kg of sandeels has a target strength of -50db at 38 kHz (Armstrong, 1986)). Nevertheless, even if one is uncertain about the precise target strength, variation in the total acoustic integral can provide an index of variation in abundance. However, their habit of burrowing in the sediment causes problems with acoustic survey methods, since at any one time, an unknown fraction of the population may in fact be buried in the sediment, and so not available to acoustic census.

The alternative to surveying sandeels in the water column is to assess their density, or abundance, in the seabed sediments. Two principal techniques have been employed to do this; dredging and grabbing, both carried out at night when the vast majority of sandeels are believed to be buried in the sediment (Winslade, 1974a; 1974b; 1974c; Wright & Bailey,1993).

Both techniques have their advantages and disadvantages. Dredges cover large areas of ground, taking samples of up to several hundred sandeels per $1000m^2$ of seabed covered. Such samples are more than adequate for population age and length structure analyses. However, catches are integrated over large areas that may include suitable, as well as unsuitable, sandeel habitat. Thus, in most cases, such samples actually underestimate the real density of sandeels in the suitable habitats. Furthermore, catchability in dredges is low, since many sandeels appear to escape ahead of the dredge, perhaps through the stimulation of an escape response caused by the vibration of the dredge along the seabed (P.J.Wright, unpublished data). In addition, relatively large mesh sizes are required (10mm) in order to prevent the dredge clogging up with sediment. As a result, catch rates of the smaller and younger sandeels tend to under-represent their actual abundance in an area.

Grab surveys provide point estimates of sandeel density, which in suitable habitats, always exceed dredge density estimates by up to a couple of orders of magnitude (S.P.R. Greenstreet, unpublished data). Sandeel catchability in grabs must therefore be relatively high, and this is particularly true for the smaller size classes, under-sampled by dredges. Another major advantage of grab surveys is that a sediment sample is always associated with each sandeel density estimate. Thus, the suitability of the habitat at each sample location can be assessed directly, at least in terms of depth and sediment particle size distribution. The principal drawback with grab surveys is that the total area sampled is small. For example, a complete survey consisting of as many as 500 grab samples will only cover $50m^2$ of seabed area, compared with the $1000m^2$ covered by a single dredge sample. Consequently, the total number of sandeels sampled in any complete grab survey will be much smaller, and rarely sufficient to assess adequately the full age structure of the sandeel population.

Assessment of sandeel biomass in a given area through the use of grab surveys relies on a detailed knowledge of the location and extent of suitable seabed habitat. Grab samples can provide estimates of the mean density of sandeels in suitable sandeel habitat which when multiplied by the area of such habitat can provide estimates of the biomass of sandeels in the region. To do this, however, requires a precise definition of what exactly constitutes suitable seabed habitat for sandeels, so that this can be adequately mapped. Sandeels are known to be extremely selective in the types of sediment which they occupy, preferring coarse, sandy substrates containing a minimum of silt (Macer 1966; Pinto *et al.*1984; Reay 1970, Wright *et al.* 2000). In this study we use a sediment map, derived using the acoustic survey technique RoxAnn (ELIFONTS 1999), to target our grab sampling preferentially towards sand, slightly gravely sand and gravely sand (Folk 1954), which include these preferred sediment types. These samples are then analysed to provide a precise definition of sandeel habitat within the Wee Bankie, Marr Bank and Berwick's Bank region of the North Sea, off the Firth of Forth, south-east Scotland.

We also present data obtained from a groundfish survey (Appendix 8). This survey was primarily directed towards assessing variation in the populations of piscivorous fish predators of sandeels in the area. However, the codend mesh size used, at 10mm, was small enough to capture samples of sandeels, Herring and Sprats. The consistent survey design each year meant that these data could also provide potentially useful indices of abundance that would reflect inter-annual variation in the abundance and distribution of these forage fish. Furthermore, this index might also be expected to provide an index of total sandeel population size. The rockhopper design of the trawl would maintain a heavy contact between the ground-gear and the seabed, and so perhaps elicit an escape response from sandeels buried in the sediment, causing them to emerge into the water column to be trapped in the following trawl.

4.2 Variation in forage fish biomass and abundance

A detailed analysis of the acoustic, demersal trawl, nocturnal grab and dredge survey data is presented in Appendix 4 where biomass and abundance estimates of sandeels, Herring and Sprats obtained from each survey type in each cruise are presented. Full age at length keys, length frequency, and age frequency distributions (by both number and biomass) for all three species are also provided, thereby illustrating the analytical procedures by which estimates of the abundance and biomass of particular length classes and age groups of each species were obtained. In this Chapter data are presented only for two age classes of each species: 0 group and 1+ aged fish. Appendix 4 provides data at finer age class resolution, partitioning the 1+ data presented here to 1 group, 2 group and 3+ aged fish.

Lesser Sandeel *Ammodytes marinus*

Table 4.2.1 provides the indices of total sandeel abundance and biomass in the study area determined using each of the three main survey techniques in each year. All three survey techniques suggested a marked increase in the total biomass following closure of the sandeel fishery in 2000, however, the precise pattern of variation differed quite markedly between survey types (Fig. 4.2.1). Acoustic survey data suggest that total sandeel biomass present in the water column increased by approximately an order of magnitude over the first two years, 2000 to 2001, followed by a decline in 2002 and 2003. However, even in 2003, sandeel biomass in the water column within the study area remained greater than in any of the three years preceding the fishery closure. The total biomass of sandeels in the study area was significantly higher in the four years when sandeel fishing was prohibited than in the three previous years when they had been fished (Mann-Whitney $U = 12$, $P = 0.034$). The demersal trawl and October nocturnal grab survey data also indicate an increase in the biomass of sandeels in the first year of the fishery closure. However, both surveys suggest that this increasing trend may have started in the previous year, 1999, when the sandeel fishery was still in operation. Both data sets imply that the response to the fishery closure was short lived, with a marked decline in sandeel abundance apparent in 2001 and 2002. Both surveys suggest a slight increase in the abundance of sandeels once again in 2003. In both instances, comparison of the index values between fishery and non-fishery years was not significant, although only just so with respect to the demersal trawl index (Mann-Whitney $U = 11$, $P = 0.077$) because the index value in 2002 just dipped below that recorded in 1999.

The abundance and biomass indices derived from the demersal trawl survey were approximately three orders of magnitude lower than those determined for the acoustic survey data, reflecting the low catchability of sandeels in the demersal trawl. The demersal trawl indices as they stand therefore do not provide an estimate of the absolute abundance and biomass of sandeels present in the area at any specific time, nevertheless they may be considered to provide an index of temporal variation in the relative abundance of sandeels. Furthermore, comparison of the length-frequency distributions of the sandeels caught in the demersal and pelagic trawl samples in each year (see Appendix 4) suggested that the larger codend mesh size on the demersal trawl resulted in of sandeels less than 9cm having lower catch rates than larger sandeels. This conclusion was born out by the observation of large numbers of small sandeels trapped in the mesh of the demersal trawl, a situation that was rarely encountered in the pelagic trawl. Examination of the age-at-length keys (see Appendix 4) indicated that the demersal trawl was failing to sample 0 group sandeels, whilst the pelagic trawl used to calibrate the acoustic integral data caught large numbers of 0 group sandeel. Consequently, a large proportion of the acoustic survey biomass estimate in each year was assigned to 0 group sandeels, while the demersal trawl abundance estimate should only be considered to provide an index of 1+ aged sandeels. Nocturnal grabs sampled both 0 group and 1+ group sandeels, and so like the acoustic survey, provided an index of abundance of both age classes.

Table 4.2.1. Between year variation in the indices of total abundance and biomass of sandeels in the study area derived from each survey technique.

Year	Acoustic Survey		Demersal Trawl		Grab Survey
	Numbers (100 million)	Biomass (1000 tonnes)	Numbers (million)	Biomass (tonnes)	Density (n.m^{-2})
1997	205.694	18.63	10.59	163	
1998	322.773	58.30	8.93	100	11.48
1999	26.225	2.80	361.82	2216	46.03
2000	524.002	134.43	745.16	5580	66.54
2001	877.357	262.48	334.91	2587	18.65
2002	1657.750	202.33	200.56	2080	26.19
2003	462.325	60.82	496.93	4452	29.49

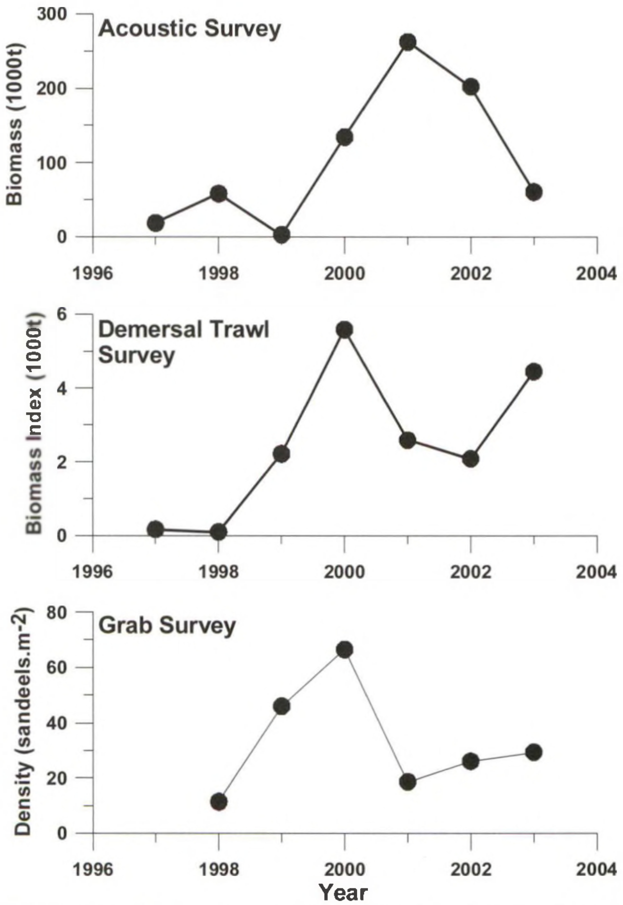


Figure 4.2.1. Between year variation in total sandeel abundance indicated by summer acoustic, summer demersal trawl and autumn nocturnal grab survey techniques.

Table 4.2.2. Between year variation in the indices of total abundance and biomass of 0 group and 1+ group sandeels in the study area derived from each survey technique.

Year	Age	Acoustic survey		Demersal trawl		Grab survey
		Numbers (100 million)	Biomass (1000 tonnes)	Numbers (million)	Biomass (tonnes)	Density (n.m^2)
1997	0 group	197.983	15.09	0.182	0	
1998		376.900	10.40	0.000	0	6.09
1999		23.579	1.63	1.935	2	41.35
2000		298.605	29.02	2.213	4	47.69
2001		338.463	27.72	0.515	1	6.72
2002		1540.927	90.98	0.182	0	17.82
2003		407.460	27.00	10.067	5	24.01
1997	1+ group	7.712	3.54	10.406	163	
1998		72.336	47.91	8.934	100	5.39
1999		3.076	1.17	359.888	2214	4.68
2000		237.779	105.41	742.948	5577	18.84
2001		548.282	234.76	334.393	2586	11.93
2002		187.094	111.35	200.374	2080	8.37
2003		74.463	32.82	486.862	4447	5.48

Table 4.2.2 gives the abundance and biomass index values for 0 group and 1+ group sandeels derived from each survey technique for each year. These data are plotted in Fig. 4.2.2 to aid comparisons between trends. Considering 1+ group sandeels first, the trends in abundance again do not appear to coincide. One obvious solution to this dilemma is that the different surveys are assessing the abundance of different components of the sandeel population. The grab sampling carried out October should have sampled the population at a time when the entire population was buried in the sediment. This survey could therefore be considered to provide an index of variation in total population abundance, albeit well after the time of concern to seabirds, the prosecution of the fishery, and the timing of the other two surveys. Furthermore, this index, as currently developed, provides only an index of relative abundance, rather than of absolute abundance. The acoustic surveys provide an index of absolute abundance, but only of that fraction of the population that is active in the water column. Acoustic survey cannot "see" sandeels buried in the sediment. The demersal trawl, with its 2m headline height, would sample an extremely limited fraction of the sandeels active in the water column. However, the heavy contact between the rockhopper ground gear and the seabed would very likely elicit an escape response from sandeels buried in the sediment, causing them to emerge into the path of the following trawl. The demersal trawl could therefore be considered to provide an index of the abundance of sandeels buried in the sediment: one that is complimentary to the acoustic survey index of sandeels active in the water column. If the differences between the acoustic and the demersal trawl survey trends can be reconciled by taking account of sandeel emergence behaviour, then these two surveys could be combined to provide an index of total abundance of 1+ sandeels present in the study area in each year. To achieve this, however, requires one further issue to be redressed; the fact that the demersal trawl, as described so far, only provides an index of variation in relative abundance rather than total abundance.

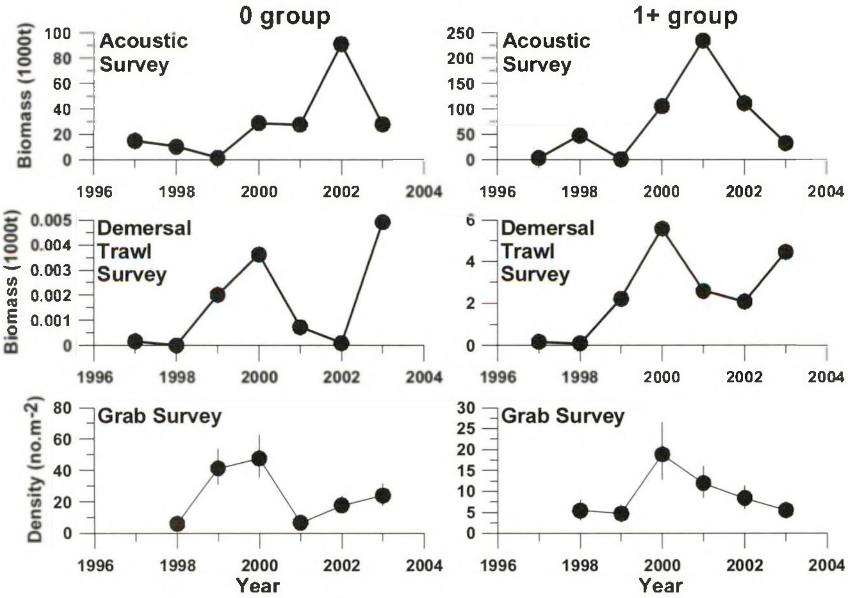


Figure 4.2.2. Between year variation in 0 and 1+ group sandeel abundance indicated by summer acoustic and autumn nocturnal grab survey techniques.

The acoustic and demersal trawl surveys were not carried out at exactly the same time each year due to variation in research vessel availability. Variation in the timing of the acoustic survey was kept to a minimum by rearranging the order in which the various bits of work were done in each summer cruise. Although the acoustic and demersal trawl surveys were always done immediately after one another, standardising the time of the acoustic survey meant that this was done first in the years 1997 to 2000, and second in the years 2001 to 2003. The Julian Day number between the acoustic and demersal trawl provides the best indication of the timing of this combined piece of work in each year (Table 4.2.3), and the difference between the earliest cruise, in 2001, and the latest cruise, in 1999, was 32 days. A 1D water column model described in chapter 3 was used to model primary production in each year of the study (Sharples *et al.* submitted). The start of the spring bloom, defined as the first day in which the surface water chlorophyll concentration exceeded 2 mg.m^{-3} for five consecutive days, ranged from 11 April (JD 101), in 2002, to 27 April (JD 117), in 2001, a range in start date spanning 16 days (Table 4.2.3). Variation in the timing of the acoustic/demersal trawl surveys relative to the start of the spring bloom was considerable, ranging from as little as 38 days in 2001 to as long as 76 days in 1999, a factor of two.

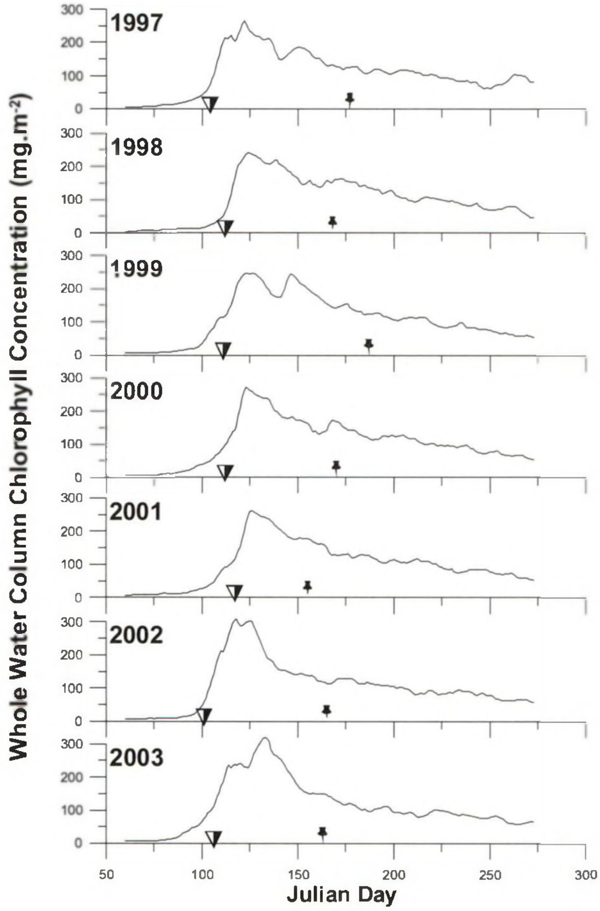


Figure 4.2.3. Daily variation in the whole water column chlorophyll concentration through out each of the years 1997 to 2003. The start of the spring bloom period and the mid-point of the acoustic and demersal trawl surveys in each year are indicated by the inverted triangle and pin symbols respectively.

Table 4.2.3. Variation between years in the timing of the acoustic/demersal trawl surveys, start of the spring bloom, duration of the production period between the start of the bloom and the surveys, and the cumulative whole water column chlorophyll concentration fuelling productivity to sandeels prior to each cruise.

Year	Day number between acoustic and demersal trawl surveys	Day number of start of spring bloom	Number of days between start of bloom and acoustic/demersal trawl surveys	Whole water column chlorophyll concentration (day.mg.m^{-2})	Cumulative whole water column chlorophyll concentration (day.mg.m^{-2})
1997	177	104	73	124.07	13866
1998	168	112	56	152.92	10959
1999	187	111	76	124.36	15508
2000	170	112	58	167.13	12412
2001	155	117	38	176.86	9709
2002	165	101	64	113.87	12948
2003	163	106	57	150.20	13906

Primary productivity, passing through the food chain, fuels the food supply to sandeels. Variation in the whole water column chlorophyll concentration through each year, output from the 1D model, is shown in Fig. 4.2.3, together with the bloom start and acoustic/demersal trawl survey dates. These plots therefore provide an indication of the potential feeding opportunity available to sandeels on any particular day. The whole water column chlorophyll concentration on the day between the acoustic and demersal trawl surveys in each year is given in Table 4.2.3. Integrating these curves up to the date of each cruise, ie the cumulative daily whole water column chlorophyll concentration (CDWWCCC), provides an indication of the total "feeding opportunity" available to sandeel up to the time of each cruise in each year (Table 4.2.3). With increase in the "feeding opportunity" prior to each cruise, sandeels should have reduced requirement for continued feeding. Consequently, with increase in the CDWWCCC prior to a survey, the proportion of sandeels active in the water column at the time of the survey should decline, with a corresponding increase in the proportion of sandeels buried in the sediment, causing the acoustic survey index to decline and the demersal trawl index to increase.

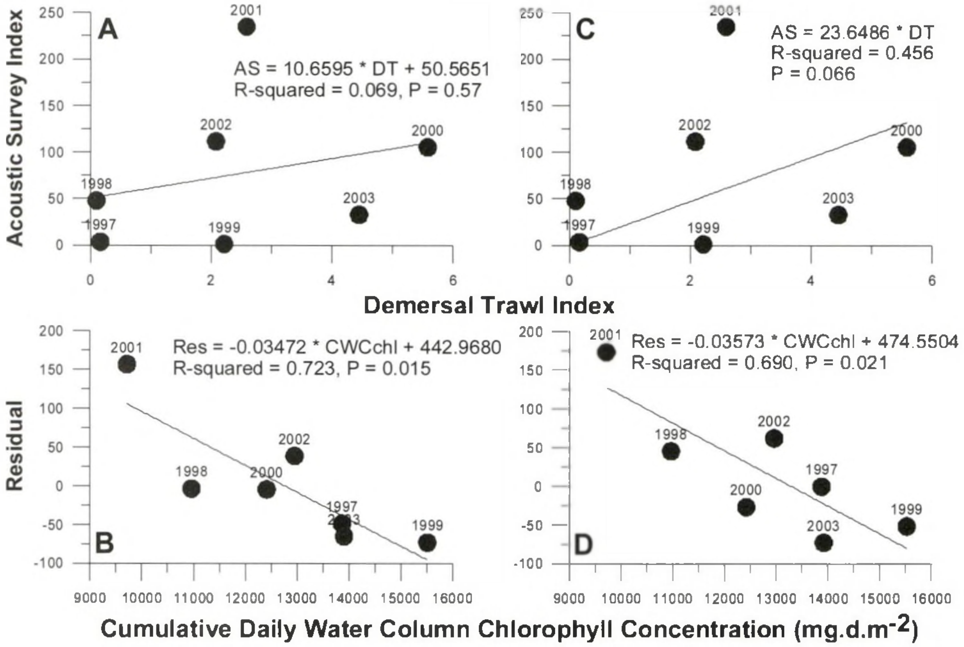


Figure 4.2.4. (A) The relationship between the demersal trawl indices and acoustic survey estimates of the biomass of 1+ sandeels in the study area. (B) Effect of cumulative daily whole water column chorophyll concentration (CDWWCCC) in the period leading up to the acoustic/demersal trawl surveys on the residuals of the relationship between the two survey index values shown in A. (C) Examination of the same relationship shown in A, but in this instance forcing the regression line through the origin. (D) Effect of CDWWCCC in the period leading up to the acoustic/demersal trawl surveys on the residuals of the relationship between the two survey index values shown in C.

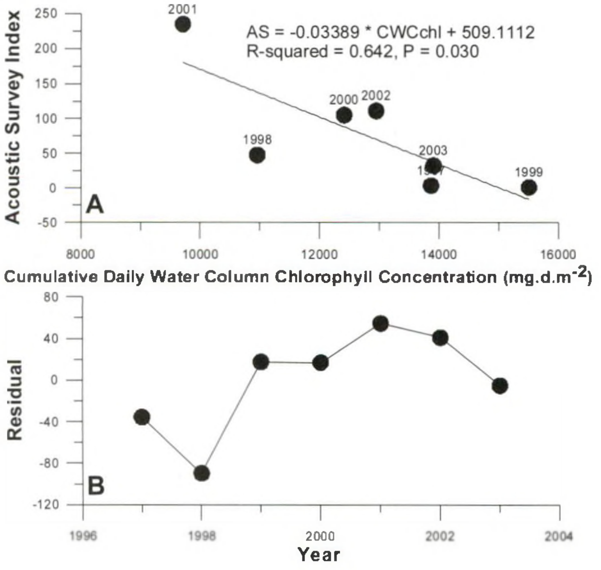


Figure 4.2.5. (A) The relationship between the acoustic survey estimate of the biomass of 1+ sandeels in the study area and the "feeding opportunity" available to sandeels prior to each survey as indicated by CDWWCCC. (B) Between year variation in the residuals from the relationship shown in A.

Fig. 4.2.4A shows the relationship between the acoustic survey and demersal trawl surveys. As anticipated from trends shown in Fig. 4.2.2, the correlation between the two indices was not significant, however 72% of residual variation between these two assessment methods could be explained by the CDWWCCC over the period leading up to each survey (Fig. 4.2.4B). As anticiapted by the hypothesis, high CDWWCCC prior to the survey results in low acoustic survey estimates relative to the demersal trawl index, and *vice versa*. This raises the possibility that much of the variation in the acoustic survey estimate of 1+ sandeel biomass shown in Fig. 4.2.2, rather than reflecting between year variation in the biomass of 1+ sandeels in the area, could instead be due to variation in the proportion of the sandeel population active in the water column, driven by differences in the timing of the acoustic/demersal trawl surveys relative to the start of the spring bloom, and consequent variation in the amount of feeding opportunity available to sandeels prior to the surveys. Relating the acoustic survey 1+ sandeel biomass estimates to CDWWCCC prior to the surveys suggested that this was indeed the case: approximately 64% of variance in the 1+ sandeel biomass estimate was explained by variation in CDWWCCC (Fig. 4.2.5A). Plotting the residuals from this relationship, in effect detrending the data and taking the effect of "feeding opportunity" prior to the surveys into account, perhaps provides a more realistic impression in the between year variation in 1+ sandeel abundance as indicated by the acoustic survey (Fig. 4.2.5B). However, in attempting to assess the total abundance of 1+ sandeels in the study area in each year, this still fails to take into account variation in the biomass of sandeels buried in the sediment.

The total sandeel biomass (B_{TOT}) present in the study area at the time of the summer surveys consists of two components, the fraction active in the water column (B_{WC}) and the fraction buried in the sediment (B_{SED}), thus:

$$B_{TOT} = B_{WC} + B_{SED} \qquad 1.$$

We are assuming that B_{WC} is assessed by the acoustic survey, and that the estimate provided by this survey (B_{AS}) is an absolute estimate of abundance, thus:

$$B_{WC} = B_{AS} \qquad 2.$$

We are also assuming that variation in B_{SED} is indicated by variation in the demersal trawl index of biomass (B_{DT}), thus:

$$B_{SED} \propto B_{DT} \qquad 3.$$

It is widely accepted that catch per unit effort (CPUE) data (such as provided by the demersal trawl survey), provides an index of the relative abundance of fish stocks and that, provided several assumptions are met, the relationship between CPUE and total stock abundance (N) is linear (King 1995), taking the form:

$$CPUE = q \, . \, N \qquad 4.$$

Unlike the general form of the equation for a linear relationship, equation 4 has no constant. The relationship is direct, passing through the origin, since it is obvious that if there are no fish present ($N = 0$), CPUE must be zero.

In respect of the demersal trawl surveys, the same fishing gear was used, fished by the same fishing officers and crew operating the same research vessel fishing the same 19 stations in each year. It therefore seems unlikely that there was any substantial variation in "fishing power" that might have influenced the performance of the demersal trawl biomass index. Furthermore, the Jackson rockhopper trawl used in these surveys had been in use for many years prior to this particular project, so no element of "learning" would have been involved. We might expect the distribution of sandeels to be non-random, being associated with particular types of seabed habitat. However, because the location of these habitats is unlikely to change substantially from year to year, fishing the same 19 stations should have resulted in the probability of fishing on sandeel seabed habitats remaining reasonably constant over the duration of the project. Thus the demersal trawl survey violates none of the assumptions underpining equation 4, and we should therefore expect this equation to hold true in respect of this survey. Since the same 19 stations were fished in each year, the only variation in effort that would have occurred between years would have been due to variation in the area swept by the gear and this was taken into account in the formulation of the demersal trawl biomass index. Thus, combining equations 3 and 4, we get:

$$B_{DT} = B_{SED} \, . \, q \qquad 5.$$

By rearranging equation 5 and combining it with equations 1 and 2, we have a model for estimating total 1+ sandeel abundance in the study area in each year. Thus:

$$B_{TOT} = B_{AS} + (B_{DT} \, . \, 1/q) \qquad 6.$$

If the proportions of 1+ sandeels buried in the sediment and active in the water column were "held" constant, then variation in both the acoustic survey biomass estimate and the demersal trawl biomass index should be directly proportional to variation in the total 1+ sandeel stock biomass, and the correlation between the two indices would be perfect at 1.0. Furthermore if the proportion of sandeels active in the water column was equal to the proportion buried in the sediment, ie the special case where 50% of the total stock is active in the water column and 50% is buried in the sediment, then the biomass of the two fractions would be identical, ie:

$$B_{WC} = B_{SED} \qquad 7.$$

Under these special circumstances, combining equation 2 and the rearranged equation 5 therefore holds:

$$B_{AS} = B_{DT} \, . \, 1/q \qquad 8.$$

Figure 4.2.4C shows this very relationship with the fitted regression forced through the origin to give the relationship:

$$B_{AS} = B_{DT} \, . \, 23.6486 \qquad 9.$$

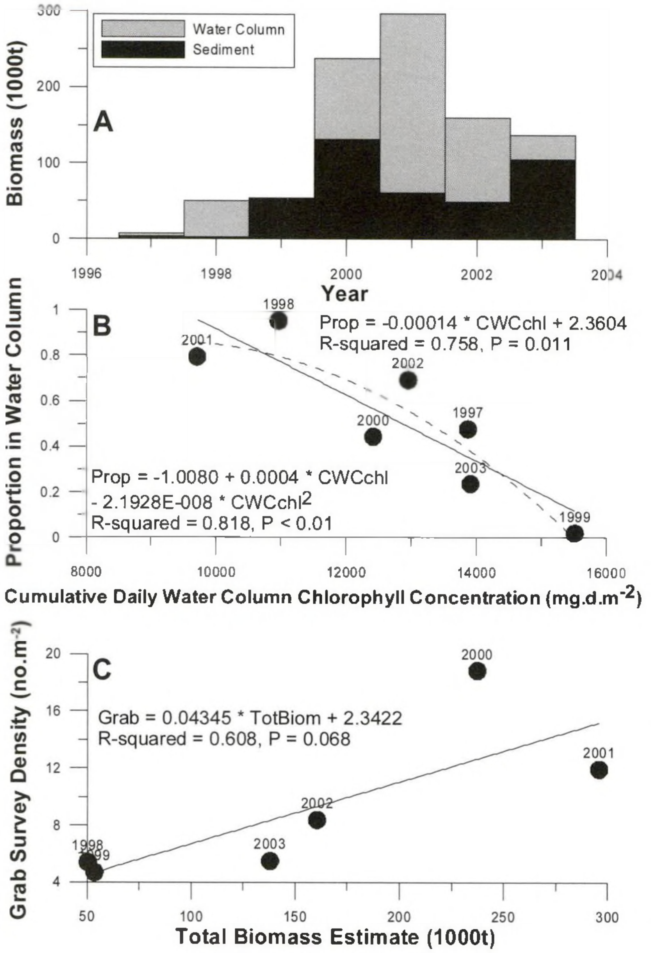


Figure 4.2.6. (A) Model output showing between year variation in the total biomass of 1+ sandeels estimated to be in the water column and in the sediment in the study area in each year over the period 1997 to 2003. (B) Relationship between the proportion of the 1+ sandeel population active in the water column and the CDWWCCC prior to each survey. (C) Relationship between model output total 1+ sandeel biomass and the density of 1+ sandeels assessed by nocturnal grab survey.

Providing this function describes the relationship where, on average, 50% of the total 1+ population is active in the water column and 50% is buried in the sediment, then it provides an estimate of the parameter 1/q in equations 6 and 8. How reasonable is this assumption? Firstly the correlation coefficient, $R = 0.675$, is far from perfect due, as already discussed, to the fact that the proportions of the 1+ sandeel population active in the water column and buried in the sediment are far from constant, being dependent on the total "feeding opportunity" available to sandeels prior to each survey. However, once again the residuals from the relationship depicted in panel C are significantly dependent on the CDWWCCC prior to each survey (Fig. 4.2.4D). In this case, although the R^2 value obtained of 0.690 is marginally lower than the value of 0.723 shown in panel B, the data points are more evenly distributed along both the X and the Y axes, providing rather more confidence in this relationship. In Fig. 4.2.4B the significance of the relationship between the residuals and CDWWCCC is heavily dependent on a single datum; 2001. Thus while it is clear that the fractions of the population in the water column and in the sediment are not constant at 50% in each, do they vary around an average of 50%? The data shown in Figs 4.2.2, 4.2.4 and 4.2.5 suggest that this must be close to being the case. In 1999 few sandeels were observed in the water column by the acoustic survey, whilst the demersal trawl index was relatively high. Thus in this year the proportion of 1+ sandeels in the water column must have been close to 0% and the proportion in the sediment close to 100%. In 2001, the reverse was clearly the case, with the proportion of the 1+ sandeel population in the sediment much closer to 0% and the proportion in the water column closer to 100%. Data for the remaining years suggest relatively evenly distributed variation between these two extremes, giving an average across all surveys close to 50% of the population in each medium. In conclusion then, the parameter 1/q in equations 6 and 8 is reasonably well estimated by the relationship obtained in Fig. 4.2.4C, and therefore equation 6, the model for estimating total 1+ sandeel biomass in the study area in each year, can be developed thus:

$$B_{TOT} = B_{AS} + (B_{DT} \,.\, 23.6486) \qquad 10.$$

Fig. 4.2.6A shows annual variation in the total biomass of 1+ sandeels determined by the model, with the biomass estimated in both in the water column and in the sediment shown seperately. Variation in the proportion of the population active in the water column was significantly related to the total "feeding opportunity" available to the sandeels prior to each acoustic/demersal trawl survey (Fig. 4.2.6B). The significant linear fit obtained between the proportion of sandeels in the water column and CDWWCCC suggested that as much as 76% of variance in the proportion of sandeels active in the water column at the time of each survey could be explained by variation in this index of the "feeding opportunity" available to 1+ sandeels. However, a polynomial relationship provided an even better fit, suggesting that as much as 82% of the variance in the proportion of sandeels in the water column could be explained by the CDWWCCC prior to each cruise. This latter fit also implies that, provided CDWWCCC prior to a survey is less than 11,000 day.mg.m^{-2}, an acoustic survey alone will provide a reasonably close estimate of the total biomass of sandeels in the area. Finally, in an attempt to validate this model, the total 1+ sandeel biomass estimate determined by the model was regressed on the estimates of mean 1+ sandeel density obtained from the October nocturnal grab surveys. A relatively strong correlation was obtained, suggesting that around 61% of the variance in grab survey sandeel density estimates could be explained by variation in the total biomass determined from the model. However, with one fewer grab survey data point available (no grab survey was carried out in October 1997), this correlation just failed to be statistically significant (*P*=0.068).

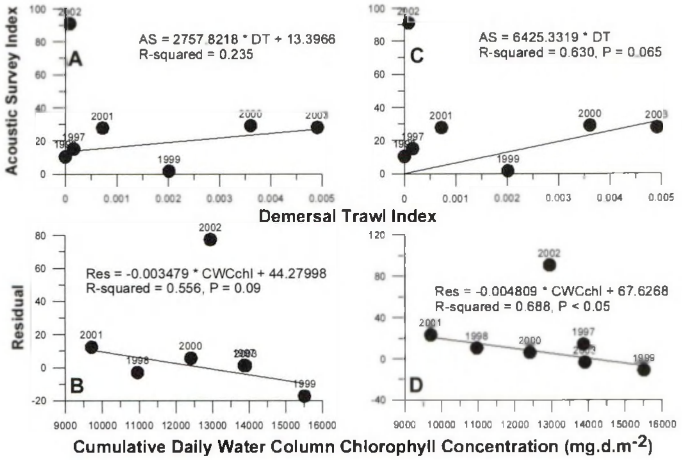


Figure 4.2.7. (A) The relationship between the demersal trawl indices and acoustic survey estimates of the biomass of 0 group sandeels in the study area. The outlier 2002 is excluded from the regression analysis. (B) Effect of cumulative daily whole water column chorophyll concentration (CDWWCCC) in the period leading up to the acoustic/demersal trawl surveys on the residuals of the relationship between the two survey index values shown in A. (C) Examination of the same relationship shown in A, but in this instance forcing the regression line through the origin. Again the outlier 2002 is excluded from the regression analysis. (D) Effect of CDWWCCC in the period leading up to the acoustic/demersal trawl surveys on the residuals of the relationship between the two survey index values shown in C.

The same approach was attempted with respect to 0 group sandeels . Fig. 4.2.7 shows the relationship between the two surveys with panel A depicting the standard regression and panel C the regression forced through the origin. In both cases the regressions were calculated with the extreme outlier 2002 excluded. In both instances, the residual variation from these relationships (excluding the 2002 outlier) was negatively correlated with the index of total "feeding opportunity" prior to the the surveys (Fig. 4.2.7B and D). In the case of the the residuals from the regression forced through the origin, the correlation was statistically significant (Fig. 4.2.7D). As with the 1+ age class sandeels, increasing CDWWCCC prior to the surveys reduced the acoustic survey biomass estimate relative to the demersal trawl survey biomass index, indicating that the an increasing fraction of the 0 group sandeel population was remaining in the sediment and not emerging to feed in the water column.

Variation in the acoustic survey estimate of 0 group sandeel biomass was not significantly related to CDWWCCC (Fig. 4.2.8A). Plotting the residuals from this regression against year produced a trend line (Fig. 4.2.8B) that was almost identical to the acoustic biomass estimate itself (Fig. 4.2.2). The acoustic survey 0 group sandeel biomass estimate was strongly influenced by year to year variation in the biomass of 0 group sandeels in the area, rather than by variation in the proportion of the sandeels remaining in the sediment as the "feeding opportunity" index increased. Nevertheless the significant relationship in Fig. 4.2.7D does suggest that the proportion of the 0 group sandeel population remaining in the sediment was increasing with increased CDWWCCC. These two apparently conflicting results are resolved if, on average across all surveys, the proportion of sandeels in the water column was higher than the proportion remaining in the sediments. The fitted trend line (Fig. 4.2.8A) suggests on average that, assuming 100% of 0 group sandeels are active in the water column at a CDWWCCC of 9000 day.mg.m^{-2}, this will have dropped to 45% at CDWWCCC values of around 15,000 day.mg.m^{-2}. On average, across all the cruises, 72.5% of 0 group sandeels would have been active in the water column, while 27.5% would have been buried in the sediment: a ratio of 2.6364.

We therefore have evidence that equation 7 does not hold, in fact the argument presented suggests instead that:

$$B_{WC} = 2.6364 \,.\, B_{SED} \qquad 11.$$

Thus equation 8 can be rewritten:

$$B_{AS} = B_{DT} \,.\, 1/q \,.\, 2.6364 \qquad 12.$$

The relationship shown in Fig. 4.2.7C provides the estimate for the parameter 1/q, but in this instance the plot does not represent the situation where BAS = BDT, rather it represents the situation where BAS = 2.6364 . BDT, so that equation 9 is rewritten thus:

$$B_{AS} = B_{DT} \,.\, 6425.3319 \,.\, 2.6364 \qquad 13.$$

Therefore the model for estimating total 0 group sandeel biomass is:

$$B_{TOT} = B_{AS} + (BDT \,.\, 6425.3319) \,.\, 2.6364 \qquad 14.$$

Fig. 4.2.9A shows variation in the model output estimate of total 0 group sandeel abundance in the study area at the time of the acoustic/demersal trawl surveys, again indicating the biomass in the water column and in the sediment seperately. In this instance variation in the proportion of the 0 group sandeel population that was active in the water column in each years was not significantly correlated with variation in CDWWCCC prior to each survey. However, the relationship was negative, suggesting some tendency for a decline in 0 group sandeel activity in the water column with increased total "feeding opportunity". The stronger correlation obtained by fitting a polynomial regression suggests that this decline in activity in the water column started to take place after a CDWWCCC of approximately 12,500 mg.d.m^{-2} (Fig. 4.2.9B). Validating the model estimates of total 0 group biomass against the 0 group density estimates obtained in the October grab surveys was not entirely convincing either. A positive correlation was obtained, but it was not statistically significant and the low R^2 value obtained suggested that only 15% of variation in 0 group density in October was explained by the model output estimate of 0 group biomass in summer (Fig. 4.2.9C).

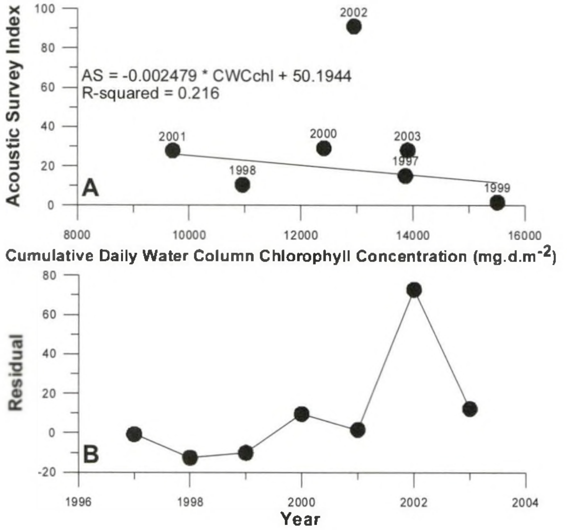


Figure 4.2.8. (A) The relationship between the acoustic survey estimate of the biomass of 1+ sandeels in the study area and the "feeding opportunity" available to sandeels prior to each survey as indicated by CDWWCCC. (B) Between year variation in the residuals from the relationship shown in A.

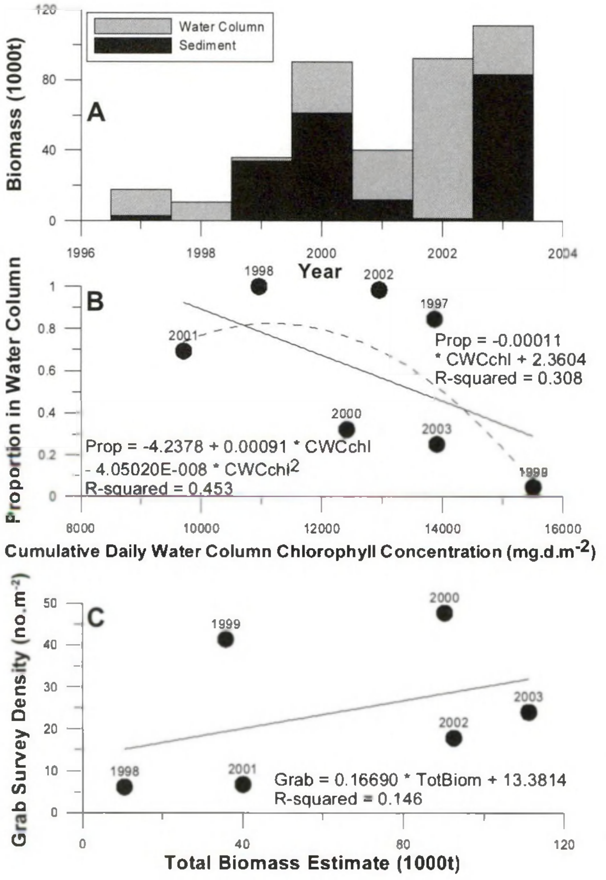


Fig. 4.2.9. (A) Model output showing between year variation in the total biomass of 0 gp sandeels estimated to be in the water column and in the sediment in the study area in each year over the period 1997 to 2003. (B) Relationship between the proportion of the 0 gp sandeel population active in the water column and the CDWWCCC prior to each survey. (C) Relationship between model output total 0 gp sandeel biomass and the density of 0 gp sandeels assessed by nocturnal grab survey.

In interpreting Fig. 4.2.8 we suggested that the acoustic survey alone might provide a reasonable estimate of interannual variation in 0 group sandeels biomass. However, correlation between the summer acoustic survey biomass and autumn grab survey density estimates was negative and the R^2 value even lower (Grab = -0.1022 * AS + 27.1437, $R^2 = 0.034$). In fact, despite our earlier reservations regarding the the ability of the demersal trawl to sample adequately small 0 group sandeels, variation in the demersal trawl survey 0 group biomass index provided a better predictor of variation in the autumn grab density estimates (Fig. 4.2.10). The linear correlation, although still not statistically significant, gave an R^2 value of 0.379, however a polynomial function provided a better and statistically significant fit ($R^2 = 0.751$, $P < 0.01$). Such a complex fit might be explained by considering the processes influencing the survival of 0 group sandeels. 0 group sandeels are the principal prey of many of the seabirds breeding in the vicinity of the study area (see later chapters). Furthermore, they also constitute a substantial fraction of the diets of the three major piscivorous fish predators in the area (Greenstreet in press). Thus favourable feeding conditions would enable 0 group sandeels to achieve an adequate body weight to survive through their first winter by an earlier date, enabling them to bury in the sediment earlier, and so reduce predation risk. Thus in years when the summer demersal trawl index registered a higher 0 group sandeel biomass in the sediment, 0 group survival through to October may have been higher. The downturn in the relationship might then be explained by some density dependence effect, whereby high abundances of 0 group sandeels in the sediment earlier on in summer might ultimately become counter productive, leading to reduced 0 group survival.

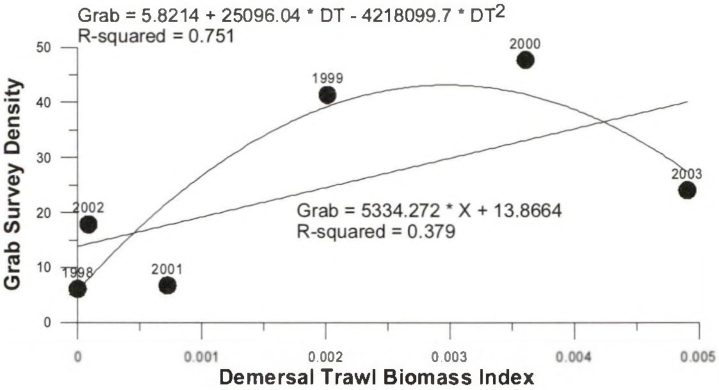


Figure 4.2.10. Relationship between the summer demersal trawl index of 0 group sandeel biomass and the autumn grab survey estimates of 0 group sandeel density.

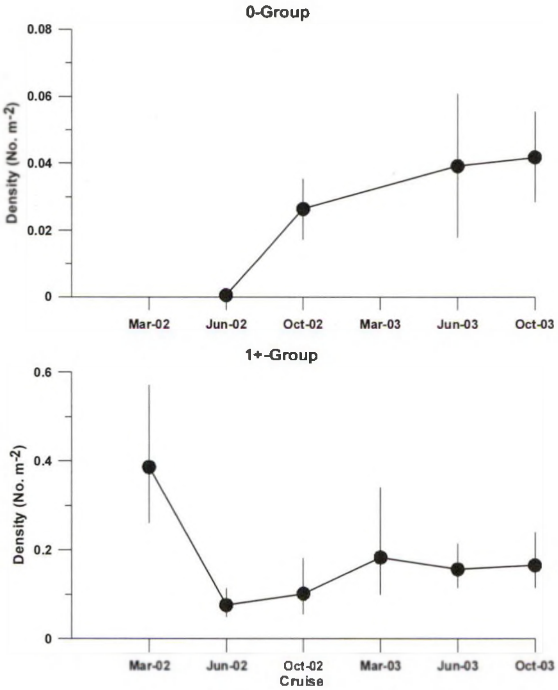


Fig. 4.2.11. Mean density (±1SE) of sandeels (no.m^{-2}) for the whole dredge survey area in 2002 and 2003. All statistics were calculated on log-transformed data but plotted on linear scale after back transformation.

Fig. 4.2.11 shows variation in the abundance of 0 and 1+ aged sandeels in the six **dredge surveys** carried out in 2002 and 2003. Samples densities were log-transformed to standardise variances and normalise the data. All analyses were carried out on the log-transformed data, however the graphs show the data plotted on a linear scale after back-transformation of the mean and upper and lower standard error values. One way ANOVA suggested no significant variation in the density of either 0 group or 1+ group sandeels between any of the cruises (confirmed with post-hoc Tukey tests comparing individual pairs of cruises). However, paired t-tests suggested that the density of 0 group sandeels was higher in October 2002 compared with June 2002 ($P < 0.05$), and that the density of 1+ group sandeels was higher in March 2002 compared with both later cruises in the same year ($P < 0.01$ in both instances). Because no significant differences between the June and October 1+ sandeel density estimates in each year were observed, these data were combined to make a more powerful between year comparison. However, a paired t test again indicated that any difference in the density of 1+ sandeels in the two years was not statistically significant. The model suggested that 1+ biomass in 2002 and 2003 differed little, despite both the acoustic and demersal trawl surveys suggesting quite marked variation, albeit in opposite directions, between the two years. The dredge data therefore tend to confirm the model estimates of total 1+ group biomass in these two years.

Herring *Clupea harengus*

Table 4.2.4 provides indices of total Herring abundance and biomass in the study area determined by the acoustic and demersal trawl surveys in each year. Variation in total Herring biomass indicated by the different surveys was significantly correlated (Fig. 4.2.12). Both survey techniques indicate a marked increase in total Herring biomass following closure of the sandeel fishery in 2000 (Mann Whitney $U = 12$, $P = 0.034$ in both instances). Variation in the Herring and sandeel acoustic survey total biomass estimates was significantly correlated ($R^2 = 0.738$, $P = 0.013$), but this was not the case with respect to the demersal trawl indices ($R^2 = 0.302$, $P = 0.202$).

In Table 4.2.5 the total Herring biomass in each year is partitioned into two age group components, 0 group Herring and Herring aged 1+. When the two age groups were considered separately, the significant correlation between the two survey types was lost (0 group $R^2 = 0.013$, 1+ group $R^2 = 0.001$). However, in both cases the year 2001 was a major outlier. In 2001 the highest recorded acoustic survey estimate of 0 group Herring biomass was obtained, yet the demersal trawl survey indicated a biomass of zero (Fig. 4.2.13). Conversely, the 2001 acoustic survey estimate of 1+ Herring biomass was the lowest recorded, yet the demersal trawl survey suggested that the abundance of 1+ Herring in this year was higher than in any other year. When the year 2001 was excluded from the two correlation analyses, both R^2 values were markedly improved, and in the case of the 1+ Herring analysis, the correlation between the two survey types was statistically significant. In 2001 over 90% of the Herring acoustic integral was associated with a single pelagic trawl sample in which 0 group Herring dominated the Herring catch. No such fish were sampled in the demersal trawl survey.

Table 4.2.4. Between year variation in the indices of total abundance and biomass of Herring in the study area derived from acoustic and demersal trawl survey techniques.

Year	Acoustic Survey		Demersal Trawl	
	Numbers (100 million)	Biomass (tonnes)	Numbers (million)	Biomass (tonnes)
1997	12.289	3,825	33.56	599.87
1998	1.231	3,173	59.37	1025.08
1999	6.137	1,703	13.21	414.28
2000	10.387	5,843	112.06	2779.31
2001	62.874	6,371	118.43	4614.57
2002	1.801	4,910	54.86	1892.19
2003	1.321	3,950	79.49	2154.55

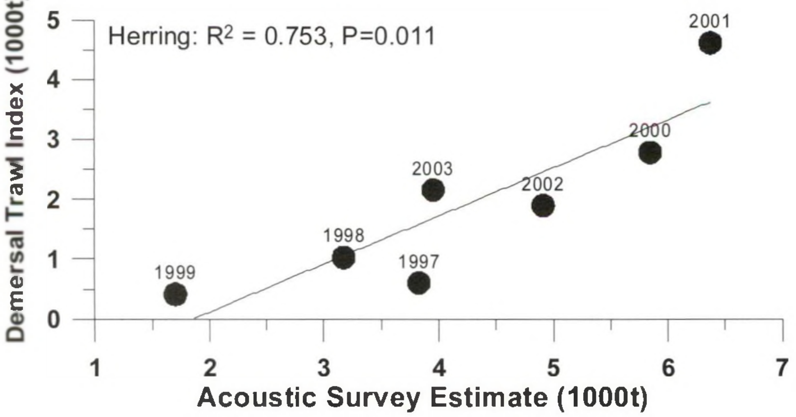


Figure 4.2.12. Relationship between the estimates of total Herring biomass obtained by the acoustic and demersal trawl surveys.

Table 4.2.5 Between year variation in the indices of total abundance and biomass of 0 group and 1+ group Herring in the study area derived from each survey technique.

Year	Age	Acoustic Survey		Demersal Trawl	
		Numbers (100 million)	Biomass (tonnes)	Numbers (million)	Biomass (tonnes)
1997	0 group	11.911	2867	2.886	9.55
1998		0.000	0	0.000	0.00
1999		6.078	1229	0.000	0.00
2000		9.033	2081	6.237	15.83
2001		63.509	6223	0.000	0.00
2002		0.440	90	0.043	2.78
2003		0.000	0	0.254	0.49
1997	1+ group	0.377	958	30.677	590.32
1998		1.714	3173	59.371	1025.08
1999		0.159	474	13.208	414.28
2000		1.599	3763	105.826	2763.48
2001		0.038	148	118.429	4614.57
2002		1.437	4820	54.813	1889.41
2003		1.377	3950	79.233	2154.05

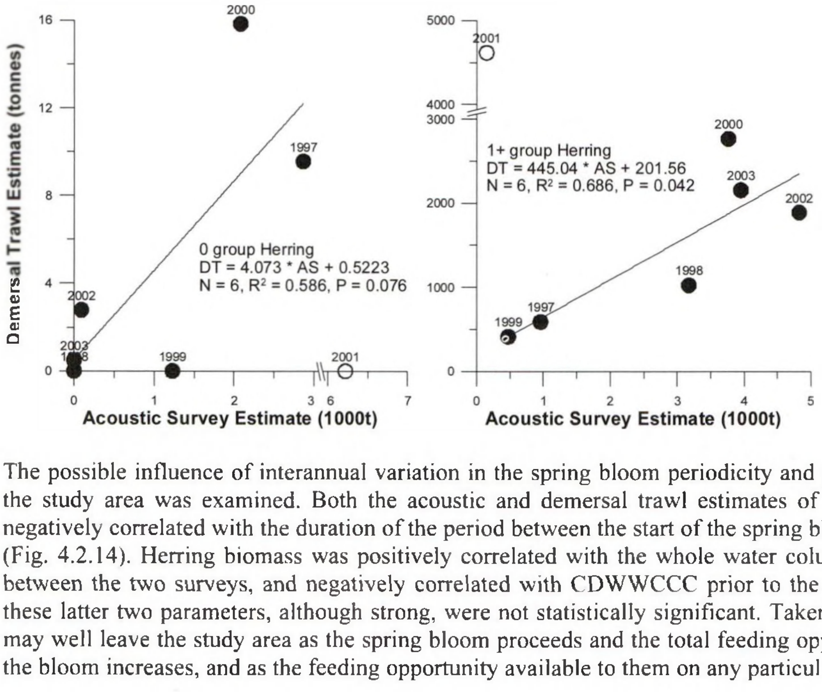


Figure 4.2.13. Relationship between the estimates of 0 group and 1+ group Herring biomass obtained by the acoustic and demersal trawl surveys. Outlier year 2001 (open circle) has been excluded from the regression in both instances.

The possible influence of interannual variation in the spring bloom periodicity and productivity on the biomass of Herring in the study area was examined. Both the acoustic and demersal trawl estimates of total Herring biomass were significantly negatively correlated with the duration of the period between the start of the spring bloom and the day between the two surveys (Fig. 4.2.14). Herring biomass was positively correlated with the whole water column chlorophyll concentration on the day between the two surveys, and negatively correlated with CDWWCCC prior to the surveys. The correlations with respect to these latter two parameters, although strong, were not statistically significant. Taken together, these data suggest that Herring may well leave the study area as the spring bloom proceeds and the total feeding opportunity experienced over the duration of the bloom increases, and as the feeding opportunity available to them on any particular day declines.

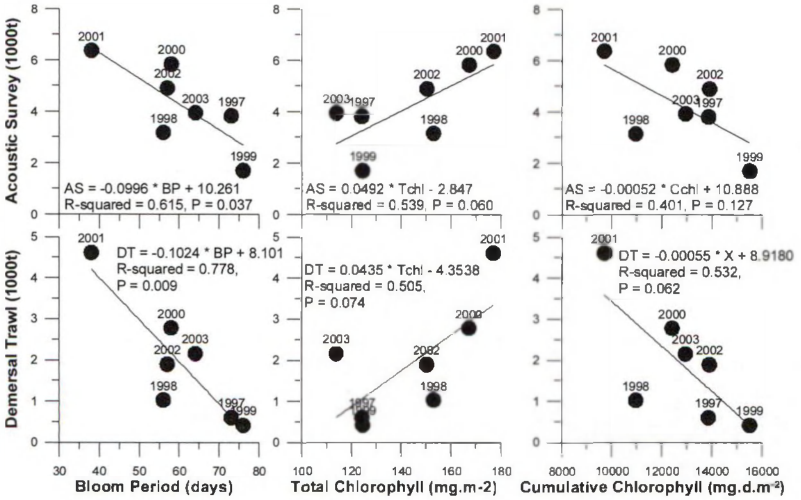


Fig. 4.2.14. Relationships between the estimates of total Herring biomass obtained by the both the acoustic and demersal trawl surveys with three parameters output from the 1D hydrography model: the duration of the period between the start of the spring bloom and the day between the acoustic and demersal trawl surveys; the whole water column chlorophyll concentration on the day between the acoustic and demersal trawl surveys; and the cumulative daily whole water column chlorophyll concentration in the period prior to the day between the acoustic and demersal trawl surveys.

Sprat *Sprattus Sprattus*

Table 4.2.6 provides indices of total Sprat abundance and biomass in the study area determined by the acoustic and demersal trawl surveys in each year. Variation in total Sprat biomass indicated by the different surveys was not significantly correlated ($R^2 = 0.127$, $P = 0.433$). Both surveys suggest that the biomass of Sprats in all years was relatively low. In such a situation where the assessment methods were attempting to track what was essentially a weak signal, the noise associated with any sampling error was probably sufficient to mask the signal in each case. Thus the likelihood of interannual variation in the estimates provided by the two surveys being correlated would be low. Neither survey suggested that variation in the biomass of Sprats was in any way related to the sandeel fishery management regime.

Table 4.2.6. Between year variation in the indices of total abundance and biomass of Sprats in the study area derived from acoustic and demersal trawl survey techniques.

Year	Acoustic Survey		Demersal Trawl	
	Numbers (100 million)	Biomass (tonnes)	Numbers (million)	Biomass (tonnes)
1997	4.173	2,606	131.26	805.23
1998	3.117	2,999	185.40	1055.83
1999	0.034	14	88.48	514.50
2000	3.803	2,468	58.79	341.26
2001	1.712	1,347	69.63	568.56
2002	0.853	451	71.03	422.37
2003	0.946	647	143.29	802.11

In Table 4.2.7 the total Sprat biomass in each year is broken down into two age components, 0 group Sprats and Sprats aged 1+. 0 group Sprats were rarely recorded in the study area. Both survey types indicated that the Sprat population in the study area consisted in all years almost entirely of fish aged 1+. Because of this, since the correlation between the total biomass estimates derived from each survey type were not correlated, interannual variation in the biomass of 1+ Sprats determined by the two surveys was not significantly related. Sprat biomass in the study area appeared unrelated to any interannual variation in the periodicity or productivity of the spring bloom as predicted by the 1D hydrography model.

Table 4.2.7. Between year variation in the indices of total abundance and biomass of 0 group and 1+ group Sprats in the study area derived from each survey technique.

Year	Age	Acoustic Survey		Demersal Trawl	
		Numbers (100 million)	Biomass (tonnes)	Numbers (million)	Biomass (tonnes)
1997	0 group	0.000	0	0.230	0.37
1998		0.000	0	0.000	0.00
1999		0.000	0	0.000	0.00
2000		0.000	0	0.000	0.00
2001		0.000	0	0.006	0.01
2002		0.012	3	0.139	0.32
2003		0.000	0	0.000	0.00
1997	1+ group	4.173	2606	131.031	804.86
1998		4.338	2999	185.402	1055.83
1999		0.035	14	88.482	514.50
2000		3.893	2468	58.789	341.26
2001		1.833	1347	69.621	568.55
2002		0.877	448	70.894	422.05
2003		0.986	647	143.287	802.11

4.3 Variation in forage fish size

Appendix 4 provides detailed information regarding the proportion of each species at age, and the abundance and biomass of each species at length and age. In this section between year variation in the length and weight of sandeels, Herring and Sprats, as determined by the various survey methods employed, is considered and summarised.

Sandeels *Ammodytus marinus*

Table 4.3.1 gives the estimates of mean length and weight of sandeels belonging to each of the four age groups determined from the summer acoustic and demersal trawl surveys, and from the autumn grab survey. The correlation matrix exploring co-variation between the various sets of estimates is provided in Table 4.3.2. Few significant correlations were detected. Co-variation between the acoustic and demersal trawl survey estimates of mean length was statistically significant with respect to 2 group sandeels, and almost significant with respect to 0 group sandeels. For all other comparisons the correlations were weak, and in one instance, apparently negative!

Table 4.3.1.The mean length and weight estimates for each age class of sandeels that were determined in each year from the summer acoustic and demersal trawl surveys, and the autumn nocturnal grab survey.

Age	Year	Length (mm) Acoustic	Length (mm) Demersal trawl	Length (mm) Grab survey	Mass (g) Acoustic	Mass (g) Demersal trawl	Mass (g) Grab survey
0	1997	6.39	6.76		0.76	0.89	
group	1998	4.55		7.35	0.28		1.11
	1999	6.13	6.96	7.48	0.69	1.04	1.18
	2000	7.02	8.19	7.66	0.97	1.63	1.05
	2001	6.76	7.09	7.18	0.82	1.41	0.88
	2002	5.95	5.58	7.17	0.59	0.48	0.85
	2003	6.32	5.62	7.48	0.69	0.49	1.05
1	1997	11.12	14.99		4.59	11.38	
group	1998	12.41	12.94	10.77	6.15	7.04	3.42
	1999	10.32	11.09	10.31	3.40	4.28	3.13
	2000	10.87	11.81	11.15	4.28	5.50	3.94
	2001	10.32	10.22	10.38	3.34	3.73	2.82
	2002	10.15	12.19	10.03	3.28	6.28	2.43
	2003	10.49	11.94	11.34	3.65	5.61	4.11
2	1997		16.23			14.65	
group	1998	13.45	14.96	13.59	7.91	10.95	7.66
	1999	12.26	13.57	13.62	6.01	7.95	7.71
	2000	12.79	14.32	14.06	7.67	10.26	8.40
	2001	12.31	13.53	12.97	6.08	8.69	6.04
	2002	12.88	13.95	13.13	7.21	9.30	6.55
	2003	12.21	13.69	12.56	5.99	8.76	5.76
3	1997		17.67			19.35	
group	1998	16.30	16.89	14.57	14.20	15.91	10.11
	1999	14.51	14.60	16.89	10.16	10.11	14.51
	2000	14.13	16.09	15.50	11.25	15.34	11.83
	2001	14.19	16.78	15.17	10.25	16.46	10.33
	2002	14.21	15.40	15.59	9.74	12.75	11.20
	2003	13.69	15.13	14.94	8.71	12.08	9.65

Table 4.3.2. Matrix of correlation coefficients and corresponding probabilities comparing interannual variation in the mean length of sandeels at age derived from the summer acoustic and demersal trawl surveys and the autumn grab survey.

Age	Survey	Survey Acoustic Survey	Demersal Trawl	Acoustic Survey	Demersal Trawl
		Correlation coefficients		Probability (*P*)	
0 group	Demersal Trawl	0.806		0.053	
	Autumn Grab Survey	0.275	0.525	0.597	0.364
1 group	Demersal Trawl	0.511		0.241	
	Autumn Grab Survey	0.326	0.280	0.528	0.591
2 group	Demersal Trawl	0.945		0.004	
	Autumn Grab Survey	0.471	0.523	0.346	0.287
3 group	Demersal Trawl	0.517		0.294	
	Autumn Grab Survey	-0.309	-0.717	0.551	0.109

Both the acoustic and demersal trawl surveys indicated the largest mean lengths of 1, 2 and 3+ group sandeels in 1997 and 1998, suggesting a possible fishing interaction. By removing a large quantity of these older aged fish, fishing may have reduced density dependence, allowing the survivors increased access to food, thereby enabling them to grow faster. Alternatively, larger fish within each cohort, with less requirement for further growth, could have buried into the sediment earlier, and so reduced their fishing mortality rates.

Table 4.3.3. Results of paired t-test analysis comparing estimates of mean length at age derived from the acoustic and demersal trawl surveys.

Age	Mean of annual mean lengths Acoustic Survey	Demersal Trawl Survey	Paired *t* test Probabilities (*P*)
0 group	6.43	6.70	0.389
1 group	10.81	12.17	0.033
2 group	12.65	14.00	0.000
3+ group	14.51	15.82	0.017

Sandeels sampled by the demersal trawl tended to have a larger mean length than sandeels sampled by the pelagic trawl during the acoustic surveys. (Table 4.3.3). The larger mesh size in the demersal trawl could be the explanation for this if the difference was restricted to just the smaller younger age class fish, but catchability ogives are normally relatively steep, thus larger fish should all be retained by both trawls. The fact that the difference is most pronounced among the older age classes suggests that the two gears are sampling different components of the sandeel population.

It is assumed that sandeels, which have reached an optimum size that should allow them to survive the following winter, will reduce their water column feeding activity and increasingly tend to remain buried in the sediment. The basis for this assumption is that buried sandeels have reduced predation mortality and lowered metabolic costs. It is further assumed that the acoustic survey samples sandeels active in the water column, while the demersal trawl samples sandeels buried in the sediment. Early in the season, sandeels will have had little chance to feed and so any difference in the size of sandeels sampled by the two gears should be minimal. As the season progresses, the larger and faster growing fish in each age class will increasingly remain in the sediment, and the difference in size between the sandeels sampled by the two methods should increase. But as the season progresses further, sandeels continuing to feed in the water column should continue to grow and the difference in size between the sandeel sampled by the acoustic and demersal trawl surveys should start to decline. Thus the model predicts that the relationships between the differences in mean length at age of sandeels sampled by the two methods and variation in total "feeding opportunity" available to sandeels prior to the surveys (CDWWCCC) should be unimodal. For the three older age classes of sandeels, this hypothesis was up-held: polynomial regressions provided better fits to all three sets of data. Furthermore, the deflexion points moved progressively to the left with increase in sandeel age. Older larger sandeels, with less need to grow further to survive the coming winter, would appear to reduce their feeding activity in the water column earlier on in the feeding season than younger, smaller fish. 0 group sandeels did not fit this pattern but, as discussed above, a much larger proportion of this age group of sandeels remained active in the water column through out the summer period. Table 4.3.1 also suggests that 0 group fish were continuing to increase in length over the period between the summer acoustic/demersal trawl surveys and the autumn grab surveys, whilst that was not case for the three older age groups. This confirms the interpretation that 0 group fish were continuing to feed in the water column after the time of the summer surveys.

Table 4.3.4. The mean length at age of sandeels determined from summer nocturnal grab survey in the three years that such surveys were carried out.

Age	Year	Mean	SE of Mean
0 group	1998	6.62	0.31
	1999	6.23	0.10
	2000	6.43	0.14
1 group	1998	10.97	0.38
	1999	10.79	0.34
	2000	11.18	0.22
2 group	1998	14.05	0.60
	1999	14.33	0.79
	2000	14.21	0.40
3 group	1998	16.71	0.41
	1999	17.21	0.83
	2000	16.94	1.03

Grab surveys were also carried out in the summers of 1998, 1999 and 2000. Although these data were considered unreliable with regard to the provision of density estimates, they still provide estimates of mean length at age for more direct comparison with similar estimates provided by the acoustic and demersal trawl surveys carried out at a similar time of year Table 4.3.4. These data also strongly support the contention that 0 group sandeels were continuing to increase in length between the summer and autumn surveys, whilst the older aged sandeels were not.

Variation in mean sandeel length at age over the six dredge surveys was examined. The data are presented in two ways. Fig. 4.3.1 shows the mean length of each age class in each survey, while Fig. 4.3.2 follows change in the mean length of individual cohorts over the course of the two years. The data again suggest that in both years 0 group sandeels continued to increase in length between the June and October surveys (one way ANOVA and post hoc Tukey's test, $P < 0.001$ in both instances). 1, 2 and 3+ group sandeels either continued to grow, showed no change in length, or even appeared to shrink over the June to October period of both years, however, any significant changes in length were relatively minor. In both years the greatest increase in the length of 1, 2 and 3+ sandeels occurred between March and June (one way ANOVA and post hoc Tukey's test, $P < 0.001$ in all instances). Fig. 4.2.17 suggests that 0 group sandeels continued to grow through the winter period from October to March (one way ANOVA and post hoc Tukey's test, $P < 0.001$). However, the apparent increase in the length of these fish (the 2002 cohort) could also explained by variable mortality rates related to fish size. Higher mortality rates among smaller 0 group sandeels compared with larger 0 group fish could bring about the same increase in mean length.

Herring *Clupea harengus*

Table 4.3.5 summarises the mean length and weight data of the different Herring age groups determined in each year from the acoustic and demersal trawl surveys. Where the data were adequate to do so, interannual variation in the mean length of Herring determined by the two different survey techniques were found to be significantly correlated (1 group Herring, $R = 0.889$, $P = 0.007$; 2+ group Herring $R = 0.99$, $P = 0.001$). Neither the plankton bloom period duration or cumulative daily whole water column chlorophyll concentration prior to the surveys, or the whole water column chlorophyll concentration at the time of the surveys, output from the 1D hydrography model, appeared to have any significant effect on the mean length and weight of Herring of any age group determined by either survey method.

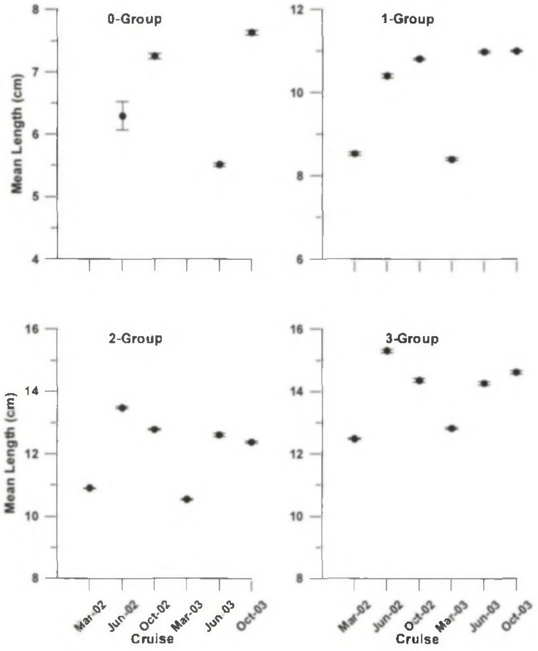


Fig. 4.3.1. Variation in mean length (± SE) at age of sandeels caught in the whole dredge study area in 2002 and 2003.

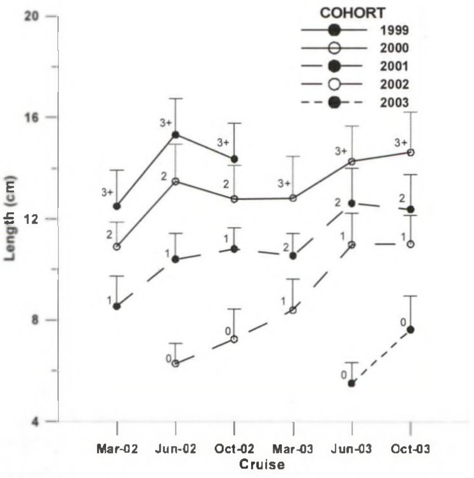


Fig. 4.3.2. Variation in the mean length (±SD) at age of different sandeel cohorts in the whole dredge survey area in 2002 and 2003. Labels indicate fish age. The 3+ aged fish will include fish from the indicated cohort and from older cohorts

Table 4.3.5. The mean length and weight estimates for each age class of Herring that were determined in each year from the summer acoustic and demersal trawl surveys.

Age	Year	Length (mm)		Mass (g)	
		Acoustic survey	Demersal trawl	Acoustic survey	Demersal trawl
0	1997	7.25	7.99	2.41	3.31
	1998				
	1999	7.05		2.02	
	2000	7.21	7.45	2.30	2.54
	2001	5.47		0.98	
	2002	6.56		2.04	
	2003	6.00	6.72	1.28	1.95
1	1997	14.92	13.65	25.10	18.50
	1998	13.82	13.57	18.52	17.27
	1999	16.02	16.25	29.87	31.35
	2000	14.67	15.09	23.53	26.11
	2001	17.21	16.82	38.47	37.42
	2002	15.76	16.05	32.02	32.54

Age	Year	Length (mm)		Mass (g)	
		Acoustic survey	Demersal trawl	Acoustic survey	Demersal trawl
	2003	15.51	15.21	28.59	26.88
2	1997	18.04		44.94	
	1998	18.00	18.00	42.16	42.16
	1999	19.00	19.00	51.54	51.54
	2000				
	2001	19.59	20.19	58.26	66.73
	2002	22.92	23.12	100.08	105.46
	2003	20.63	21.22	72.15	79.05

Table 4.3.6. The mean length and weight estimates for each age class of Sprat that were determined in each year from the summer acoustic and demersal trawl surveys.

Age	Year	Length (mm)		Mass (g)	
		Acoustic	Demersal Trawl	Acoustic Survey	Demersal Trawl
0 group	1997		6.00		1.60
	1998				
	1999				
	2000				
	2001	5.50	5.50	1.23	1.52
	2002	6.71	6.71	2.33	2.33
	2003				
1 group	1997	9.16	9.08	5.93	5.78
	1998	9.60	8.97	6.35	5.12
	1999	7.91	8.81	3.65	5.13
	2000	9.23	9.29	6.30	5.79
	2001	9.14	8.70	5.64	5.63
	2002	8.47	9.02	4.79	5.71
	2003	9.50	9.00	6.49	5.53
2 group	1997	10.48	10.41	8.59	8.52
	1998	10.36	10.43	7.86	8.15
	1999	10.35	10.17	8.24	7.78
	2000	10.81	10.80	9.67	9.02
	2001	10.64	10.93	8.90	10.34
	2002	11.29	11.01	11.39	10.65
	2003	10.01	9.66	7.61	7.00

Sprats *Sprattus Sprattus*

Table 4.3.6 summarises the mean length and weight data of the different Sprat age groups determined in each year from the acoustic and demersal trawl surveys. Variation in the mean length of 1 group Sprats determined by the two survey methods was only weakly correlated, however, the two estimates of 2+ group Sprat mean length were significantly correlated ($R = 0.89$, $P = 0.007$). Neither the plankton bloom period duration or cumulative daily whole water column chlorophyll concentration prior to the surveys, or the whole water column chlorophyll concentration at the time of the surveys, output from the 1D hydrography model, appeared to have any significant effect on the mean length and weight of 1 and 2+ Sprats determined by acoustic survey. The same held for the demersal trawl Sprat biomass estimates with one exception. 2+ Sprat mean length appeared to be positively correlated with the whole water column chlorophyll concentration at the time of the surveys ($R = 0.84$, $P = 0.019$). Given that the length of fish of this age is most likely to be heavily influenced by an accumulation of vary conditions earlier on in life, the length of this age group of fish was the least likely to by directly affected by current growth conditions. Furthermore, since high whole water column chlorophyll concentrations tended to be associated with earlier phases of the spring bloom, the direction of this relationship ran counter to expectations. At present therefore this single significant result is tentatively put down to a type 1 error, to be expected given the number of correlation analyses actually performed.

4.4 Sandeel abundance and distribution east of Scotland, 2001-2004

FRV *Tridens* provided a platform for sea-based seabird surveys in the western part of the central North Sea during the ICES coordinated international hydro acoustic survey for Herring in 1991-2004 (Camphuysen 2005). The acoustic data collected as a routine, used to estimate the spawning stock of Herring en Sprat by means of echo integration, were analysed to make an abundance estimate and to provide spatial patterns of sandeels during, 2001-2004 (Appendix 9). The idea was to provide a broad image of sandeel distribution over a wider area and to evaluate the variability in broad scale spatial patterns over the years.

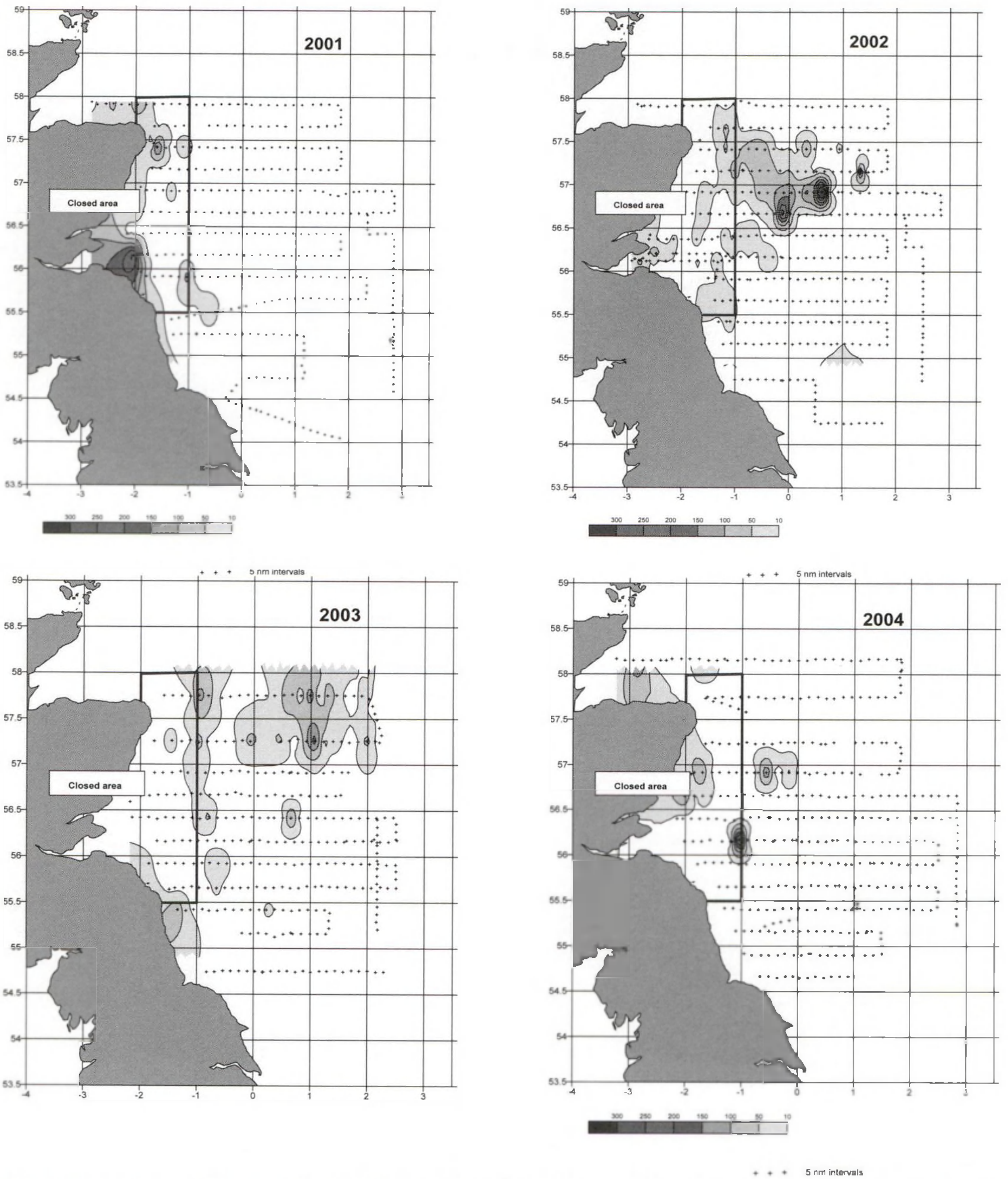


Figure 4.4.1. Relative distribution of sandeelS during the North Sea Hydro Acoustic Survey for Herring and Sprat in the area surveyed by FRV "Tridens". Contour units are Nautical Area Scattering Coefficients (NASC's: m^2/nm^2).

Spatial patterns were different in each of the years of survey. High concentrations of sandeels in the water column occurred much closer to the coast in 2001 and 2004 than in 2002 and 2003 (Fig. 4.4.1). In 2001 the main concentrations were found on Wee Bankie and towards the coast to the east of Bass Rock. In 2002, the year when the Wee Bankie area was particularly well covered, the main concentrations were found far offshore and north of the Devil's Holes. In 2003 the distribution pattern was more spread out over an even larger area in northeastern direction. 0-group sandeels sampled in 2002 were 5% shorter and 30% less in body mass than 0-group sandeels sampled in 2003, which is roughly in accordance with patterns found earlier in each year during acoustic surveys in the principal study area.

Assigning echo's to sandeel is problematic. The acoustic Target strength of a sandeel is very low compared to fishes with a swimbladder. The applied target strength (Anon. 2004) of a sandeel, is approximately 180 times as low as a Sprat or Herring of the same length. This means that concentrations of sandeel that are "polluted", even if only slightly, with Sprat/Herring may result in a biased abundance estimate of sandeel. Most likely, the amount of sandeel is overestimated. Normally surface schools of sandeel are fairly good recognizable, but some faulty identification is unavoidable. Therefore the contour-plots in figure 2, are presented in acoustic values, NASC's. The plots give approximate distribution patterns. Some concentrations were found at the end of a transect, close to the coast. Transects stopped there because Herring is not expected so close to the coast. It is possible that one would have recorded much more sandeel along coast if the transects would have been extended towards the shore. Only in 2002, survey transects were extended into the Firth of Forth. Relatively few sandeel were recorded in that year.

4.5 Discussion

In all the analyses presented above where the operation or not of a sandeel fishery was used as a categorical variable to explore the effects of the fishery, 1999 was treated as a "fishery in operation" year. Technically this is correct since the fishery was not closed until 2000. However, this is somewhat misleading. Although still legally allowed to operate in the area, fishing effort in the area was much lower and the total sandeel catch taken was actually no higher than the catches made for scientific monitoring in all the ensuing years when the area was technically closed to fishing. Thus for example, when comparing the Demersal trawl biomass estimates in fishery and non-fishery years, no significant effect of the fishery was detected. This was because the 1999 index exceeded the 2002 value. 1999 was treated as a fishing year, but in fact the impact of the fishery in 1999 was little different from the impact in 2002. The two years during the course of this study when sandeel removals by the fishery were particularly high, 1997 and 1998, produced the two lowest demersal trawl index values in the time series.

Field work on board FRV Clupea (courtesy Marine Laboratory Aberdeen)

Chapter 5 Setting the scene (3): colony based and at-sea data on seabirds

5.1 Introduction

The aim of this chapter is to set the scene for the work on avian predators by presenting results of the long-term monitoring both for the breeding colonies and the at-sea surveys. These results form the basis of the more detailed analysis in chapters 7 and 8, where the data are integrated with information on the physical environment, lower trophic levels and fish, and where the importance of marine climate and the sandeel fishery for seabird breeding phenology and success are examined.

5.2 Breeding population trends, 1997-2003

Population size

Whole colony counts of Shags, Kittiwakes and Guillemots were carried out each year by Scottish Natural Heritage on the Isle of May, using standard methods (Walsh et al. 1995; Fig 5.2.1). Whole colony counts of Gannets on the Bass Rock were carried out in 1994 (Murray & Wanless 1997) and 2004 (Wanless et al. 2004) and indicated that numbers increased from 39 751 to 48 065 apparently occupied sites (AOSs). Assuming a constant rate of increase over the period indicated that there were c45 000-48 000 AOSs on the Bass Rock during the IMPRESS project. Breeding population trends differed among the four species. Counts of Shag nests declined sharply in 1999 due to a large proportion of adults not breeding that year, a regular occurrence in this species (Aebischer 1986), but numbers subsequently increased. Breeding populations of Guillemots and Gannets both increased markedly. In contrast, there was a continuous decline in Kittiwake numbers between 1997 and 2003.

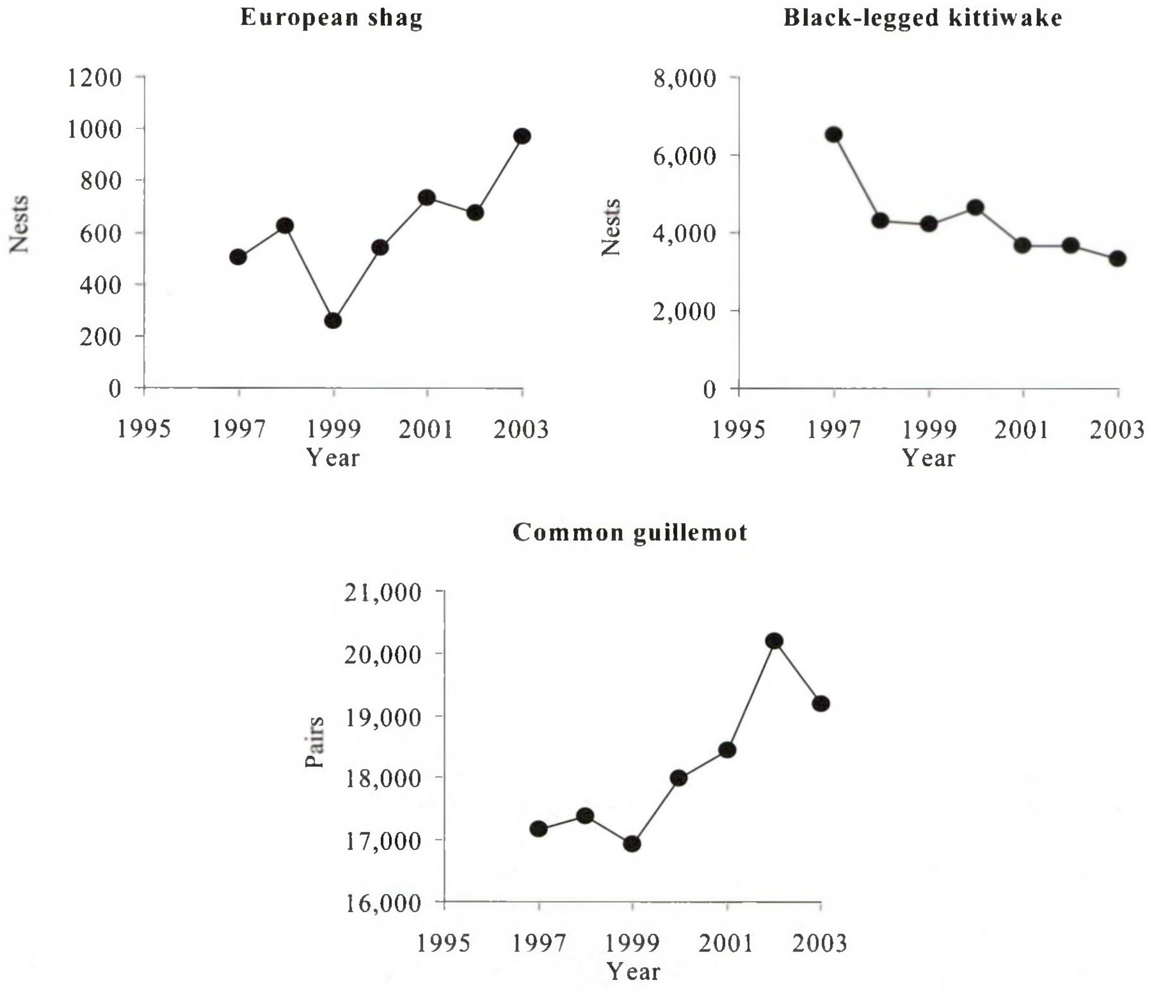


Figure 5.2.1 Breeding population size of the four study species between 1997 and 2003.

Breeding success

Breeding success was recorded for each species using standard protocols (Walsh *et al.* 1995). Shags showed a general increase in breeding success over the period, except for the non-breeding year in 1999 when success was low. In contrast, Guillemot breeding success showed an overall decline. The number of chicks fledged per pair in Kittiwake was very variable, but there was no clear trend during the study period (Fig. 5.2.2). Breeding success of Gannets on the Bass Rock was only available for 2002 and 2003 but, as in previous years, was consistently high (Nelson 2002). Breeding success during the three IMPRESS field seasons (2001-2003) also varied markedly among the species. Breeding success of Shags was the highest recorded at the Isle of May over the last 20 years. In contrast, values for Guillemots were some of the lowest recorded. Kittiwake breeding success fluctuated, but was generally higher than during the late 1990s. Breeding success was higher in 2003 than in 2002 or 2001 in all four species (Fig. 5.2.2).

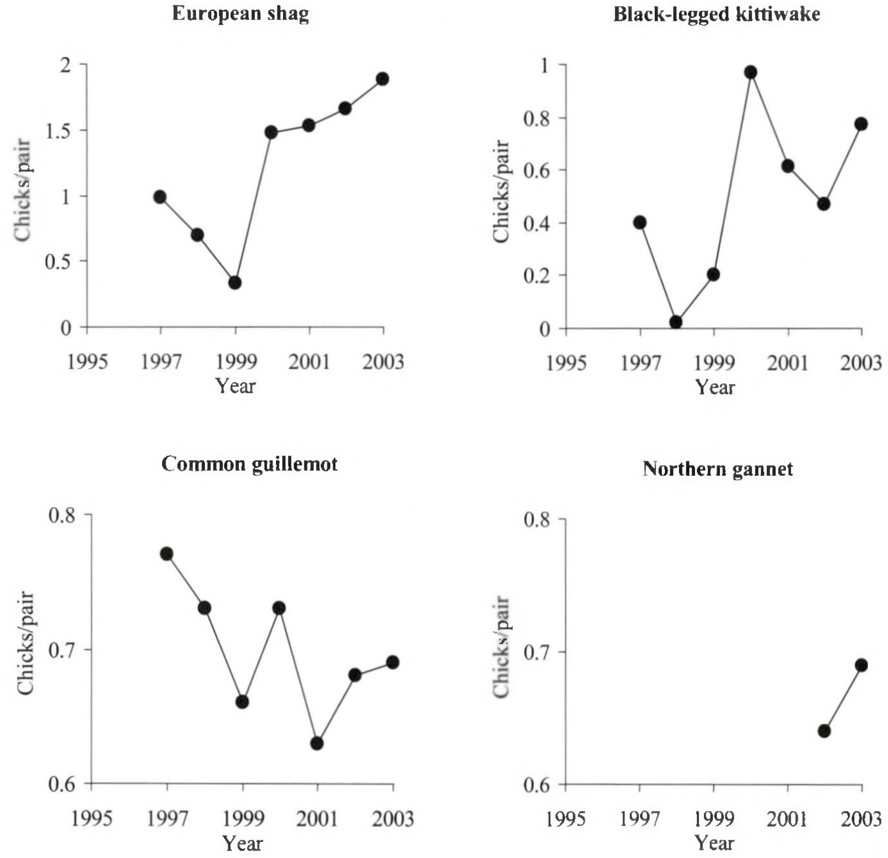


Figure 5.2.2 Breeding success (number of chicks fledged per pair) of the four study species from 1997-2003.

Timing

A summary of first and median dates of laying and fledging (1997-2003) is provided in Table 5.2.1 for the species nesting on the Isle of May. Note that median laying and fledging dates were not recorded for Kittiwakes prior to 2001.

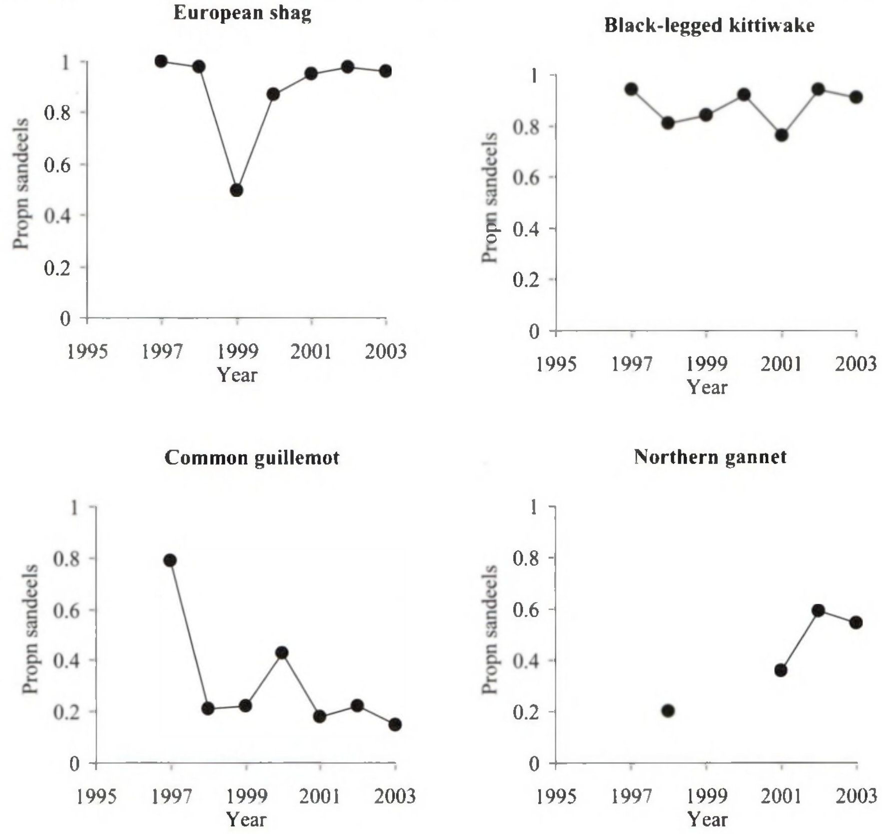
Table 5.2.1. First and median dates of laying and fledging of European Shags, Black-legged Kittiwakes and Common Guillemots nesting on the Isle of May, 1997-2003.

	Shag				Kittiwake				Guillemot			
	laying date		fledging date		laying date		fledging date		laying date		fledging date	
	first	median	first	median	first	median	first	median	first	median	first	median
1997	12-Mar	11-Apr	06-Jun	06-Jul	10-May		14-Jul		21-Apr	30-Apr	13-Jun	22-Jun
1998	01-Mar	05-May	26-May	30-Jul	13-May		17-Jul		01-May	10-May	23-Jun	02-Jul
1999	30-Apr	28-May	25-Jul	22-Aug	16-May		20-Jul		23-Apr	08-May	15-Jun	30-Jun
2000	18-Mar	06-May	12-Jun	31-Jul	05-May		09-Jul		20-Apr	04-May	12-Jun	26-Jun
2001	20-Apr	28-Apr	15-Jul	23-Jul	17-May	26-May	21-Jul	30-Jul	23-Apr	06-May	15-Jun	28-Jun
2002	16-Apr	30-Apr	11-Jul	25-Jul	10-May	19-May	14-Jul	23-Jul	23-Apr	05-May	15-Jun	27-Jun
2003	23-Mar	12-Apr	17-Jun	07-Jul	09-May	27-May	13-Jul	31-Jul	17-Apr	02-May	09-Jun	24-Jun

5.3 Seabird diets

General diet patterns 1997-2003

Diet samples were obtained annually between 1997 and 2003 for the three Isle of May study species, and in 1998, 2001, 2002 and 2003 for Gannets. Samples were collected and analysed using standardised methods (IMPRESS Report 2001.004). Figure 5.3.1 shows the proportion of Lesser Sandeels (by biomass) in the diet of each species. Shags were almost completely dependent on sandeels, with the exception of 1999, the year in which breeding success was low and a large proportion of birds did not breed. Kittiwakes also depended heavily on sandeels. In contrast, the main prey brought in by Guillemots for their chicks was Sprats. Gannets, took a wide variety of prey. Guillemots and Gannets showed contrasting trends in the importance of sandeel in the diet during the period, with the proportion decreasing in the former and increasing in the latter.


European shag

Black-legged kittiwake

Common guillemot

Northern gannet

Figure 5.3.1 Proportion of sandeels (by biomass) in the diet of the four study species during the chick-rearing period 1997-2003.

Detailed diet analysis 2001-2003

More intensive sampling of diet was carried out throughout the breeding season in all four species between 2001 and 2003 (Table 5.3.1). This enabled within season patterns of diet composition to be examined in detail. In **Europan Shags**, 1+ sandeels completely dominated the diet in 2002 but, in 2001 and 2003 0 group sandeels were also taken (Fig. 5.3.2). The timing of 0 group occurrence differed, being intermittent throughout 2001, but confined to the end of the season in 2003. In all three years, **Black-legged Kittiwakes** switched from a diet dominated by 1+ group sandeels at the beginning of the season to 0 group sandeels later in the season. Whilst sandeels dominated the diet throughout 2002, clupeids were also important in the latter half of June and early July in 2001, and to a lesser extent in 2003 (Fig. 5.3.3). Clupeids comprised a large component in the diet of **Common Guillemot** chicks in all three years. There was a strong seasonal pattern in both 2001 and 2003, with clupeids becoming increasingly important and 1+ group sandeels less important (Fig 5.3.4). In 2002, the proportion of 1+ group sandeels initially declined, but then increased so that there was a second peak of occurrence in late June. 0 group sandeels and other smaller species were rarely recorded.

In 2003, we carried out the first detailed study of seasonal patterns of diet in adult Guillemots (Wilson *et al.* in press). Adult diet was quantified by water-offloading, under UK Home Office licence. Sampling took place from the middle of May to the end of June. Analysis of presence/absence data revealed the importance of 0 group sandeels in the diet of adults. 1+ group sandeels were less important and showed a seasonal decline. In contrast, clupeids, gobies and gadoids increased in importance during the season, such that by the second half of June clupeids and gobies were found as frequently in the stomach flushings as 0 group sandeels (Fig 5.3.5). The results for 1+ group sandeels and clupeids mirrored seasonal changes in chick diet composition, though clupeids occurred more frequently in the latter. However, the finding that gobies, and in particular 0 group sandeels, are taken by adult Guillemots is important, as previous studies of Guillemot chick diet had not indicated that these prey types were taken (full details in Wilson *et al.* in press).

A total of 114 regurgitates (mass = 13.6 kg) was collected from **Northern Gannets**, of which 22 were from confirmed breeders, four were from chicks and the remainder were from non-breeders or possible breeders. In 2003, 92 samples (mass = 10.2 kg), of which 10 were from confirmed breeders and none were thought to have come from chicks. In both years, the most abundant prey item in terms of both frequency of occurrence and biomass was 0 group sandeel (Tables 5.3.2-5.3.3). This contrasts with 1998, when Mackerel was the most common prey item (Hamer *et al.* 2000) and with 2001, when the diet comprised similar proportions of Mackerel and sandeel (Lewis et. al. 2003). Together, these data suggest a progressive increase in the proportion of sandeel in the diet since 1998. There were no consistent seasonal changes in diet composition in 2002 or 2003, but this can be partly explained by differences in the sampling periods in the two years. In 2002 0 group sandeel was the most abundant prey item in both July and August (Fig 5.3.6). In 2003, where sampling started earlier, clupeids were the predominant prey item in late June but by July, sandeels were the most common prey (Fig 5..3.7). Lengths of fish taken by Gannets ranged from 50 mm (0 group sandeel) to 400 mm (Mackerel) in 2002 (Table 5.3.4) and from 52 mm (0 group sandeel) to 379 mm (haddock) in 2003 (Table 5.3.5).

Table 5.3.1 Number of food samples obtained for the four study species using the four sampling methods.

	Northern Gannet		**European Shag**		**Black-l. Kittiwake**		**Common Guillemot**	
2001	Date	*n*	Date	*n*	Date	*n*	Date	*n*
Regurgitations	Not collected		9/5-29/7	113	8/5-6/8	144	n/a	
Observations of prey delivery	n/a		n/a		n/a		13/5-14/7	823
Dropped fish	n/a		n/a		n/a		22/6-1/7	8
2002	Date	*n*	Date	*n*	Date	*n*	Date	*n*
Regurgitations	1/7-25/8	114	28/5-21/7	75	16/5-18/7	118	n/a	
Observations of prey delivery	n/a		n/a		n/a		30/5-3/7	2278
Dropped fish	n/a		n/a		n/a		22/6-1/7	8
2003	Date	*n*	Date	*n*	Date	*n*	Date	*n*
Regurgitations	24/6-4/8	92	29/5-5/7	38	4/5-4/8	161	n/a	
Observations of prey delivery	n/a		n/a		n/a		30/5-3/7	2967
Stomach contents	n/a		n/a		n/a		17/5-28/6	91
Dropped fish	n/a		n/a		n/a		13/6-21/6	12

Interspecific comparisons

The previous sections indicate the importance of sandeels in the diet of the seabird predators and provide evidence of similarities in patterns of seasonal change with a consistent shift from 1+ group to 0 group. There were however, significant differences in the size of 0 group sandeels taken by each species, differences between years, and an interaction between species and year. Guillemots took the smallest 0 group, followed by Kittiwakes and Gannets (Table 5.7). Fish were larger in 2002 than 2003, particularly those taken by Gannets, resulting in a significant interaction between species and year (GLM: species: $F_{1,170} = 3{,}425.10$, $P < 0.001$; year: $F_{1,170} = 2{,}392{,}90$, $P < 0.001$, species*year: $F_{1,170} = 52.8$, $P < 0.001$; all other interactions ns). The difference in sandeel size among the species was largely due to interspecific differences in the timing of breeding, rather than selection of different sized sandeels. By plotting sandeel length against date (Figure 5.9), the increase in sandeel length is evident as a non-linear change over time. The relationship suggests that the different predators were sampling from the same sandeel population since in neither year were there marked discontinuities between the length/date relationships for the individual species. Sandeels were larger for a given date in 2002, and there was a significant interaction between year and date (GLM: species: $F_{1,170} = 0.24$, ns; log(julian date): $F_{1,170} = 424.57$; $P < 0.001$; year: $F_{1,170} = 9.01$, $P < 0.001$, year*log(julian date): $F_{1,170} = 12.95$, $P < 0.001$; all other interactions ns).

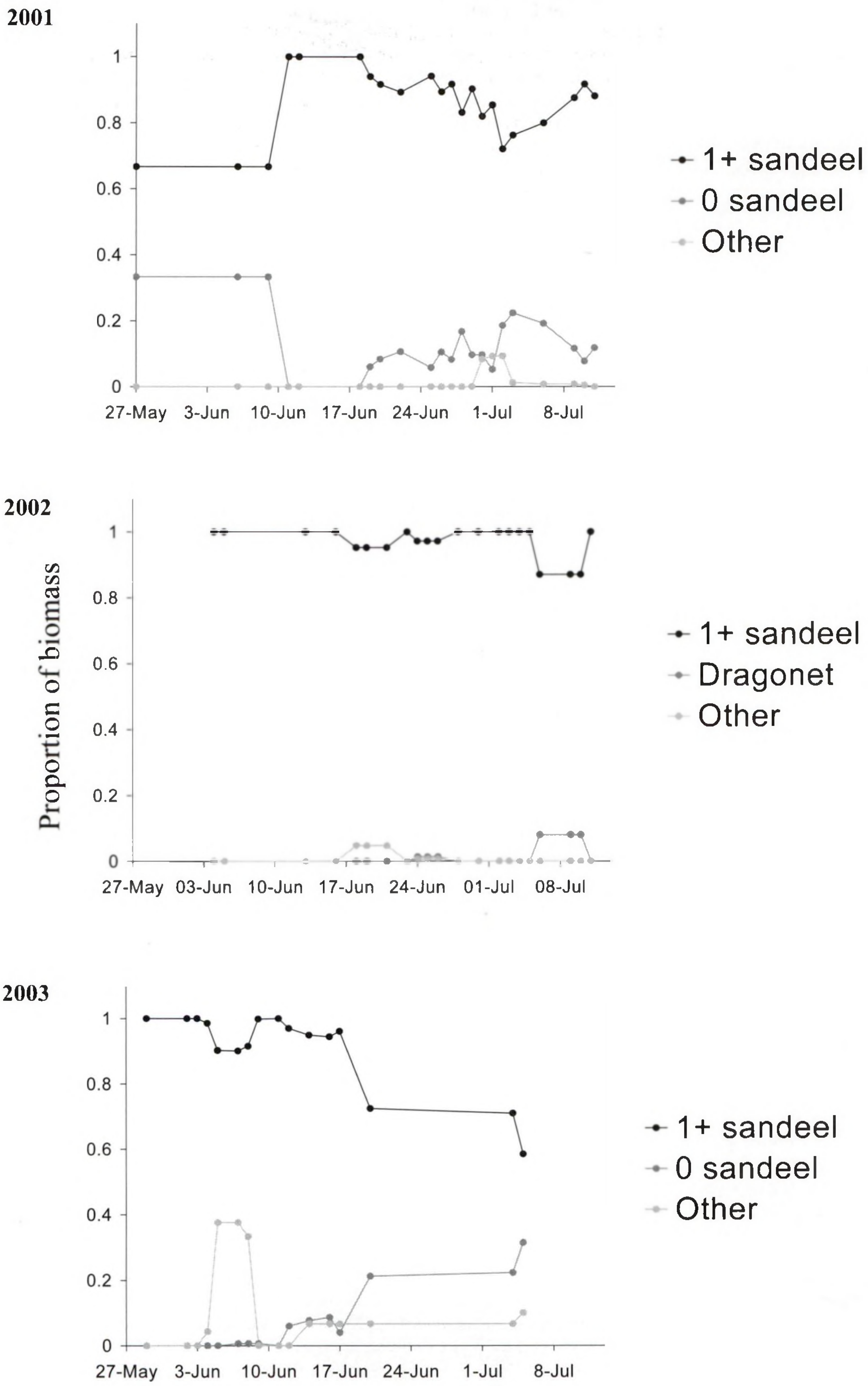


Fig. 5.3.2. Seasonal changes in diet composition for the Shag in three study years. Values are running means of biomass proportions.

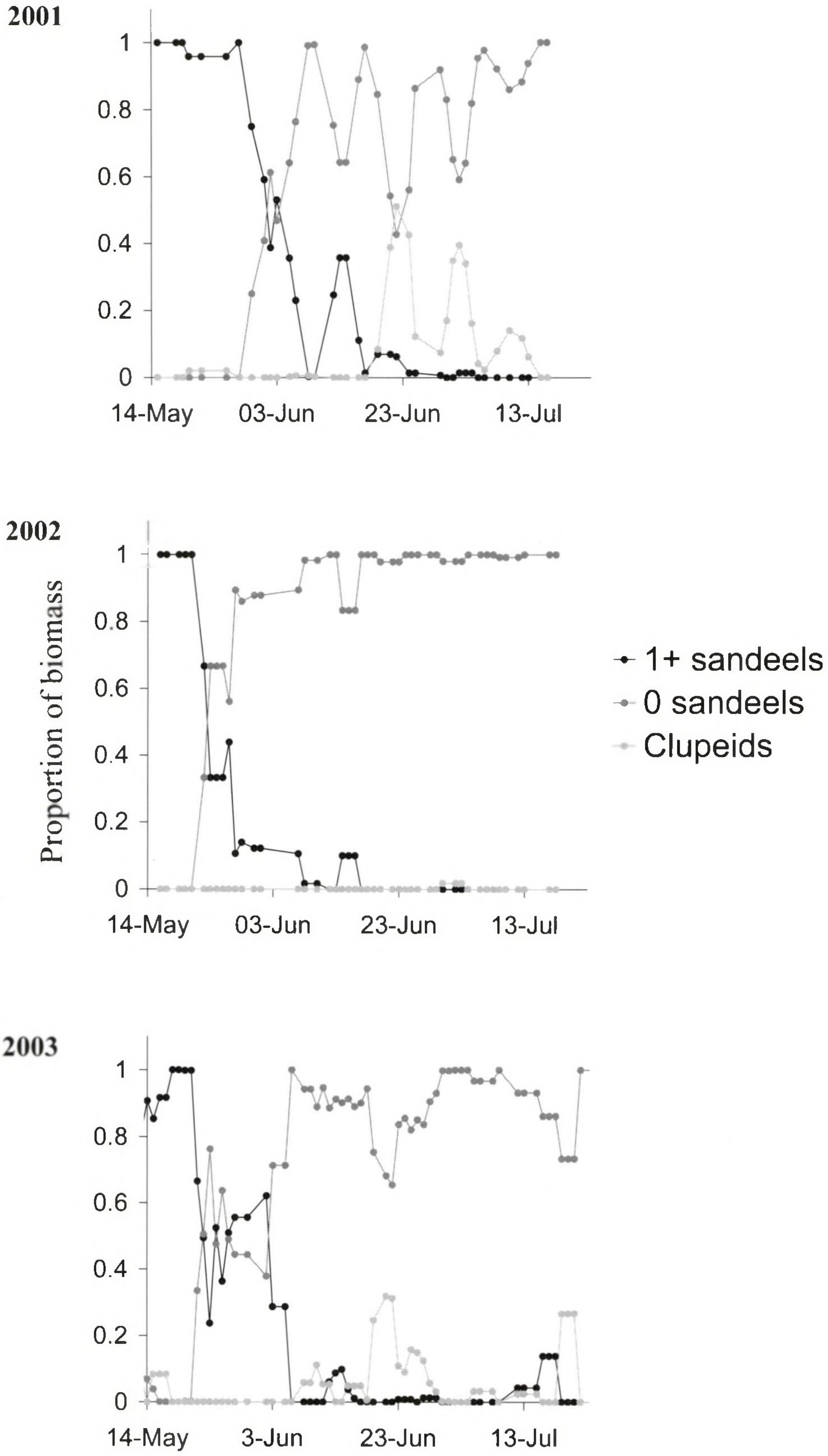


Fig. 5.3.3. Seasonal changes in diet composition for Kittiwake in the three study years. Values are running means of biomass proportions.

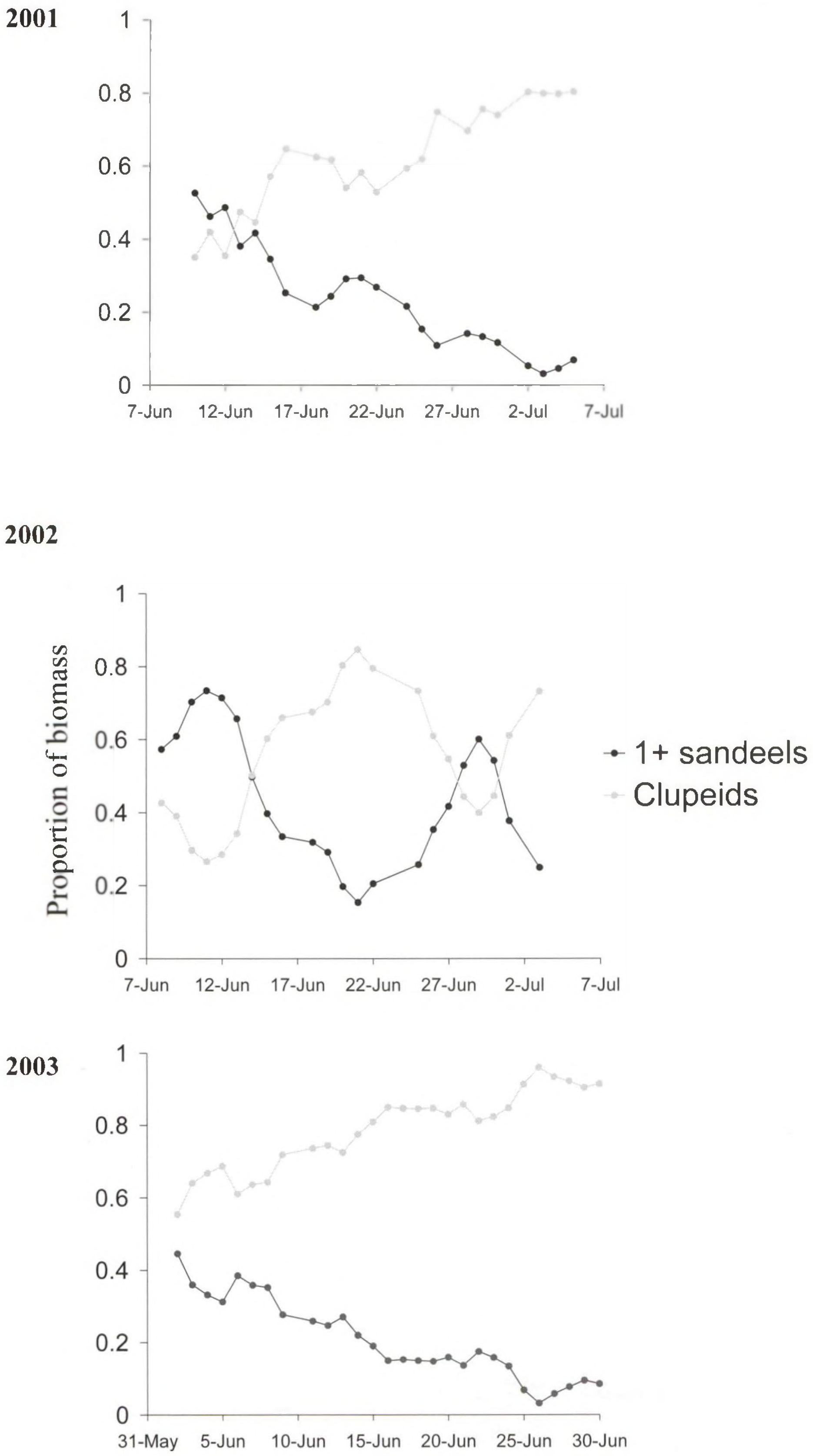


Fig. 5.3.4. Seasonal changes in diet composition for Guillemot in the three study years. Values are running means of biomass proportions.

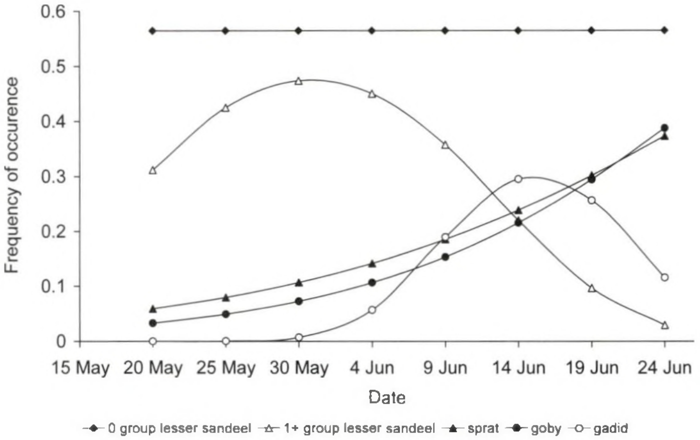


Fig. 5.3.5. Predicted values of frequency of occurrence of different prey types in adult Guillemot diet through the season in 2003.

Table 5.3.2 Diet of Gannets expressed as frequency of occurrence, based on 114 regurgitates in 2002 and 92 regurgitates in 2003.

	Frequency of occurrence (%)	
Family	2002	2003
Ammodytidae (0 group)	68.4	68.5
Ammodytidae (1+ and older)	1.8	6.5
Scombridae	21.1	18.3
Clupeidae	13.4	32.6
Gadidae	17.5	13.0
Pleuronectidae	1.8	1.1
Triglidae	1.8	0.0
Callionymidae	0.9	0.0
Carangidae	0.0	1.1
Belonidae	0.0	1.1

Table 5.3.3 Diet of Gannets expressed as proportion of biomass, based on 114 regurgitates (mass = 13.6 kg) in 2002 and 92 regurgitates (mass = 10.2 kg) in 2003.

	Proportion of biomass (%)	
Family	2002	2003
Ammodytidae (0 group)	55.0	51.4
Scombridae	23.6	14.6
Clupeidae	7.7	18.8
Gadidae	10.7	10.4
Other	2.9	4.8

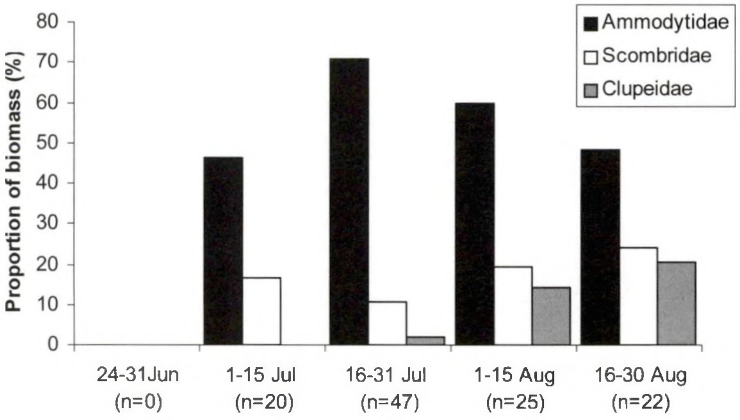


Fig. 5.3.6. Seasonal changes in diets of Gannets for the three main prey types in 2002.

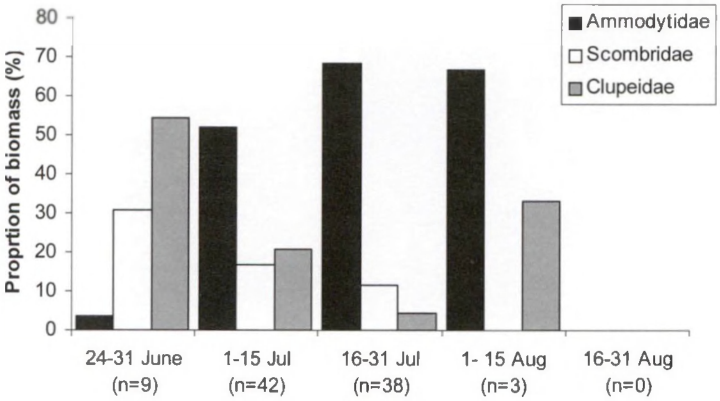


Fig. 5.3.7. Seasonal changes in diets of Gannets for the three main prey types in 2003.

Table 5.3.4 Mean lengths (mm) and total number of fish present in 114 food samples in 2002. 22 fish (19 Gadidae plus 3 Pleuronectidae) could not be identified to the species level.

Family	Species	*n* fish	Mean length (mm)	SD (mm)	Min – max length (mm)
Ammodytidae	Lesser Sandeel 0 gp	7477	81.5*	4.3	50.9 - 85.8
Ammodytidae	Lesser Sandeel 1+	2	110.0	-	113.0 - 107.0
Scombridae	Mackerel	28	320.1	44.1	233.3 - 400.0
Clupeidae	Herring	21	244.4	70.7	96.9 - 306.0
Clupeidae	Sprat	21	88.0	30.5	57.1 - 153.1
Gadidae	Whiting	19	209.4	51.9	124.0 – 323.0
Gadidae	Haddock	5	351.6	31.6	314.0 - 400.0
Gadidae	Cod	2	322.7	92.3	257.4 - 388.0
Triglidae	Red gurnard	2	**		
Callionymidae	Dragonet	1	229		

*based on a subsample of 3230 otoliths; ** vertebrae only.

Table 5.3.5 Mean lengths (mm) and total number of fish present in 114 food samples in 2003. Six fish (2 Gadidae, 2 Pleuronectidae, 2 unknown) could not be identified to species level.

Family	Species	*n* fish	Mean length (mm)	SD (mm)	Min – max length (mm)
Ammodytidae	Lesser Sandeel 0gp	5177	77.3*	7.6	51.9 - 99.8
Ammodytidae	Lesser Sandeel 1+	77	97.0	5.1	89.0 - 113.8
Ammodytidae	Greater sandeel 1+	3	161.6	6.6	156 - 169
Scombridae	Mackerel	18	305.3	37.9	212.5 - 362.5
Clupeidae	Herring	41	175.6	71.8	71.8 - 252.6
Clupeidae	Sprat	35	106.0	16.2	82.9 - 163.1
Gadidae	Whiting	2	278.2	30.5	244.2 - 303.3
Gadidae	Haddock	7	327.1	51.6	217.0 - 379.0
Belonidae	Garfish	1	360.0	-	-
Carangidae	Scad	1	383.0	-	-

* based on a sub-sample of 2470 otoliths.

Table 5.3.6 Mean size (mm) of 0 group sandeels (calculated from otoliths) from regurgitations or water-offloading from seabirds in 2002 and 2003.

	2002		2003	
	mean ± SD	*n*	mean ± SD	*n*
Black-legged Kittiwake	69.15 ± 9.75	3548	65.76 ± 11.08	6975
Northern Gannet	83.07 ± 7.26	3229	77.31 ± 7.60	2469
Common Guillemot			52.53 ± 9.39	272

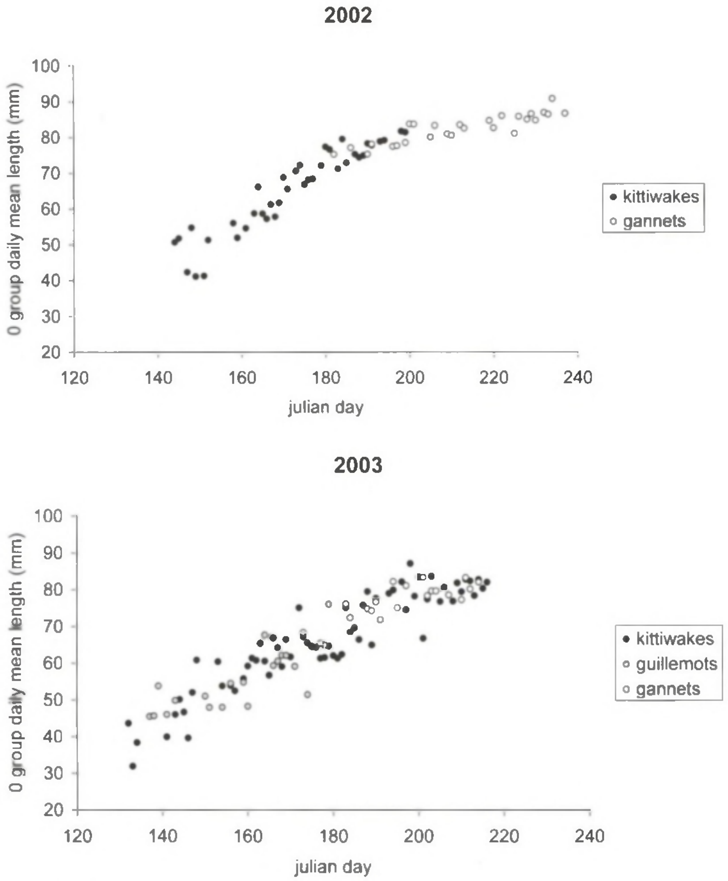


Fig. 5.3.8 Seasonal changes in daily mean 0 group sandeel length in the diets of Kittiwakes, Gannets and Guillemots in 2002 and 2003 (Guillemots in latter year only).

5.4 At-sea distribution and abundance of seabirds

Material used

Surveys were conducted onboard the fisheries research vessels *Clupea* and *Tridens* and onboard the research vessel *Pelagia* (see Chapter 1.5). Seabird survey techniques onboard *Clupea* on the one hand and onboard *Pelagia/*Tridens on the other hand were similar, but not identical. Rather than changing methods to harmonise techniques during the *IMPRESS* project period, it was chosen to keep methods on either platform intact and to take the opportunity to imbed the survey results into a longer series of data collected according to either method. The *Clupea* worked entirely within the principal study area, mostly in June (4 June-5 July) between 1997 en 2003, usually in connection with acoustic work on sandeels and/or oceanographical observations and was manned by ornithologists from the Marine Laboratory in Aberdeen. The *Tridens* was engaged in the annual ICES Herring acoustic survey from mid-June to late-July since the early 1990s, worked a much larger area (the 'study area at large'; Fig. 1.5.4), was manned by ornithologists from Royal NIOZ on Texel during 10 seasons between 1991 and 2004. *Tridens* observers focussed on foraging behaviour and (multi-species) feeding associations (MSFAs) (Camphuysen & Webb 1999). The cruise onboard RV *Pelagia* was a dedicated survey in June 2003, largely within the principal study area, and hydroacoustic information was collected simultaneously with seabird censuses. Ornithologists onboard were the same and were using identical methods (with emphasis on foraging behaviour and feeding flocks) as on the *Tridens*.

Special sets of data were collected onboard *Pelagia* and *Clupea* as so-called "mini-surveys". In the *Pelagia* cruise, carefully selected hotspot areas within the principal study area were worked for 25-hours (covering the tidal cycle twice) each, to examine the interplay between (tidal) currents and seabird foraging activity. Onboard FRV *Clupea*, a mini-survey was steamed in June 2001, centred on the Isle of May and a small-scale repeated survey was steamed in June 2002 to examine the effects of day, time of day, and tidal state on seabird usage of the Wee Bankie area. Details of these mini-surveys can be found in Appendices 2-3.

The results are presented as three discrete sets of data: FRV *Tridens* and RV *Pelagia* surveys 1991-2004 (focussing on broad distribution patterns and foraging behaviour patterns within and beyond the principal study area), FRV *Clupea* surveys 1997-2003 (focussing on trends in seabird abundance, with distribution patterns relative to oceanographic features and fish abundance within the principal study area illustrated in Appendix 2), and "mini-surveys" of RV *Pelagia* (focussing on diurnal patterns and tidal rhythms in seabird foraging behaviour).

Seabird community

From wide-ranging surveys in the study area at large onboard FRV Tridens and RV Pelagia (1991-2004), the offshore seabird community comprised at least 37 different species (Table 5.4.1). Of a total number of 53,365 birds observed in transect within the principal study area, the most abundant 15 seabird species were (in declining order of numerical abundance) Common Guillemot (48.5%), Atlantic Puffin *Fratercula arctica* (21.4%), Black-legged Kittiwake (11.9%), Razorbill *Alca torda* (10.7%), Northern Gannet (5.9%), Northern Fulmar *Fulmarus glacialis* (0.6%), Herring Gull *Larus argentatus* (0.5%), European Shag (0.2%), Lesser Black-backed Gull *Larus fuscus* (0.1%), Arctic Tern *Sterna paradisaea* (0.1%), Manx Shearwater *Puffinus puffinus* (0.1%), European Storm-petrel *Hydrobates pelagicus* (0.0%), Common Gull *Larus canus* (0.0%), Arctic Skua *Stercorarius parasiticus* (0.0%), Great Skua *Stercorarius skua* (0.0%), and Great Black-backed Gull *Larus marinus* (0.0%). In comparison with the study area at large, the overall abundance of Guillemots, Puffins, Kittiwakes, Razorbills and Gannets is relatively high, whereas the abundance of Northern Fulmars is fairly low. It should be noted that the number of Shags observed is very low, this being the result of their inshore distribution (see Chapter 5.5); coastal areas where sea-going research vessels engaged in offshore censuses seldom venture.

Table 5.4.1. Seabirds observed in the study area at large (NW North Sea; 54-59°N, 3°W-2°E) and in the principal study area (Wee Bankie area; 56°N-56°30'N, 3°W-1°W), 1991-2004 (FRV Tridens and RV Pelagia surveys combined). Mean densities (birds per km²) are calculated from all individual birds observed in transect, whereas the other indicator of relative abundance (n per km) is the total number of birds observed (whether or not in transect) divided by the distance travelled. (Table sorted from high to low values on densities in the principal study area).

		Study area at large		**Principal study area**	
		Density	N per km	Density	N per km
Common Guillemot	*Uria aalge*	9.6	3.6	36.2	12.2
Atlantic Puffin	*Fratercula arctica*	2.0	0.7	16.0	5.6
Black-legged Kittiwake	*Rissa tridactyla*	2.7	1.9	8.9	5.7
Razorbill	*Alca torda*	1.3	0.4	8.0	2.2
Northern Gannet	*Morus bassanus*	1.0	1.3	4.4	5.7
Herring Gull	*Larus argentatus*	0.1	0.1	0.4	0.5
Northern Fulmar	*Fulmarus glacialis*	1.7	1.8	0.4	0.5
European Shag	*Phalacrocorax aristotelis*	0.0	0.0	0.2	0.1
Lesser Black-backed Gull	*Larus fuscus*	0.0	0.0	0.1	0.1
Arctic Tern	*Sterna paradisaea*	0.1	0.1	0.1	0.1
Manx Shearwater	*Puffinus puffinus*	0.0	0.0	0.0	0.0
European Storm-petrel	*Hydrobates pelagicus*	0.0	0.0	0.0	0.0
Common Gull	*Larus canus*	0.0	0.0	0.0	0.0
Arctic Skua	*Stercorarius parasiticus*	0.0	0.0	0.0	0.0
Great Skua	*Stercorarius skua*	0.0	0.0	0.0	0.0
Great Black-backed Gull	*Larus marinus*	0.0	0.0	0.0	0.0
Great Cormorant	*Phalacrocorax carbo*	0.0	0.0	0.0	0.0
Little Gull	*Larus minutus*	0.0	0.0	0.0	0.0
Sabine's Gull	*Larus sabini*	0.0	0.0	0.0	0.0
Common Tern	*Sterna hirundo*	0.0	0.0	0.0	0.0
Red-throated Diver	*Gavia stellata*	0.0	0.0		
Black-throated Diver	*Gavia arctica*	0.0	0.0		
Sooty Shearwater	*Puffinus griseus*		0.0		0.0
Leach's Storm-petrel	*Oceanodroma leucorhoa*	0.0	0.0		
Common Eider	*Somateria mollissima*		0.0		
Black Scoter	*Melanitta nigra*	0.0	0.0		0.0
Velvet Scoter	*Melanitta fusca*		0.0		
Common Goldeneye	*Bucephala clangula*		0.0		
Red-breasted Merganser	*Mergus serrator*		0.0		
Red-necked Phalarope	*Phalaropus lobatus*		0.0		
Pomarine Skua	*Stercorarius pomarinus*		0.0		0.0
Long-tailed Skua	*Stercorarius longicaudus*		0.0		
Black-headed Gull	*Larus ridibundus*	0.0	0.0		0.0
Ring-billed Gull	*Larus delawarensis*		0.0		
Sandwich Tern	*Sterna sandvicensis*	0.0	0.0		0.0
Black Tern	*Chlidonias niger*		0.0		
Black Guillemot	*Cepphus grylle*	0.0	0.0		

Seabird distribution

From Clupea surveys, the variability in numbers and distributions of Guillemot, Razorbill, Puffin, Kittiwake, Gannet, and Shag, were determined from 1997 to 2003 (Appendix 2ab). Puffin distributions were strongly linked to the Isle of May. Guillemot and Razorbill distributions differed considerably among years. Shags were rarely encountered offshore and again their distributions appeared to be restricted to the area around the Isle of May. Kittiwakes recorded on the water tended to have a relatively coastal distribution, whilst birds recorded in flight were distributed widely across the study area. Gannet distributions, both of birds recorded on the water and in flight, differed between years. In June 2001 the area in the immediate vicinity of the Isle of May was found to be of great importance to most species breeding on the island, or on the nearby Bass Rock.

During the first three years of study, 1997 to 1999, an active industrial fishery for sandeels was prosecuted. Most fishing effort occurred during the months of May and June. *Clupea* surveys were timed to coincide more or less with this period, also the time of year when sandeels were most active in the water column and therefore most "visible" to acoustic survey. During the latter four years of the study, 2000 to 2003, this industrial fishery was closed, and only extremely limited fishing for scientific purposes was allowed. Guillemot, Puffin and Kittiwake numbers in the area all seemed to generally higher in the four years that sandeel fishing was prohibited (Figure 5.4.1; Appendix 2ab). No obvious effect of the closure of the sandeel fishery on the distributions of the six sandeel specialist seabird predators was immediately apparent.

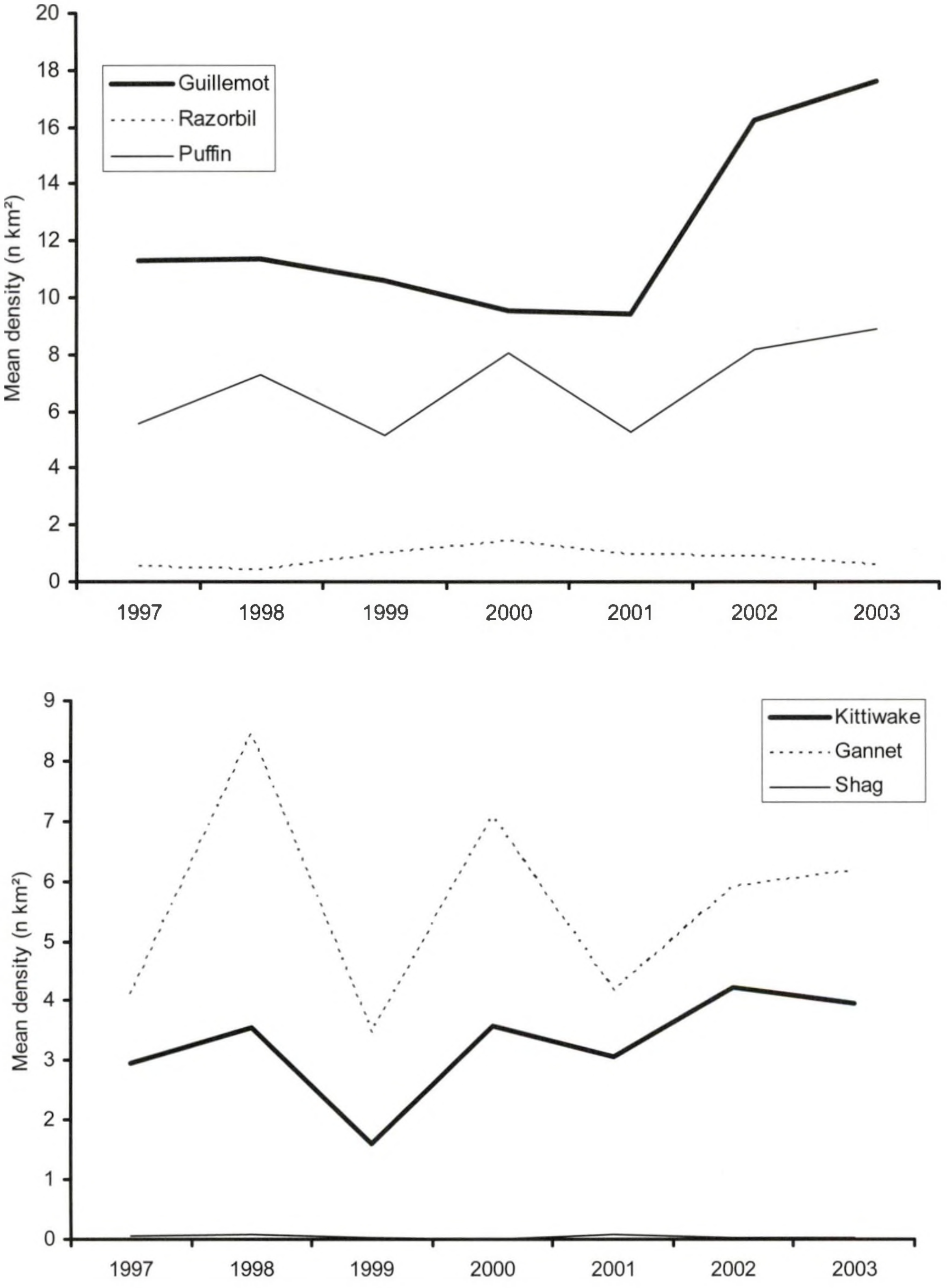
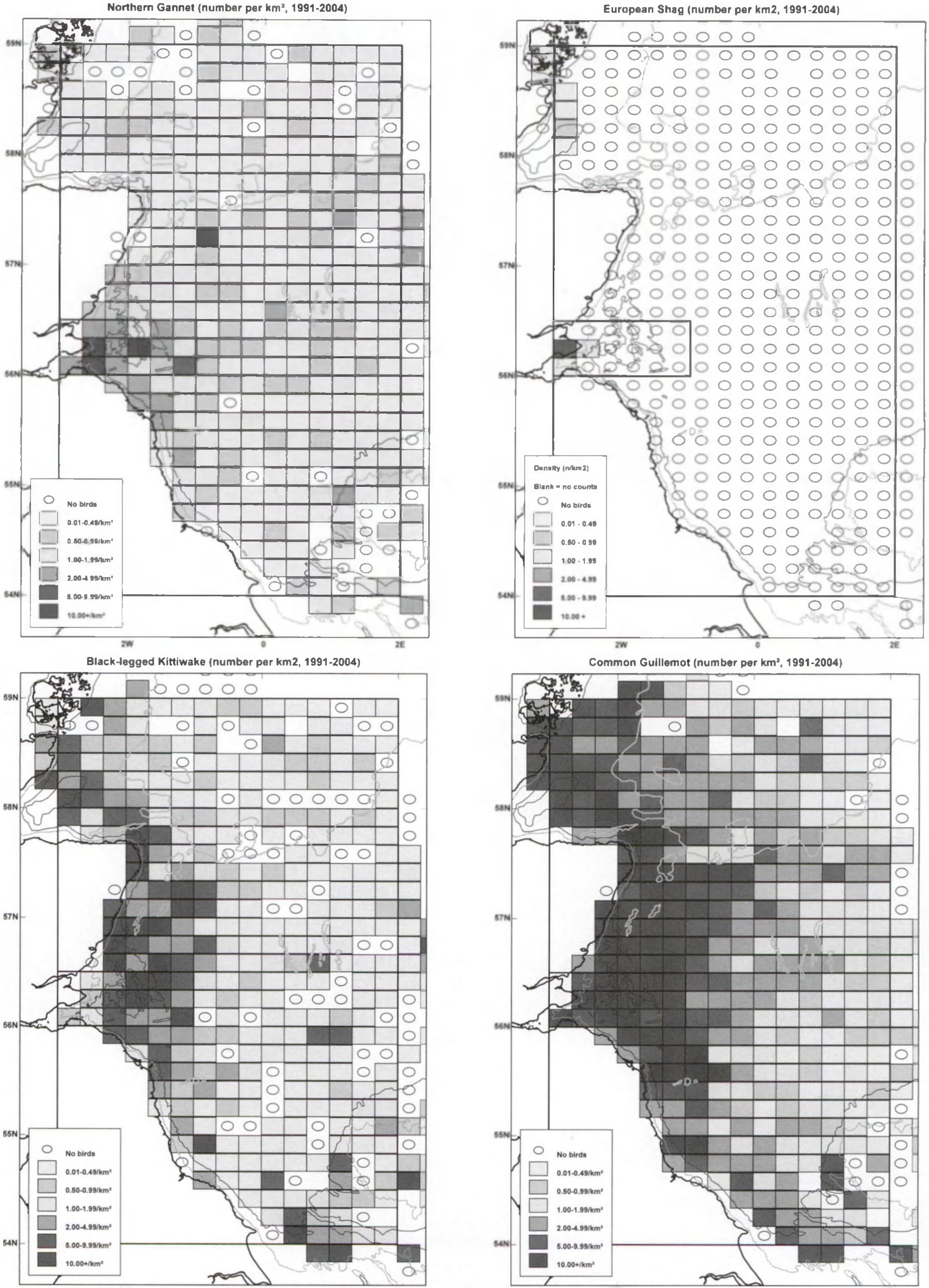


Figure 5.4.1. Mean densities of six seabird species in the principal study area form ship-based surveys onboard FRV Clupea, June-July 1997-2003.


Northern Gannet (number per km², 1991-2004)

European Shag (number per km2, 1991-2004)

Black-legged Kittiwake (number per km2, 1991-2004)

Common Guillemot (number per km², 1991-2004)

Figure 5.4.2. Generalised distribution patterns of Northern Gannet, European Shag, Black-legged Kittiwake, and Common Guillemot, from ship-based surveys, June-July, 1991-2004 onboard FRV Tridens and RV Pelagia.

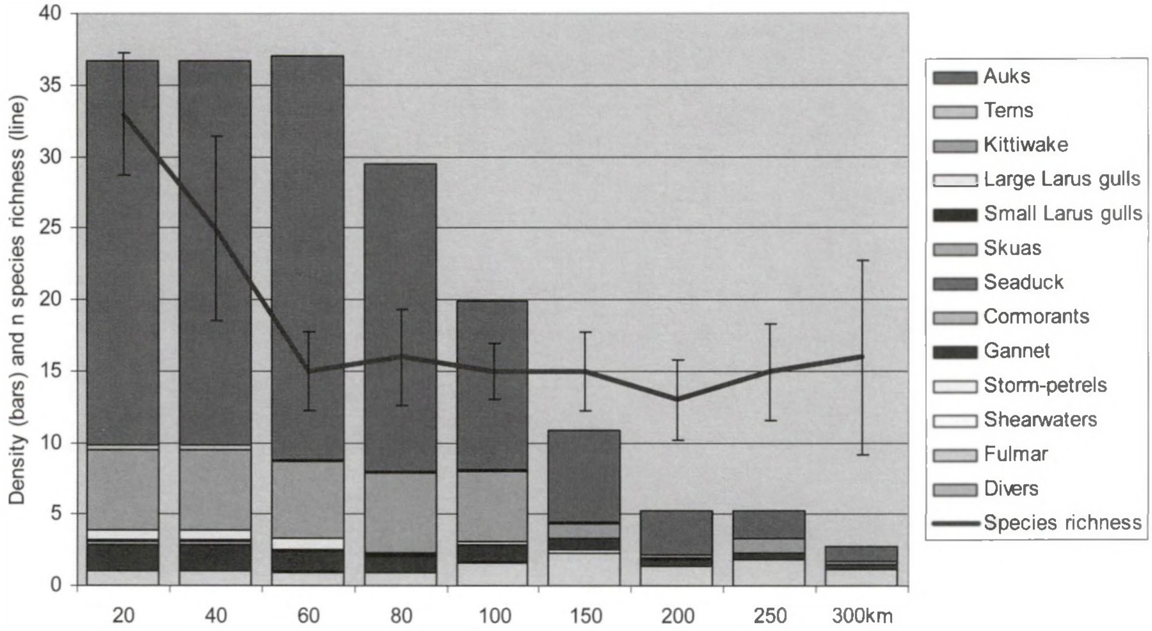


Figure 5.4.3. Changes in top-predator community with distance from land as densities (n km^{-2}*; stacked bars) and jackknife estimate of species richness (n ± 95% CI; line; Krebs 1989), based on large-scale ship-based surveys 1991-2004 in the study area at large onboard FRV Tridens and RV Pelagia.*

From the large scale surveys onboard FRV Tridens and RV Pelagia (1991-2004), rather clear-cut, generalised distribution patterns can be derived (Figs. 5.4.2), with Gannets far-ranging, Guillemots and Kittiwakes highly concentrated in the western (nearshore) half of the study area at large, and with Shag concentrated in inshore waters (not well covered in these surveys). From these surveys, it is obvious that the main feeding area for East Scottish auks and Kittiwakes can be found within approximately 100km from the coast, with peak densities usually slightly nearer the coast. Somewhere within that zone is the outer limit of the breeding birds from the Isle of May study colonies, whereas the Gannets, while "filling up" the entire study area at large, probably travel even further away into the North Sea on single foraging trips from the Bass Rock. Seabird densities and species richness declined and species composition altered with increasing distance to the UK coast (Fig. 5.4.3). The principal study area is almost entirely within 90 km from land and, as such, well within the areas with highest mean top-predator densities and diversity of the northwest North Sea.

Foraging and feeding

The behaviour of seabirds and marine mammals was studied, categorised and recorded for as many as possible individuals after counts were completed, with emphasis on foraging activities (Camphuysen & Garthe 2004). In the study area at large, of the commoner species, between 17.5% (Common Gull) and 73.4% (Sandwich Tern) were recorded as foraging (Table 5.4.2). It should be realised, however, that diving seabirds such as auks and cormorants were frequently disturbed by the approaching observation platform and their feeding activities may therefore have been underestimated. It is interesting to note that in the study area at large, a significantly higher proportion of Gannets was recorded as foraging (35.6%, n = 44,818) than in the principal study area (21.4%, n = 13,637; G_{adj}= 1024, df= 1, P< 0.001). The opposite was true for Kittiwakes (G_{adj} = 516, df= 1, P< 0.001; Table 5.4.2) and Guillemots (G_{adj} = 617, df= 1, P< 0.001; Table 5.4.2). Most birds that were recorded as feeding participated in feeding flocks and most these flocks comprised several species (multi-species feeding associations, MSFAs). In the study area at large, in 12 out of 18 common species recorded, at least 80% of the feeding individuals were joining some sort of MSFA (Table 5.4.2). Notable (abundant) exceptions were Atlantic Puffin (74.8%, n = 4404), Arctic Tern (46.2%, n = 1549), European Storm Petrel (15.0%, n = 606), and Shag (22.6%, n = 190). Within the principal study area, a similar pattern emerged, with three (abundant) species showing a lower tendency to participate in multi-species feeding frenzies (<80% feeding in flocks): Kittiwake (56.5%, n = 8452, Arctic Tern (18.7%, n = 107), and Shag (0%, n = 28).

Feeding techniques were rather diverse in Gannets and Kittiwakes, but pretty specific in Guillemots (Table 5.4.3). Feeding Gannets were mostly deep plunge-diving or scooping and the latter activity was much more common within the principal study area than in the area at large. Scooping was entirely associated with multi-species feeding associations and has never been observed (so far) when Gannets were feeding alone or with conspecifics. Gannets associated with dolphins were typically deep plunge-diving and solitary Gannets were either shallow- or deep plunge-diving. Feeding Kittiwakes were dipping or shallow plunge-diving. Guillemots were observed pursuit diving from the surface mostly, but were occasionally pursuit plunging in attempts to keep up with fast moving fish shoals. Pursuit plunging was mainly seen within the principal study area and only frequently in 2004.

Table 5.4.2. Seabirds observed (n), the fraction foraging and feeding (n, % of all observed) and those foraging in multi-species feeding flocks (n, % of all feeding), in the study area at large and within the principal study area. The right-hand 4 columns give proportion of feeding individuals associated with fishing vessels (trawlers), following hunting marine mammals (cetaceans), participating in 'natural' multi-species feeding associations (multi-sp), or as individuals or in flocks with just a single species (single-sp).

Study area at large		***n***		**Flock-**		% of feeding individuals			
Species	*n*	**feeding**	**%**	**feeding**	**%**	**trawlers**	**cetaceans**	**multi-sp**	**single sp**
Common Guillemot	122649	19978	16.3	16187	81.0	0.3	0.1	80.6	19.0
Black-l. Kittiwake	66013	33966	51.5	27264	80.3	8.9	2.5	68.9	19.7
Northern Fulmar	60438	30284	50.1	27975	92.4	89.5	0.3	2.6	7.6
Northern Gannet	44818	15961	35.6	13094	82.0	42.8	18.6	20.7	18.0
Atlantic Puffin	23297	4404	18.9	3294	74.8	0	0	74.8	25.2
Razorbill	14045	3300	23.5	2857	86.6	0	0	86.6	13.4
Herring Gull	5400	3161	58.5	2942	93.1	26.9	0.3	65.9	6.9
Arctic Tern	2196	1549	70.5	715	46.2	0.1	0.4	45.6	53.8
Lesser Bl.-backed Gull	1319	690	52.3	667	96.7	73.5	0.1	23.0	3.3
Europ. Storm-petrel	1066	606	56.8	91	15.0	11.2	2.5	1.3	85.0
Guillemot/Razorbill	857	660	77.0	655	99.2	0	0	99.2	0.8
Great Bl.-backed Gull	699	347	49.6	336	96.8	66.0	0	30.8	3.2
Great Skua	671	250	37.3	231	92.4	48.8	2.4	41.2	7.6
European Shag	582	190	32.6	43	22.6	0	0	22.6	77.4
Manx Shearwater	461	155	33.6	140	90.3	2.6	2.6	85.2	9.7
Black-headed Gull	434	188	43.3	63	33.5	30.3	1.1	2.1	66.5
Sandwich Tern	323	237	73.4	68	28.7	0	0	28.7	71.3
Arctic Skua	233	100	42.9	87	87.0	13.0	0	74.0	13.0
Common Gull	206	36	17.5	21	58.3	36.1	0	22.2	41.7
Other species	338	140	41.4	27	19.3	2.1	0	17.1	80.7

Principal study area		***n***		**Flock-**		% of feeding individuals			
Species	*n*	**feeding**	**%**	**feeding**	**%**	**trawlers**	**cetaceans**	**multi-sp**	**single sp**
Common Guillemot	29048	6567	22.6	5802	88.4	0	0.1	88.2	11.6
Northern Gannet	13637	2913	21.4	2346	80.5	18.2	6.3	56.0	19.5
Black-l. Kittiwake	13619	8452	62.1	4775	56.5	6.0	1.1	49.4	43.5
Atlantic Puffin	13287	2965	22.3	2498	84.2	0	0	84.2	15.8
Razorbill	5155	1617	31.4	1455	90.0	0	0	90.0	10.0
Northern Fulmar	1194	526	44.1	489	93.0	83.1	0.8	9.1	7.0
Herring Gull	1112	700	62.9	630	90.0	21.4	0	68.6	10
Lesser Bl.-backed Gull	349	183	52.4	172	94.0	57.4	0	36.6	6.0
European Shag	314	28	8.9		0.0	0	0	0	100
Guillemot / Razorbill	281	250	89.0	250	100.0	0	0	100	0
Arctic Tern	132	107	81.1	20	18.7	0	0	18.7	81.3
Manx Shearwater	70	34	48.6	31	91.2	0	0	91.2	8.8
Other species	108	35	32.4	22	62.9	8.6	0	35.8	55.6

Table 5.4.3. Feeding and foraging behaviour observed (% of categorised sample) in the area at large and in the principal study area for Gannets, Kittiwakes and Guillemots, as mono-specific activities (solitary individuals or flock consisting of a single species; top half of the table) and as participants of multi-species foraging assemblages (bottom half of the table).

Mono-specific feeding activities	**Area at large**			**Principal study area**		
Behaviour observed	Gannet	Kittiwake	Guillemot	Gannet	Kittiwake	Guillemot
Holding fish	0	0.1	40.7	0	0	14.0
Feeding young at sea	0	0	0.6	0	0	0.1
Feeding, method unspecified	0	0.5	0.1	0	0.5	0
Aerial pursuit	0	0.0	0	0	0	0
Scavenging	0	0.0	0	0	0.0	0
Scavenging at fishing vessel	1.7	0.3	0	0	0	0
Dipping	0	46.2	0	0	62.9	0
Surface seizing	0	0.1	0	0	0	0
Surface pecking	0	2.4	0	0	0.4	0
Deep plunging	29.6	0.1	0	46.7	0.1	0
Shallow plunging	0.5	8.1	0	2.5	2.1	0
Pursuit diving, or bottom feeding	0	0	55.9	0	0	82.6
Actively searching	68.2	42.2	2.8	50.8	33.9	3.3
Not feeding, mono-species occurrence	28326	22135	89648	10566	3604	19215
Feeding mono-species occurrence	2867	6702	3791	567	3677	765
% Feeding	9.2	23.2	4.1	5.1	50.5	3.8

Table 5.4.3 continued

Multi-species flocks	**Area at large**			**Principal study area**		
Behaviour observed	Gannet	Kittiwake	Guillemot	Gannet	Kittiwake	Guillemot
Holding fish	0	0.0	1.0	0	0.0	0.0
Without fish	0	0	0.3	0	0	0.1
Feeding young at sea	0	0	0.0	0	0	0
Feeding, method unspecified	0	0.4	0.1	0	0	0.1
Scooping prey from surface	5.3	0	0	16.3	0	0
Aerial pursuit	0	0.1	0	0	0.0	0
Scavenging at fishing vessel	35.3	6.8	0	27.2	9.0	0
Dipping	0	39.2	0.5	0	48.3	0
Surface seizing	0.2	0.9	0	0	0.6	0
Surface pecking	0	1.4	0	0	2.5	0
Deep plunging	24.7	0.0	0	37.1	0	0
Shallow plunging	0.6	34.2	0	2.4	20.9	0
Pursuit plunging	0	0.0	3.1	0	0	7.9
Pursuit diving, or bottom feeding	0.1	0.4	94.8	0.1	1.5	91.5
Actively searching	33.8	16.5	0.3	17.1	16.8	0.4
Kleptoparasitising	0	0.1	0	0	0.3	0
Not feeding, in multi-species flock	531	9912	13023	158	1563	3266
Feeding, in multi-species flock	13094	27264	16187	2346	4775	5802
% Feeding	96.1	73.3	55.4	93.7	75.3	64.0
Monospecific	31193	28837	93439	11133	7281	19980
Multi-species	13625	37176	29210	2504	6338	9068
Totals	44818	66013	122649	13637	13619	29048

Table 5.4.4. Composition of human-induced multi-species feeding associations (associated with fishing activities) from ship-based surveys in June-July 1991-2004 in the study area at large and in the principal study area. Shown are number of flocks, mean (± SE) number of species and number of individual seabirds and marine mammals per flock and numbers of individuals, mean flock size and presence (flocks) of individual species.

	Area at large				**Principal area**			
	No of indiv	Mean	SE	Flocks	No of indiv	Mean	SE	Flocks
Bird species		3.5	0.1	243		3.4	0.6	9
Marine mammal species		0.0	0.0			0.1	0.1	
Bird numbers		239.3	24.7			203.9	128.8	
Marine Mammal numbers		0.1	0.0			0.1	0.1	
Fulmar	32762	176.1	25.6	186	437	145.7	82.7	3
Gannet	9154	56.2	10.1	163	530	176.7	107.8	3
Kittiwake	3138	25.9	3.7	121	510	127.5	71.0	4
Large gull sum	1641	17.6	3.2	93	256	28.4	7.8	9
Herring Gull	855	16.8	3.4	51	150	16.7	6.3	9
Lesser Black-backed Gull	515	9.2	2.7	56	105	11.7	2.5	9
Great Black-backed Gull	271	6.5	1.5	42	1	1.0		1
Great Skua	150	2.4	0.3	62				
Storm-Petrel	78	5.6	1.8	14				
Black-headed Gull	70	5.0	1.9	14	2	2.0		1
Common Gull	18	1.3	0.1	14				
Arctic Skua	15	1.2	0.1	13				
Minke Whale	7	2.3	0.7	3				
Harbour Porpoise	4	2.0	1.0	2				
Manx Shearwater	4	1.3	0.3	3				
Arctic Tern	2	2.0		1				
Cormorant	2	1.0	0.0	2				
Common Tern	2	1.0	0.0	2				
Ring-billed Gull	1	1.0		1				
Grey Seal	1	1.0		1	1	1.0		1

Flock formations (MSFAs)

Multi-species foraging assemblages (MSFAs) are an important strategy used to obtain prey by numerous species of seabirds (Hoffman et al. 1981; Ballance et al. 1997; Camphuysen & Webb 1999). During the extensive surveys in the northwest North Sea, three major types were recognised on the basis of the underlying attraction: (1) human induced feeding flocks (birds associated with (fishing) vessels), (2) marine mammal-induced feeding flocks (birds attracted to hunting cetaceans or seals), and (3) 'natural' feeding flocks (seabirds, sometimes with marine mammals, jointly exploiting a shared resource). Between species, the importance of either flock type was very different. Of Guillemots for example, in the study area at large, 0.3% of the feeding individuals (n = 19 978) were recorded in association with a fishing vessel, and only 0.1% were attracted by foraging cetaceans, whereas 80.6% were found in 'natural' MSFAs and a final 19.0% were feeding solitary or with conspecifics only. Quite the opposite was found in Northern Fulmars (89.5%, 0.3%, 2.6%, and 7.6% respectively, n = 30 284; Table 5.4.2). Northern Gannets clearly 'spread the attention' and were represented substantially in each of these conditions (42.8%, 18.6%, 20.7%, and 18.0% respectively, n = 15 961). Kittiwakes were closer to Guillemots with 68.9% in 'natural' MSFAs and 19.7% as solitary or at least single-species feeders. A similar pattern was found within the principal study area (Table 5.4.2), but with a stronger emphasis on 'natural' MSFAs in both Guillemots (88.2%, n = 6567) and Gannets (56.0%, n = 2913), and with a slightly stronger tendency to feed among conspecifics in Kittiwakes (43.5%, n = 8452; 49.4% in 'natural' MSFAs).

Table 5.4.5. Composition of cetacean-induced multi-species feeding associations (associated with hunting marine mammals) from ship-based surveys in June-July 1991-2004 in the study area at large and in the principal study area. Shown are number of flocks, mean (± SE) number of species and number of individual seabirds and marine mammals per flock and numbers of individuals, mean flock size and presence (flocks) of individual species.

		Area at large				**Principal area**		
	No of indiv	Mean	SE	Flocks	No of indiv	Mean	SE	Flocks
Bird species		1.1	0.0	465		1.5	0.2	12
Marine mammal species		1.0	0.0			1.1	0.1	
Bird numbers		10.8	1.1			23.8	6.6	
Marine Mammal numbers		6.4	0.7			3.4	0.6	
Gannet	3596	8.7	0.9	412	184	18.4	8.0	10
Kittiwake	836	18.6	4.5	45	89	14.8	4.7	6
Fulmar	110	6.9	3.6	16	4	4.0		1
Guillemot	18	6.0	2.1	3	9	9.0		1
Storm-Petrel	15	1.9	0.4	8				
Large gull sum	9	3.0	1.2	3				
Herring Gull	8	4.0	1.0	2				
Arctic Tern	6	3.0	1.0	2				
Great Skua	6	1.5	0.3	4				
Manx Shearwater	6	1.0	0.0	6				
Black-headed Gull	2	2.0		1				
Lesser Black-backed Gull	1	1.0		1				
White-beaked Dolphin	1287	6.4	0.3	200	28	4.0	0.8	7
White-sided Dolphin	874	43.7	14.0	20				
Harbour Porpoise	652	2.9	0.2	226	9	3.0	0.6	3
Common Dolphin	128	42.7	13.9	3				
unidentified dolphin	14	3.5	0.9	4				
Minke Whale	12	1.3	0.3	9				
Grey Seal	9	1.1	0.1	8	4	1.3	0.3	3
Common Seal	1	1.0		1				

Table 5.4.6. Composition of 'natural' multi-species feeding associations (not human-induced, not as a result of marine mammal activity) from ship-based surveys in June-July 1991-2004 in the study area at large and in the principal study area (see Table 5.4.5 for conventions).

		Area at large				**Principal area**		
	No of indiv	Mean	SE	Flocks	No of indiv	Mean	SE	Flocks
Bird species		2.5	0.0	3972		2.5	0.0	1193
Marine mammal species		0.0	0.0			0.0	0.0	
Bird numbers		29.2	1.7			23.7	2.3	
Marine Mammal numbers		0.1	0.0			0.0	0.0	
Kittiwake	41523	16.8	0.9	2471	6951	8.6	0.7	811
Guillemot	36105	12.3	0.6	2935	10901	15.2	1.8	719
Razorbill	6794	4.1	0.2	1642	2662	6.5	0.8	412
Puffin	4959	4.9	0.9	1020	3307	6.1	1.6	541
Gannet	4127	7.4	0.8	561	1793	9.3	2.0	192
Large gull sum	3305	10.2	1.4	325	672	6.8	2.5	99
Herring Gull	2819	10.9	1.6	259	579	7.3	2.9	79
Fulmar	1865	5.8	1.4	320	61	1.9	0.3	32
Arctic Tern	1037	14.6	2.4	71	39	4.3	1.0	9
Lesser Black-backed Gull	302	3.1	0.6	99	88	2.8	0.5	32

		Area at large				Principal area		
	No of indiv	Mean	SE	Flocks	No of indiv	Mean	SE	Flocks
Manx Shearwater	241	2.3	0.2	105	40	1.7	0.3	23
Great Black-backed Gull	184	4.4	0.8	42	5	1.3	0.3	4
Harbour Porpoise	157	2.8	0.3	57	20	2.9	0.3	7
Great Skua	150	3.0	1.0	50	3	1.0	0.0	3
Sandwich Tern	133	10.2	4.7	13				
Arctic Skua	100	1.8	0.2	55	9	1.5	0.3	6
Minke Whale	85	1.9	0.3	46	20	1.3	0.1	16
Shag	43	14.3	7.3	3				
Common Tern	35	5.0	1.5	7	1	1.0		1
Grey Seal	33	2.1	0.7	16	5	1.7	0.3	3
Black-headed Gull	28	3.5	0.7	8				
Common Gull	22	1.5	0.1	15	4	1.3	0.3	3
Storm-Petrel	11	1.4	0.3	8				
Harbour Porpoise	10	2.0	0.0	5	2	2.0		1
Sabine's Gull	2	1.0	0.0	2				
Fin Whale	1	1.0		1				
White-beaked Dolphin	1	1.0		1				

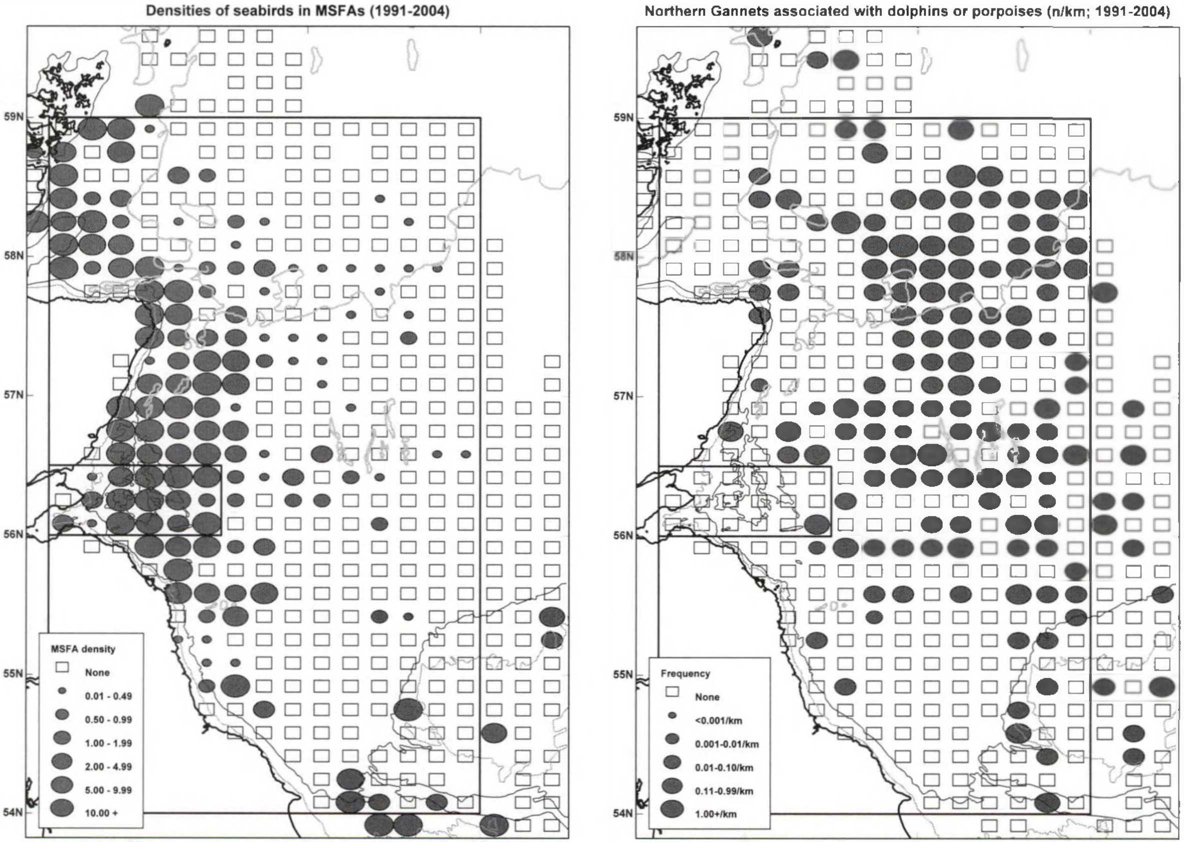


Figure 5.4.4. Distribution patterns of auk-driven multi-species feeding assemblages and of foraging associations between Gannets and cetaceans in the northwest North Sea, based on large-scale ship-based surveys 1991-2004 in the study area at large onboard FRV Tridens and RV Pelagia.

Geographical distribution of MSFAs

The three types of MSFAs, human induced, cetacean driven and 'natural' did not have a similar distribution. 'Natural' MSFAs were generally formed in coastal waters of very high seabird density (Fig. 5.4.4) and were nearly all encountered within 100km from the nearest coast (Fig. 5.4.5). Comparing Figs. 5.4.2 and 5.4.4, it is obvious that most these flocks were formed where Guillemots and Kittiwakes co-occur in high densities (Fig. 5.4.6). The relationship between densities of cetaceans and the occurrence of MSFAs around hunting marine mammals is a lot weaker, mainly because within c. 80km from the coast cetaceans were largely ignored by seabirds (Fig. 5.4.4). Distance to the coast (Fig. 5.4.7) and water depth (Fig. 5.4.8) were two key parameters underlying the frequency of formation of cetacean-driven MSFAs.

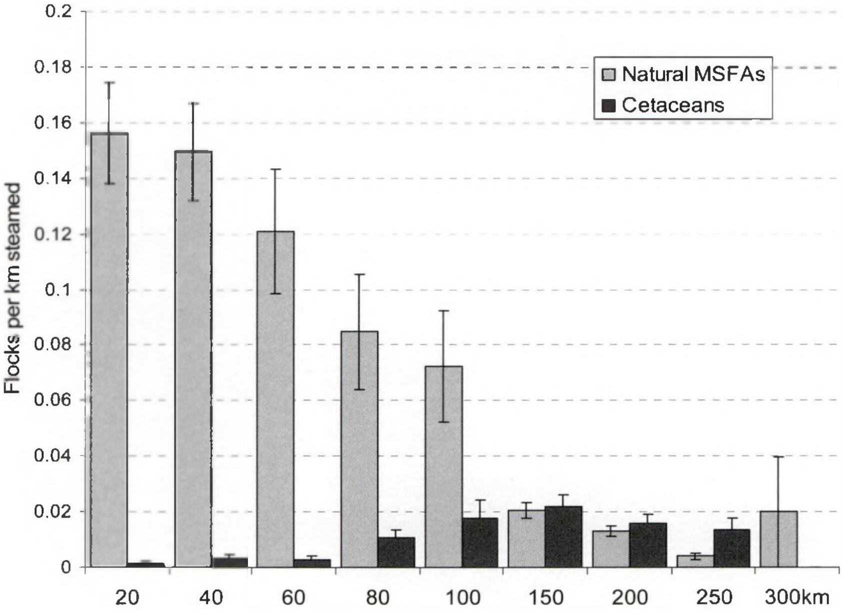


Figure 5.4.5. Average number (± SE) of MSFAs per km surveyed with distance to the UK coast (km), from ship-based surveys, June-July 1991-2004, based on 20 transects perpendicular to the coast in the study area at large. Shown are seabird flocks associated with hunting marine mammals (dark grey), and 'natural' feeding frenzies (light grey, seabirds, sometimes with marine mammals, jointly exploiting a shared resource).

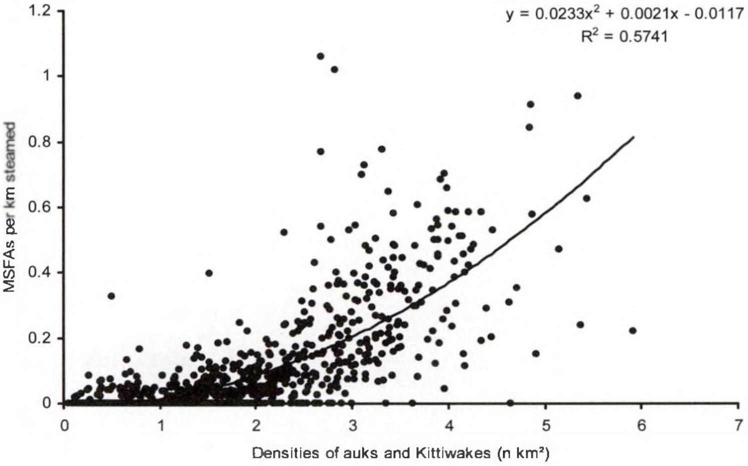


Figure 5.4.6. Frequency of 'natural' MSFAs (flocks observed per km steamed) with density of large auks (Guillemots and Razorbills) and Kittiwakes, as calculated for 1116 5'x10'rectangles where at least 5 km (1.5 km²) has been surveyed, June-July 1991-2004.

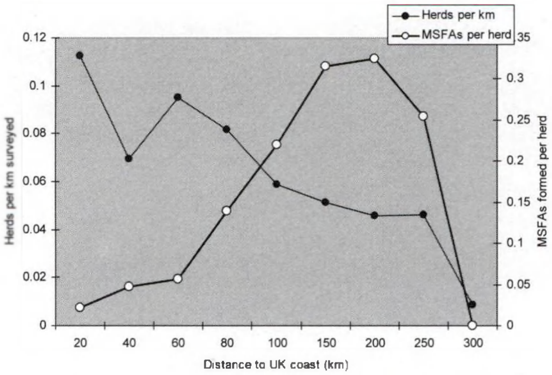


Figure 5.4.7. Relative abundance of cetacean herds with increasing distance to the UK coast (n km^{-1}) and frequency of MSFAs formation (bird flocks associated with cetaceans as a fraction of all herds of marine mammals observed), June-July 1991-2004.

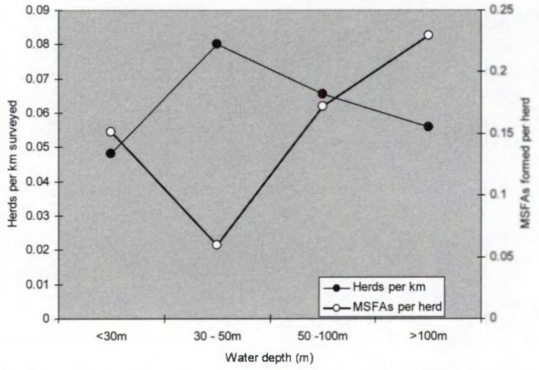


Figure 5.4.8. Relative abundance of cetacean herds with increasing water depth (n km^{-1}) and frequency of MSFAs formation (bird flocks associated with cetaceans as a fraction of all herds of marine mammals observed), June-July 1991-2004.

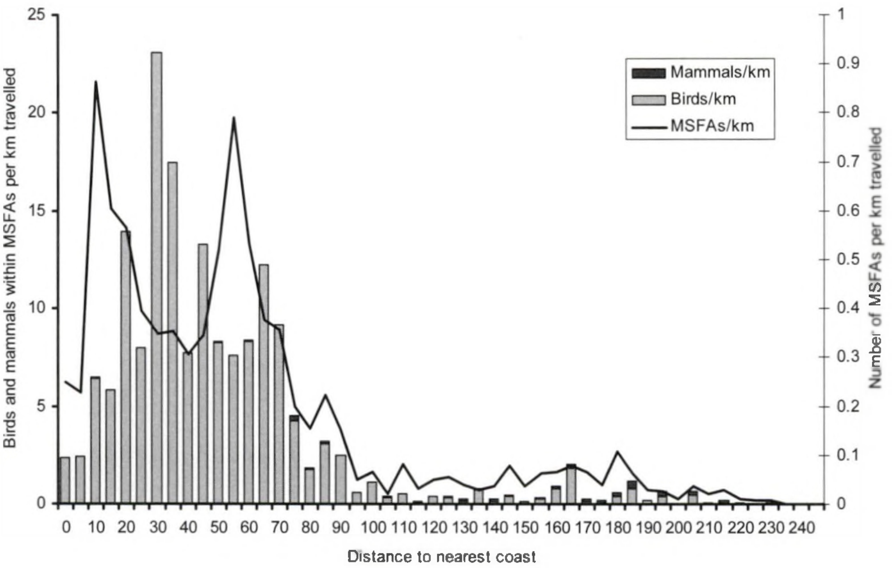


Figure 5.4.9. ***(A)*** *Numbers of seabirds and marine mammals per km participating in MSFAs (bar graph; types 2 and 3 combined) and the number of MSFAs per km (line graph) with distance to the nearest UK coast within the principal study area (0-90km from the coast; 56°-56°30'N, 3°W-1°W) and further eastward (>90km from the coast; same latitude interval; 1°W-2°E).*

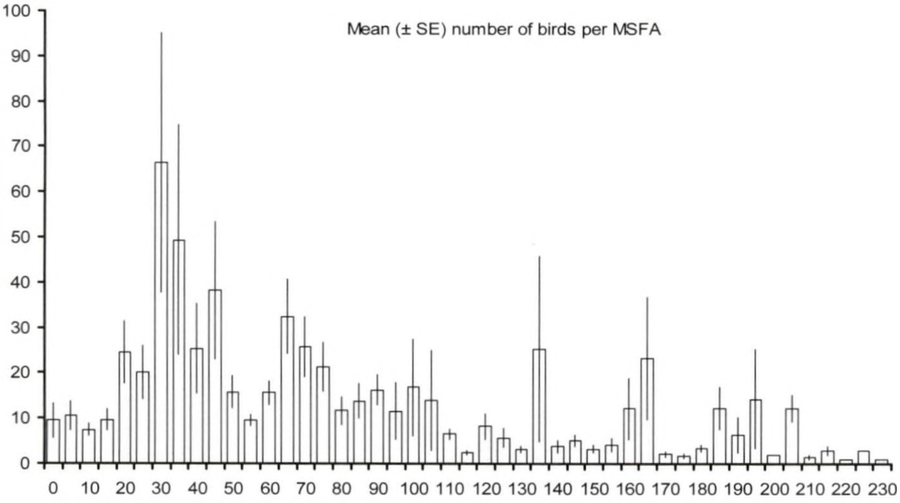


Figure 5.4.9. (B) *Mean (± SE) numbers of flock participants in multi-species feeding frenzies with distance to the nearest UK coast within the principal study area (0-90km from the coast; 56°-56°30'N, 3°W-1°W) and further eastward (>90km from the coast; same latitude interval; 1°W-2°E). 'Natural' MSFAs and cetacean-induced assemblages combined.*

Flock size and frequencies of MSFAs varied with distance to the coast, with relatively many, but small MSFAs near the coast. Within the principal study area, numerous smaller MSFAs were formed at very short distances to the coast (0-20km), fewer and larger flocks at 20-50km distance, numerous small flocks at 50-70km distance and a declining level in most parameters further away from the coast (Fig. 5.4.9). Summarising variations in the density of MSFAs per unit area surveyed within the principal study area, and the mean numbers of seabirds within flocks in broad habitat zones defined by variation in bathymetry and hydrography in the area (Fig. 3.2.8), it appears that mixed waters can be characterised as having rather few and consistently very small MSFAs (mean 8.2 ± 1.2 seabirds, n = 164 MSFAs, when shallow and deeper waters are combined). Freshwater influenced waters (Firth of Forth and approaches) and offshore stratified waters have consistently larger flocks (15.1 ± 2.6, n = 121 and 17.7 ± 2.0, n = 372 MSFAs), while the bank areas had a rather variable pattern, but with on average by far the largest MSFAs (34.6 ± 4.8, n = 536 MSFAs, when all three bank areas were combined; Fig. 5.4.10)

Energy requirements

In biomass terms, the seabird community in the principal study area was dominated by auks (Guillemot, Puffin and Razorbill), Gannets and Kittiwakes (98.0% of all birds found in transect; Fig. 5.4.11). Following this, the energy requirements of the seabird community in the principal study area was overwhelmingly dominated by the same species (99.8% of the energy requirements of all seabirds present; Table 5.4.7). The energy requirements per unit area within the principal study area (118,380 kJ day^{-1} km^{-2}) were on average 3.9x higher than those for the study area at large (30,260 kJ day^{-1} km^{-2}). Figure 5.4.12 illustrates the relative importance of the nearshore sector between Moray Firth and Farne Islands, and particularly of the Firth of Forth approaches (principal study area of the project), in terms of (potential) daily energy utilisation by seabirds simply based on mean densities observed, 1991-2004.

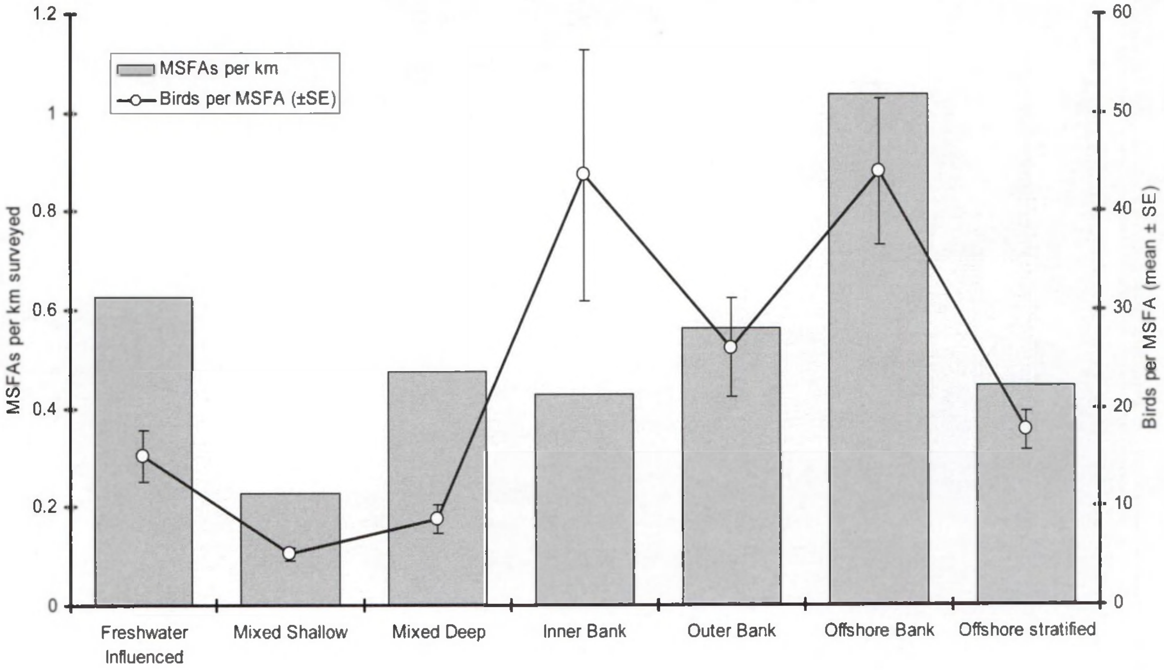


Figure 5.4.10. Mean (± SE) numbers of flock participants (line) in 'natural' multi-species feeding frenzies and frequency of MSFAs encounters (n km^{-1}) in broad habitat zones defined by variation in bathymetry and hydrography in the principal study area (1991-2004 surveys). See Fig. 3.2.8 for partitioning of the study area.

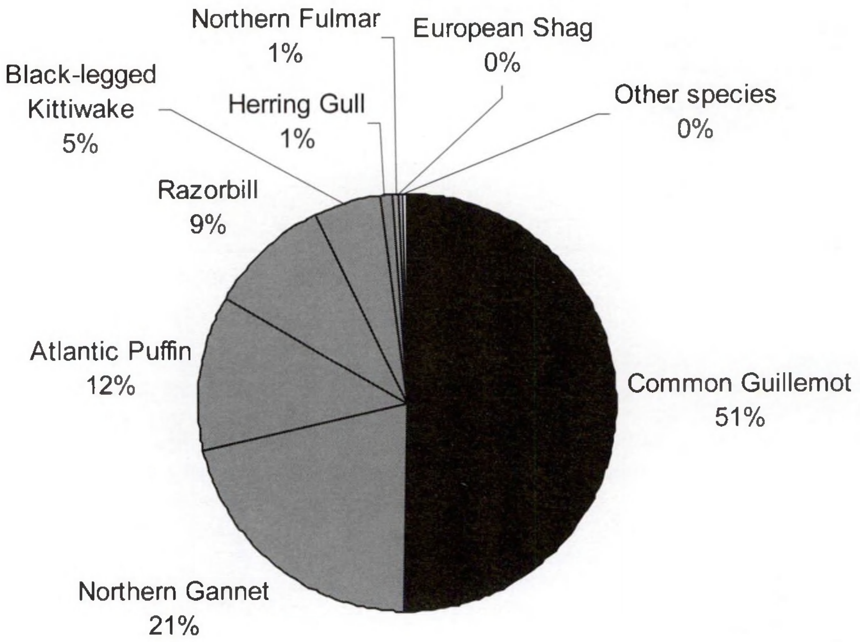


Figure 5.4.11. Relative abundance by biomass of seabirds in the principal study area off the Firth of Forth, based on ship-based surveys on board FRV Tridens and RV Pelagia, 1991-2004.

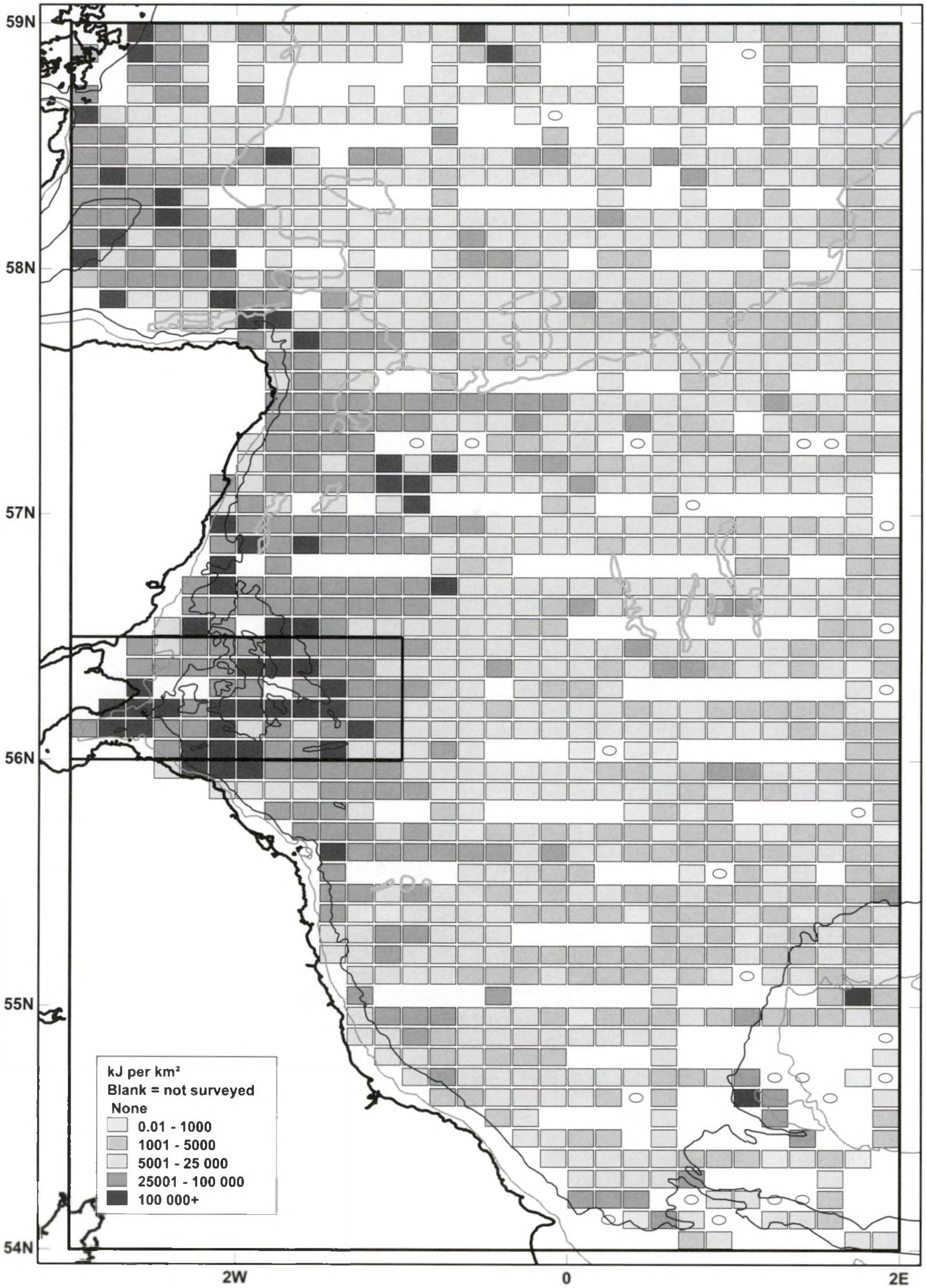


Figure 5.4.12. Daily energy utilisation by seabirds per km² per 5'x10'rectangle based on mean seabird densities in June-July 1991-2004 and species-specific Field Metabolic rates (FMR) within and beyond the primary study area off the Firth of Forth (Tridens and Pelagia surveys combined).

Table 5.4.7. Estimated total number of seabirds in the study area at large (NW North Sea; 54-59°N, 3°W-2°E) and in the principal study area (Wee Bankie area; 56°N-56°30'N, 3°W-1°W), from mean densities observed in June-July 1991-2004 (FRV Tridens and RV Pelagia surveys combined) and energy requirements (kJ x 10⁶) per species in either area. BMR values after Camphuysen 1996, assuming FMR =3.9 BMR for breeding birds and 2.5 BMR for non-breeding birds. Energy requirements are calculated for the mean number of individuals present over a 61-day period (June-July).

	Area at large (54°-59°N)			**Study area (56°-56°30'N)**		
Species	Estimated number	Energy requirements kJ x 10^6	%	Estimated number	Energy requirements kJ x 10^6	%
Common Guillemot	1,331,700	136,862.1	53.6	220,200	22,630.6	51.5
Northern Gannet	133,000	35,546.2	13.9	26,700	7,147.6	16.3
Atlantic Puffin	273,100	16,838.6	6.6	97,400	6,005.9	13.7
Razorbill	186,500	15,331.0	6.0	48,500	3,989.6	9.1
Black-legged Kittiwake	370,400	22,842.7	8.9	53,900	3,323.6	7.6
Herring Gull	19,200	2,366.3	0.9	2,500	306.7	0.7
Northern Fulmar	229,200	23,558.1	9.2	2,600	267.8	0.6
European Shag	2,400	501.5	0.2	1,000	208.3	0.5
Other species	36,700	1,577.5	0.6	1,500	89.5	0.2
Totals	2,582,200	255,424.1	100	454,300	43,969.6	100

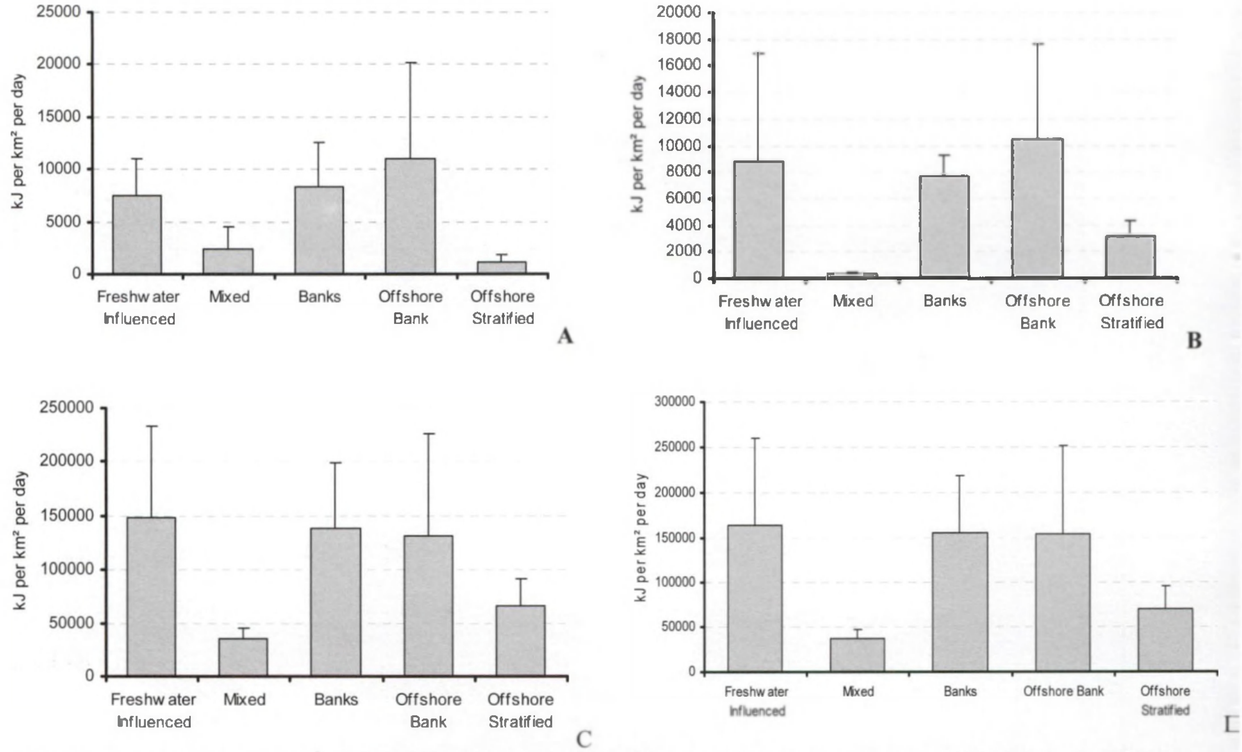


Figure 5.4.13. Energy acquired (kJ km⁻² d⁻¹) by (A) Northern Gannets, (B) Black-legged Kittiwakes, (C) Common Guillemots and (D) these thre species combined within 5 broad zones defined by bathymetry and hydrography (see Chapter 3, mixed shallow and deeper waters and inner an outer bank areas combined). Calculations based on densities of actively foraging Gannets and Kittiwakes and densities of swimming Guillemot 1991-2004 surveys RV Tridens and RV Pelagia, within the principal study area..

When summarising variations in the density of the study species (n km^{-2}) within the principal study area in broad habitat zones defined by variation in bathymetry and hydrography in the area (Fig. 3.2.8), it is important to discriminate between 'plain densities' (birds recorded in transect, irrespective of behaviour) and foraging individuals when the actual energy intake has to be estimated. For aerial seabirds this is most straightforward, because foraging and/or feeding individuals can be readily separated. For pursuit-diving seabirds, this is less easy, because avoidance behaviour of swimming birds may influence their behaviour when encountered. 'Present swimming' was taken as a proxy for foraging distribution in Guillemots, thereby omitting birds in flight recorded as 'in transect' by the snapshot method. Foraging (searching) or feeding birds were selected for Gannets and Kittiwakes.

The results suggest that within the principal study area, corrected for the size of the respective zones defined by bathymetry and hydrography, Northern Gannets acquired 24% of their energy by feeding in freshwater influenced waters, 11% in mixed waters (mostly in deeper waters), 59% over the banks and 7% in offshore stratified waters (Fig. 5.4.13A). Note that Gannets travelled far beyond the boundaries of the principal study area, so that this budget should not be applied to the Bass Rock Gannetry as a whole, but just to the birds foraging within the principal study area. For Kittiwakes, 53% of the energy was acquired on the banks, 18% in offshore stratified waters, 27% in freshwater influenced waters and only 2% in mixed waters (Fig. 5.4.13B). A fairly similar picture emerged for Guillemots, with 48% of the energy being acquired on the banks, 20% in offshore stratified waters, 24% in freshwater influenced waters and only 8% in mixed waters (Fig. 5.4.13C). A combination of all data suggests that for these three species the bank areas are the most important foraging grounds (49% of the energy acquired) and that mixed waters near the coast are relatively unimportant (8%) (Fig. 5.4.13D).

All Shags observed during surveys within the principal study area were foraging in waters that have been categorised as freshwater influenced and this is the area where these birds seemingly acquire most (if not all) the energy required (not included in Fig. 5.4.13D).

5.5 Foraging locations and depth utilisation

Methods to obtain locational data

Locational data were obtained using VHF telemetry for Kittiwakes and Shags in 2001, compass loggers for Kittiwakes, Shags and Guillemots in 2002 and for Guillemots in 2003, satellite tags for Gannets in 2002 and 2003, and GPS loggers for Gannets in 2002 and for Gannets and Shags in 2003. Technical details for each of these instruments are provided in Chapter 1.6 and Appendix 1. Adults were caught at the nest using a crook or noose pole. Loggers were attached to feathers on the back or central tail feathers using Tesa© tape. The temperature sensor of the compass and GPS-TD loggers was secured with an L-shaped piece of thermoplastic and Tesa© tape, so that it hung beneath the tail feathers. Attachment time of loggers was 5-25 mins, depending on the species and logger.

In 2001, locations were obtained using **VHF telemetry**, by attaching radio transmitters (Biotrack Ltd) to the birds and following the direction and strength of the signal from two tracking stations. In the case of the Kittiwake and Guillemot, both offshore feeders, the first station was on the Isle of May (height 73 m) and the second at the Cairn O' Mount (56°55'N, 02°34'W; height 450 m). The two stations were in constant contact by mobile phone. Each frequency was monitored for 5 minutes once every 20 minutes. The accuracy of fixes was assessed by placing a radio transmitter on FRS RV *Clupea*, whose exact location was known. The ship was radiotracked continuously on 6 and 7 June, while she was operating in the study area.

For the Shag, an inshore feeder, one tracking station was on the Isle of May and the second tracking station was mobile, operating from a car travelling up and down the roads along the south Fife coast. The mainland observer was notified by mobile phone every time a Shag departed on a foraging trip and advised of a suitable site to enable successful triangulation with a fix from the Isle of May. For the majority of trips, fixes were made from more than one point along the coast but, because of time constraints, only the location of the first dive bout of a trip was determined.

Considerable post-processing of the data was required for the two offshore feeders due to: (1) the larger distances involved leading to greater error in the estimated locations; (2) birds regularly being out of range of either or both stations; and (3) in the case of the Kittiwake, the method of foraging leading to much more complex foraging trips compared to those made by Guillemots and Shags. When a foraging bird was in receiving range of both tracking stations, fixes were derived by triangulation. An estimate of error was obtained by taking the mean error of fixes at different distances recorded for a test transmitter placed on FRV *Clupea*. In cases where the bird was out of range of one, or both, stations, fixes were extrapolated using the last known bearing prior to signal loss, or first known bearing following signal loss, combined with dead reckoning based on the average flight speed (values given below).

For the Shag, birds were always in range of both tracking stations, so post-processing was more straightforward. The same error margins were derived from the *Clupea*'s position, but the errors were much smaller because triangulation was usually from three rather than two locations, and distances between the tracking stations and the birds were generally much smaller.

The method of obtaining fixes from **compass loggers** follows on the principal of dead reckoning, whereby a foraging track is generated from a series of joined vectors. The direction of each vector is provided by two perpendicular compass vector sensors, and the length of the vector is derived from published mean flight speeds for each species (13.1 $m.s^{-1}$ for Kittiwake, 15.4 $m.s^{-1}$ for Shag, 19.1 $m.s^{-1}$ for Guillemot, Pennycuick 1997). Thus, when the bird is not flying, the vector has zero length. Each vector was corrected for wind speed and direction, using hourly weather data from Leuchars weather station, 20 km north of the Isle of May, and for the orientation of the logger on the birds' back, estimated from photographs.

The initial step of the process involved identifying sections of flight. Different activities (colony, flight, sea surface and diving) were readily identified from the output of the logger (see WP7 interim report 2002 for details). The second step was to plot compass1 values against compass2 values. For true bearings to be calculated from the data, this scatter plot must take the form of a ring of data points, from which accurate estimates of maximum compass1 values (referring to south) and maximum compass2 values (referring to east) can be made. The coded flights, with associated bearing estimate, were then combined in Mulitrace-route (Jensen Software Systems) to produce a foraging track. Each foraging track was viewed in Excel. A filtering process was carried out to remove those tracks that did not produce a satisfactory output. The criteria for this decision were: 1) a close association between the start and end point (in reality these are in the same place, i.e. the nest site); and 2) a track shape consistent with existing information from VHF telemetry, i.e. travelling flights were relatively direct. This step appears somewhat arbitrary but, in practice, it was clear which tracks to retain and which to discard. Among discarded tracks, a second check was made to ensure that the flights had been correctly coded. If no improvements could be made at this point, the track was discarded. For retained tracks, the vectors were run through an algorithm in Excel to correct for drift. This method brings the end point to the same location as the start point and distributes the drift evenly between all flight vectors.

The three steps detailed above were all required for a foraging track to be deemed satisfactory, namely: 1) successful coding of flights; 2) identifiable ring of data points in scatter plots between compass1 and compass2; and 3) close association between start and end points of the foraging track. Table 5.5.1 summaries this filtering process for the three species. In Shags and Guillemots, the majority of foraging trips recorded produced acceptable tracks. However, for Kittiwakes, the percentage of unacceptable tracks was much higher due to problems determining a ring of data points and/or wide disparity between start and end points. The likely explanation for the former problem was the Kittiwake's mode of flight. The two compasses are affected by tilt of the logger. Shags and Guillemots have a powerful, direct flight that apparently causes negligible tilt in the logger. However, the indirect, meandering flight of Kittiwakes presumably causes tilt to such an extent that no scatter ring is detected, and thus no bearing can be derived. The likely explanation for the second problem was that it was not possible to satisfactorily separate travelling flight from foraging/hovering flight on the logger traces. A number of vectors were probably incorrectly assumed to be the former, when in reality the bird was in a bout of foraging flight, when x-y location may not change at all. For these tracks, we were confident that the first flight (outward) and last flight (inward) represented travelling flight, and could therefore derive departure and arrival bearing for these trips. The difficulty in deriving foraging tracks from compass loggers for this species was the major reason for not deploying them in 2003.

Satellite transmitters (platform terminal transmitters, PTTs) provided locations of Gannets at sea during early to mid chick rearing (chicks 2-7 weeks post-hatching) in 2002 (24 June – 5 Aug) and 2003 (3 July – 4 Aug). In 2002, two combinations were used: (1) seven adults were fitted with a PTT (Microwave Telemetry Inc, Columbia, USA; mass = 30g); (2) nine birds were fitted with a PTT plus a stomach-temperature logger under licence from the UK Home Office. In 2003, nine adults were equipped with a PTT only. PTTs were attached as described by Hamer *et al.* (2000) and had a duty cycle of continuous transmission. On recapture, devices were removed and a blood sample of less than 0.1 ml was taken, under Home Office licence, for determination of sex from DNA, based on the principle that males and females differ in their CHD I genes (Griffiths et. al. 1998). Data generated by the PTTs were processed using the ARGOS facility (CNES, Tolouse, France) and were provided in latitude/longitude format. Only high-quality locations (classes A, 0, 1, 2, and 3) were used in the analysis. Locations of Gannets at sea were overlaid on a geographic co-ordinate system (GCS_WCS_1984) in ArcGIS. Trip duration, destination and average travel speed over complete foraging trips were determined following Hamer *et al.* (2000).

Table 5.5.1 Number (and%) of acceptable trips remaining after filtering of data recorded by compass loggers in the three species.

Species	Year	Foraging trips	Flight coded	Scatter ring	Acceptable tracks	
Black-legged Kittiwake	2002	27	25	13	4	(15%)
European Shag	2002	41	38	38	31	(76%)
Common Guillemot	2002	35	35	28	26	(74%)
Common Guillemot	2003	24	22	22	18	(75%)

Table 5.5.2 Sample sizes of logger deployments for the four species.

Species	year	breeding period	logger	*n* birds	*n* trips	*n* locations
Gannet	2002	chick-rearing	Satellite telemetry	16	46	510
	2002	chick-rearing	GPS	10	8	901
	2003	chick-rearing	Satellite telemetry	9	50	442
	2003	chick-rearing	GPS	23	24	6177
Shag	2001	chick-rearing	VHF telemetry	44	45	48
	2002	chick-rearing	Compass	20	31	66
	2003	chick-rearing	GPS	10	32	48
Kittiwake	2001	incubation	VHF telemetry	11	11	124
	2001	chick-rearing	VHF telemetry	22	28	255
	2002	chick-rearing	Compass	17	4	491
Guillemot	2001	chick-rearing	VHF telemetry	10	0	0
	2002	chick-rearing	Compass	9	26	78
	2003	chick-rearing	Compass	8	18	37

For all **GPS loggers**, data were collected in longitude and latitude format with a precision of 3-19 m. For Gannets, sampling intervals were 3 (n = 5), 15 (n = 3) and 20 (n = 2) mins in 2002, whereas all GPS-loggers and GPS-TDs had sampling intervals of 3 mins in 2003. Deployment dates were 8 August - 15 August 2002 and 8 July and 2 August 2003. In 2002, 5 birds were given a GPS-log and a PreciTD and 5 birds were given a GPS-log and also fed a Minitemp-xl stomach-temperature logger. In 2003, 4 birds were given a GPS-log, a PreciTD and a Minitemp-xl stomach-temperature logger; and 19 birds were deployed with a combined GPS-TDlog and a Minitemp-xl logger. Upon recapture, devices were removed, and a blood sample of less than 0.1 ml was taken for determination of sex. For Shags, sampling interval was 5 mins (n = 8) or continuous (minimum 1 fix per second, n = 2), and birds carried the loggers for 1 day. Output from GPS loggers required little post-processing because the latitude and longitude were present in the raw data. By combining the high number of fixes of compass loggers, with a better accuracy than satellite tags, the GPS loggers developed in this project dramatically improved the quality of data on foraging location. The current limitation of this technology is that the logger unit is large compared to the other devices described above, and therefore could not be deployed on Kittiwakes or Guillemots. Table 5.5.2 shows the sample sizes after analysis was complete.

Statistical analysis

When comparing differences between years, sexes and species, REML (Residual Maximum Likelihood) analyses were carried out in Genstat. The relevant independent variables were entered into the models as fixed effects, with bird identity included as a random effect to account for pseudoreplication of data for individual birds (Patterson and Thompson 1971; Genstat 1993). Comparison of the deviances of models with and without bird identity then tested whether or not differences in the behaviour of individual birds accounted for any of the observed variation in the dependent variables. Stepwise deletions of fixed effects from the minimum adequate model were carried out and the significance of the fixed effects was estimated from the Wald statistic (W), which has a χ^2 distribution. Means are presented ± 1 S.E. unless otherwise stated.

Foraging areas from logger data

European Shags used three main foraging areas: (a) inshore, west of the colony; (b) inshore, north of the colony; and (c) close to the island (Fig. 5.5.1). Location a) was the most frequently used. The usage of foraging locations in each year is given in Table 5.5.3. Birds used area c) least in 2001, and most in 2003. In contrast, area a) was used very extensively in 2002, and least in 2003. These differences resulted in a significant difference in foraging range between the years (all locations: 2001: 9.5 ± 3.1 km, n = 48 locations; 2002: 8.1 ± 4.1 km, n = 66 locations; 2003: 5.5 ± 4.2 km, n = 48 locations; REML: W = 7.15, $P < 0.001$; maximum range per trip: 2001: 9.5 ± 3.1 km, n = 48 trips; 2002: 8.0 ± 4.4 km, n = 31 trips; 2003: 5.2 ± 4.6 km, n = 32 trips; REML: W = 6.25, $P < 0.01$).

The improved quality of data obtained from more sophisticated loggers is well demonstrated by results from Shags, where VHF telemetry was used in 2001, compass loggers in 2002 and GPS loggers in 2003. VHF provided single fixes per foraging trip. Compass loggers provided foraging tracks with unknown variations due to sea and wind drift. GPS loggers gave very accurate locations (Appendix 1) and accounted for any drift. Thus, GPS loggers enabled small, lateral movements of birds whilst they were foraging or in flight to be tracked accurately for the first time (Figure 5.5.2).

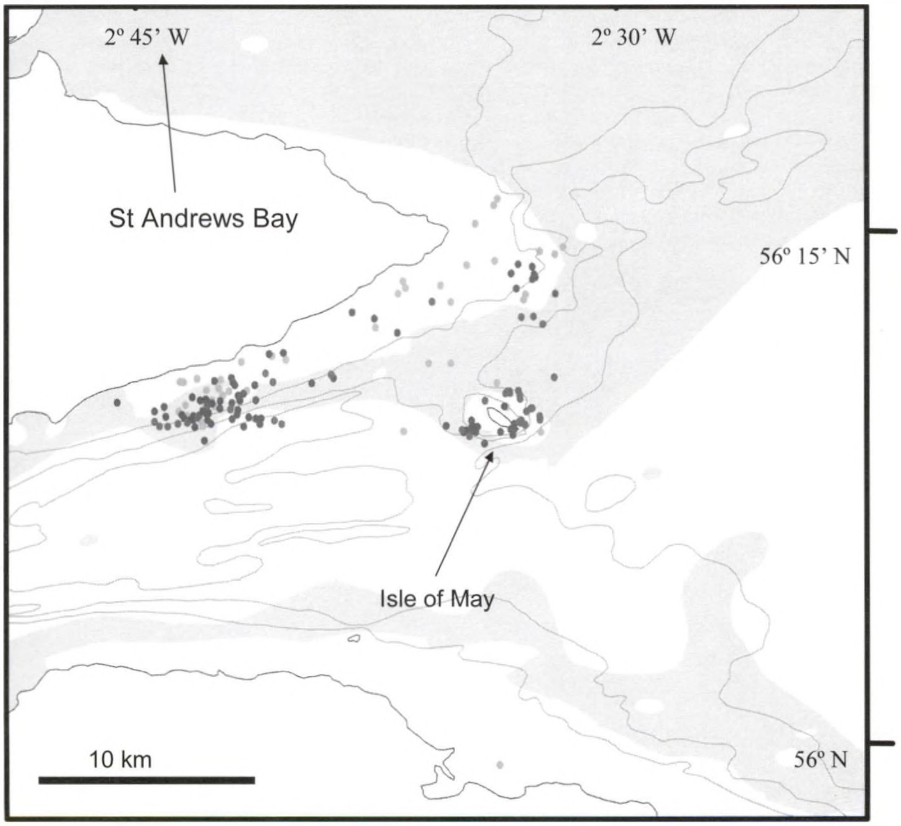


Fig. 5.5.1. Foraging locations of Shags derived from VHF telemetry in 2001 (green, n = 48 locations, 48 birds), derived from compass loggers in 2002 (red, n = 66 locations, 20 birds) and derived from GPS loggers in 2003 (blue, n = 48 locations, 10 birds). 20 m, 30 m and 40 m contours are shown. Grey areas are sandy substrates, white areas non-sandy substrates.

Table 5.5.3. Distribution of Shag foraging locations in the three main feeding areas.

	Area a	 b	 c	 other	 total
2001	25	22	1	0	48
2002	43	3	16	4	66
2003	13	21	23	0	48

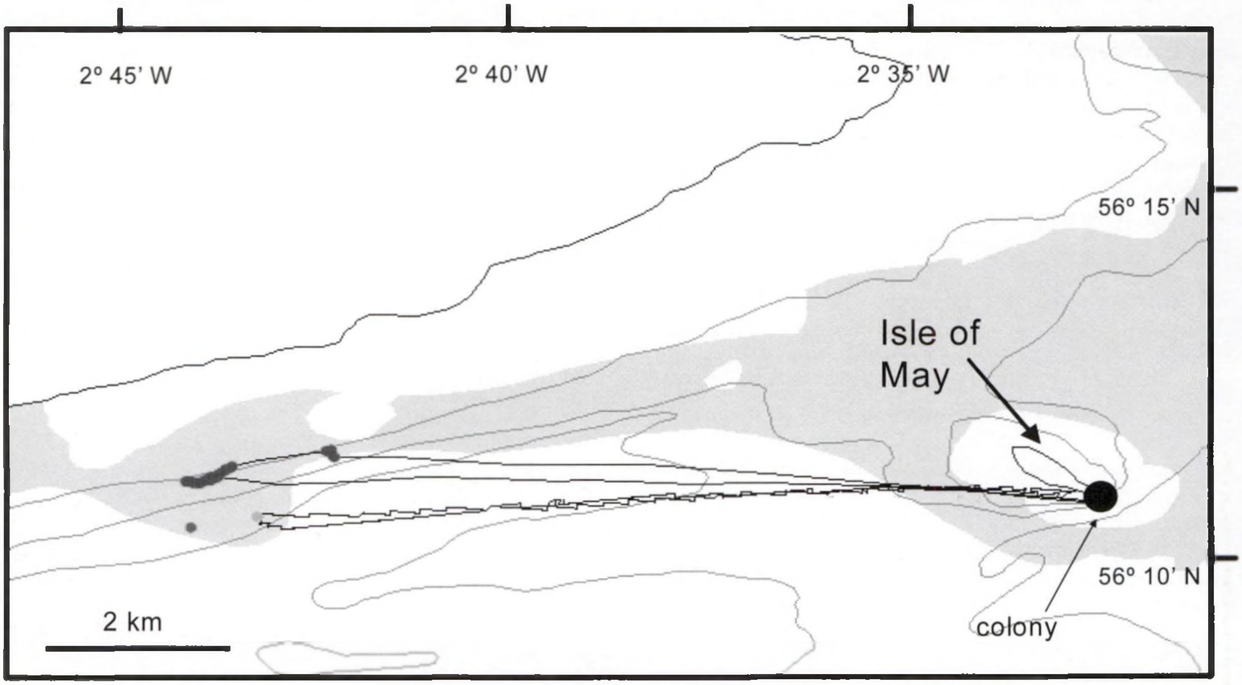


Figure 5.5.2. At sea locations for three birds foraging in a similar area but obtained from three different logger types. VHF telemetry (blue dot), gave a single foraging fix in our study. The compass logger data (black line for flight track, green dot for foraging location) provides a complete foraging track, but cannot quantify lateral drift on the water and only one fix per foraging bout is obtained. In addition, it uses a fixed wind drift correction during flight, because wind data are only available at hourly intervals. The GPS data (black line and red dots) record a complete foraging track, and quantify lateral drift both during flight and on the sea at an accuracy of <20 m (see section Appendix 1). The result is a much more complete picture of the foraging trip in which lateral drift is accurately recorded both during foraging and flight. In this example, the bird carried out two foraging bouts (n = 36 fixes and 4 fixes respectively), tracking the 20m contour in an east-west direction. The resolution of the data are also finer, hence the smoother flight track than that measured by the compass logger. 20 m, 30 m and 40 m contours are shown; grey areas are sandy substrates, white areas non-sandy substrates.

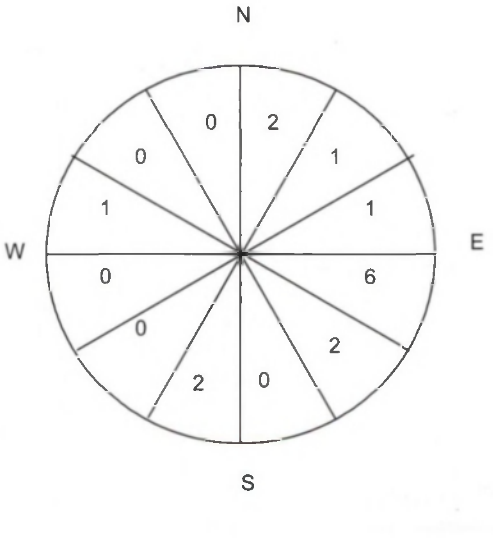


Fig. 5.5.3. Combined departure and arrival directions of Guillemots in 2001 obtained using VHF telemetry (bearings are expressed relative to the Isle of May).

Until recently, VHF telemetry was the only technology available to obtain **Common Guillemot** foraging locations. In such studies, a large proportion of birds fly out of range of one or both tracking stations. This was the case in 2001, when VHF transmitters were attached to 10 Guillemots. Few fixes were obtained during three tracking sessions during chick rearing, largely because birds were out range of both tracking stations. The problem was probably compounded by the difficulties of picking up signals from a species that spends its time away from the colony either flying low over the water, underwater or on the sea surface. In the majority of cases Guillemots were foraging out of range of the Isle of May as well as the Cairn O' Mount station, so the only data obtained were departure and arrival bearings from the island tracking station. These data indicated that birds foraged over a wide area using both inshore areas, e.g. St Andrews Bay and between the Isle of May and the Fife coast, as well as offshore of the colony. Ten out of 15 (67%) arrival or departure bearings were between 60° and 150° relative to the Isle of May (Figure 5.5.3).

In 2002 and 2003, compass loggers were available, allowing fine scale locational data to be obtained. Figure 5.5.4 shows that Guillemots were foraging much closer to the colony than expected from previous at-sea surveys (Camphuysen & Webb 1999), with the furthest distance from the colony estimated at 25.3 km. No birds flew to the Wee Bankie/Marr Bank region. Some birds foraged close to the coast west of the colony. There was a slight, but not statistically significant, tendency for foraging range to be greater in 2002 (all locations: 2002: 10.1 ± 6.6 km, n = 78 locations; 2003: 8.0 ± 5.9 km, n = 37 locations; REML: W = 2.79, p = 0.10; maximum range per trip: 2002: 12.4 ± 6.6 km, n = 26 trips; 2003: 8.5 ± 5.3 km, n = 18 trips; REML: W = 2.09, p = 0.14).

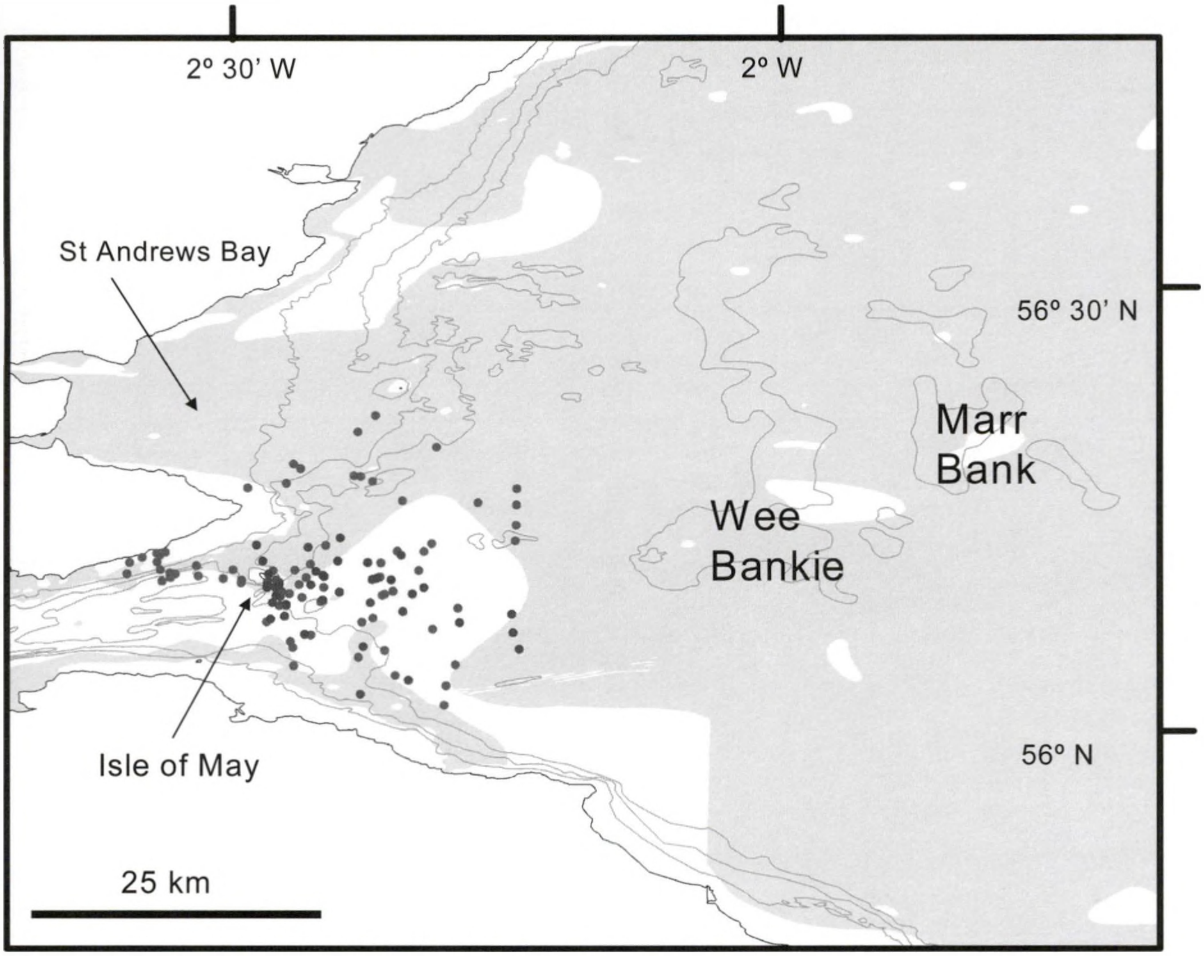


Fig. 5.5.4 Foraging locations of Guillemots derived from compass loggers in 2002 (blue, n = 78 locations, 9 birds) and 2003 (red, n = 37 locations, 8 birds). Grey areas are sandy substrates, white areas non-sandy substrates.

During the 2001 breeding season, **Black-legged Kittiwakes** used a wide variety of foraging areas, from inshore coastal areas in St Andrews Bay area out to the Wee Bankie/Marr Bank region (see Fig 5.5.5). Mean maximum foraging range per trip was 37.0 ± 16.3 km (range 13.6 – 83.5 km). Throughout June and early July, Kittiwakes were distributed throughout this region, but in mid July foraging locations became more concentrated on the western edge of the Wee Bankie. However, there was no difference in maximum foraging range between the three time periods (early June: 43.0 ± 19.9 km; late June/early July: 34.9 ± 17.0 km; mid July: 37.7 ± 14.6 km; REML: W = 0.59, ns), nor between incubating and chick-rearing birds (incubation: 38.7 ± 19.0 km; chick-rearing: 35.9 ± 15.5 km; REML: W = 0.17, ns).

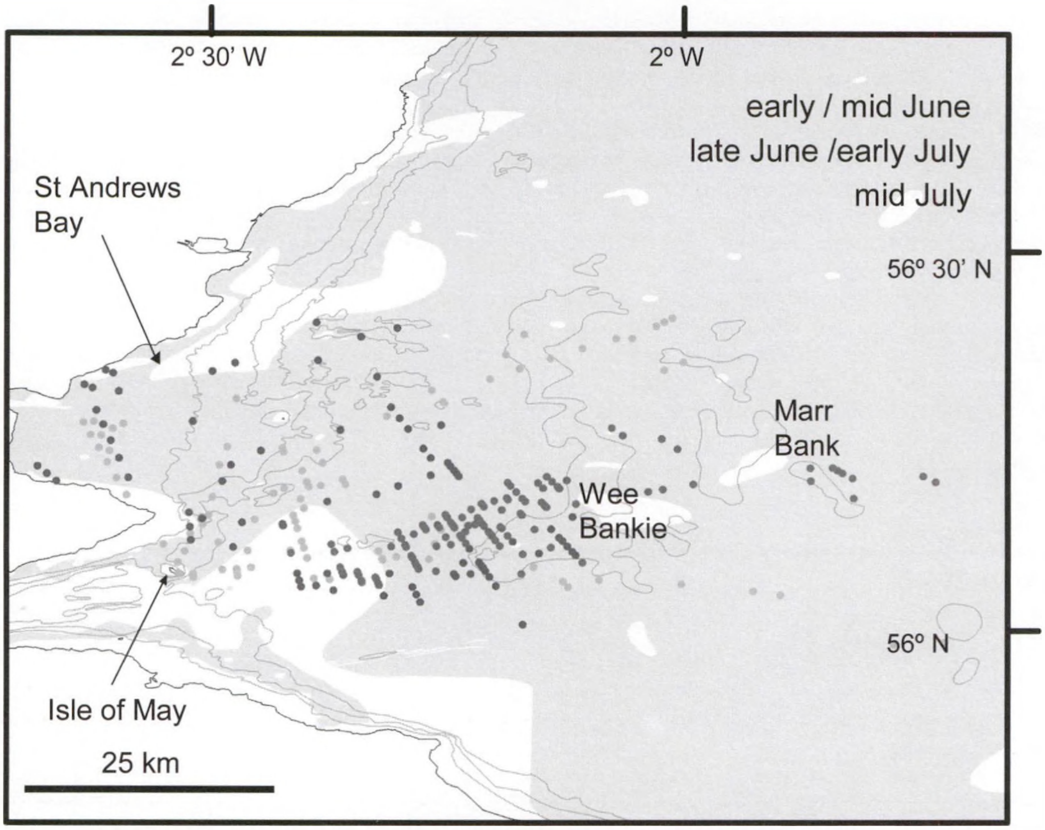


Fig. 5.5.5.Foraging locations of Kittiwakes derived from radio telemetry in early June 2001 (n =113 locations, 8 birds), late June 2001 (n = 120 locations, 14 birds) and early July 2001 (n =135 locations, 8 birds).

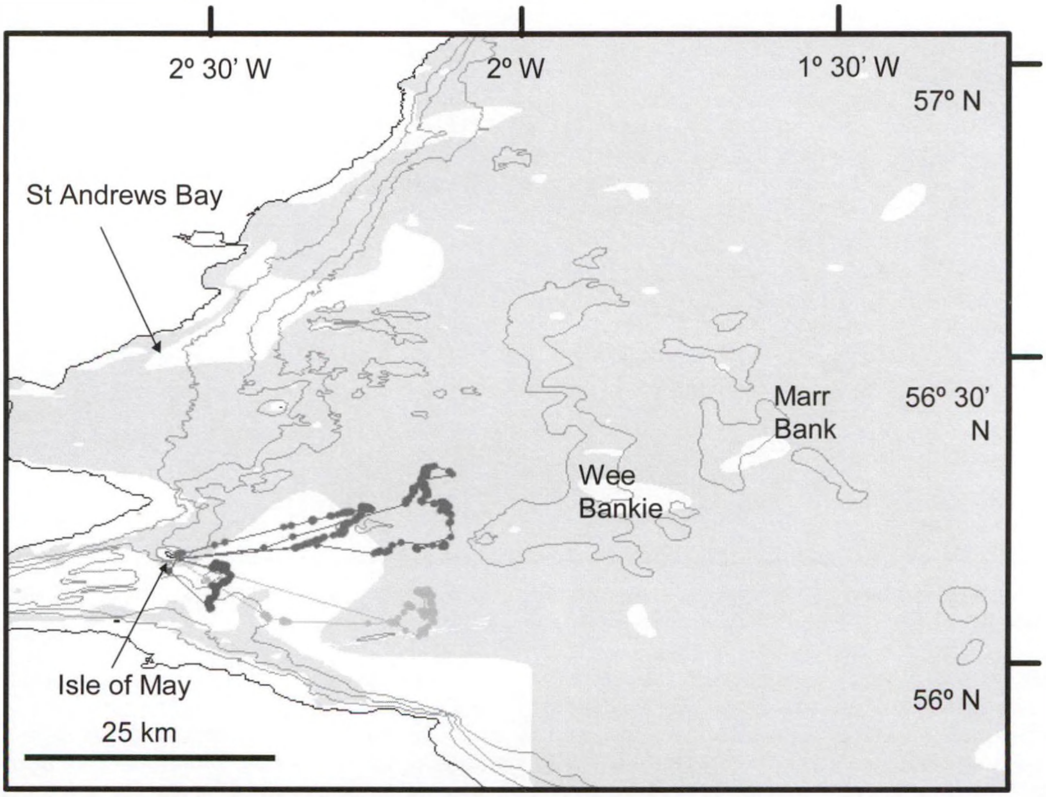


Fig. 5.5.6. Foraging tracks of Kittiwakes derived from compass loggers in 2002 (n = 491 locations, 4 birds). 20 m, 30 m and 40 m contours are shown; grey areas are sandy substrates, white areas non-sandy substrates.

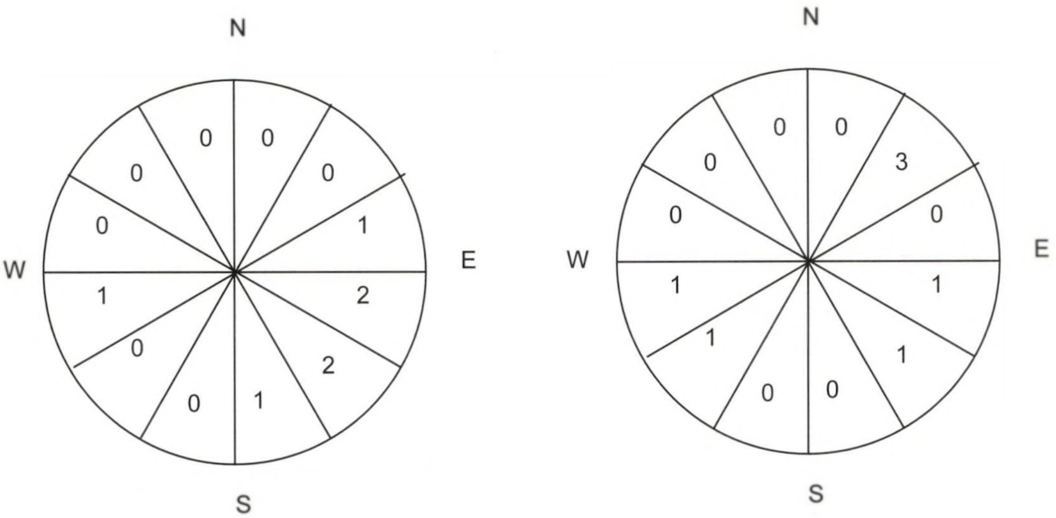


Fig. 5.5.7. Departure directions (left) and arrival directions (right) of Kittiwakes in 2002 derived from compass loggers (bearings are expressed relative to the Isle of May).

Compass loggers did not produce useable results for most foraging trips. Only four tracks were derived during chick rearing in 2002 (Fig 5.5.6), when foraging trips are shorter and flights are more direct than during incubation. For the nine trips for which heading data were available, departure and arrival directions could be calculated in seven cases (Fig 5.5.7). These data indicated that, as in 2001, Kittiwakes were using a wide variety of foraging locations, both inshore of the Isle of May and offshore out to the Wee Bankie region.

We obtained 762 high-quality locations over 147 PTT-days in 2002 and 727 high-quality locations over 110 PTT-days in 2003 for **Northern Gannets**. Locations extended to the Bergen/Viking Bank (West Norway), Halibut Bank (NE Scotland), Fisher Bank (north central North Sea), Dogger Bank (south central North Sea) and Outer Silver Pit (southern North Sea) (Figs 5.5.8 and 5.5.9). There were sufficient locational fixes to determine durations and destinations of foraging trips for 46 trips from 14 birds in 2002 and for 50 trips from 8 birds in 2003.

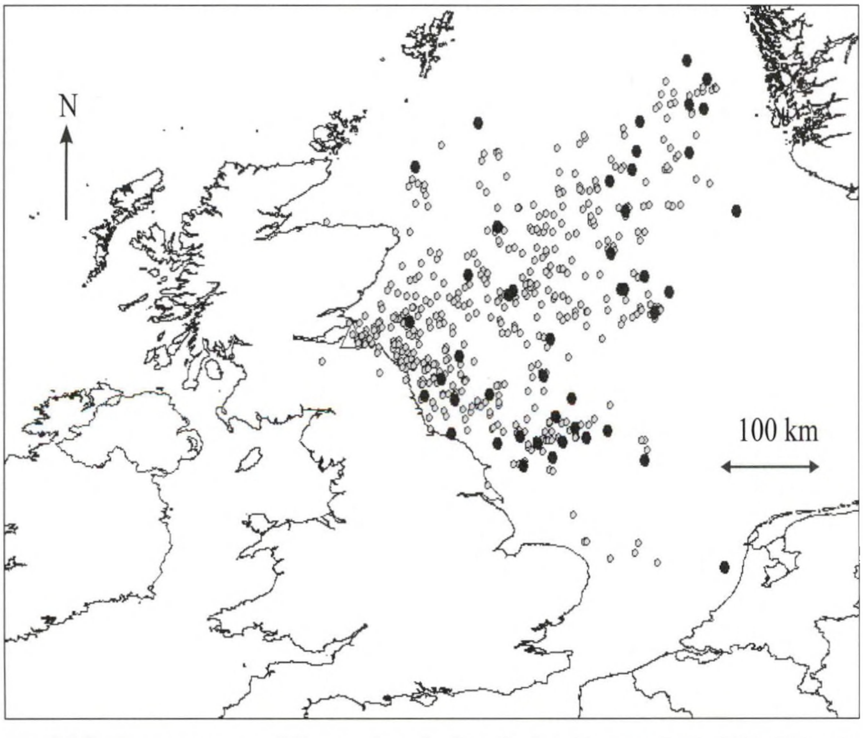


Fig. 5.5.8. Foraging ranges of Gannets from the Bass Rock (white triangle) in 2002. White circles are locations at sea; black circles are destinations of individual foraging trips.

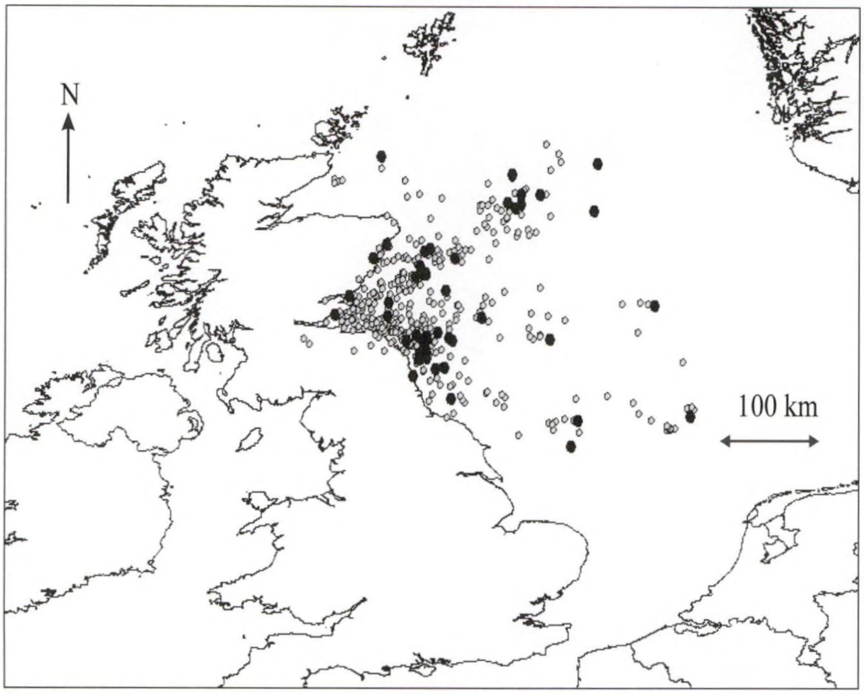


Figure 5.5.9. Foraging ranges of Gannets from the Bass Rock (white triangle) in 2003. White circles are locations at sea; black circles are destinations of individual foraging trips.

Gannets made significantly longer trips in 2002 (41.2 ± 2.8 h) than in 2003 (24.6 ± 1.7 h; REML: $W = 23.23$, $P < 0.001$). There was no difference in trip duration between sexes (males, mean = 29.6 ± 2.2 h; females, mean = 37.6 ± 3.0 h; REML: $W = 0.11$, $P > 0.1$) and no interaction between year and sex (REML: $W = 0.26$, $P > 0.1$). There was no difference in the deviances of models with and without bird identity, indicating no consistent differences among birds in trip duration.

In addition to making trips of longer duration, Gannets travelled further from the colony on foraging trips in 2002 (mean = 312 ± 18 km; Fig 5.5.8) than in 2003 h (mean = 162 ± 15 km; Fig 5.5.9; REML: $W = 20.89$, $P < 0.001$). There was no difference in range between sexes (males, mean = 198 ± 106 km; females, mean = 299 ± 145 km; REML: $W = 1.99$, $P > 0.1$). There was no interaction between factors and no consistent variation among birds. Bearings to destinations of foraging trips (indicated by locations at maximum distance from the colony during each trip) did not differ significantly between years (REML: $W = 0.01$, = 1, $P > 0.1$; Figs 5.28 and 5.29) or between sexes (REML: $W = 0.29$, $P > 0.1$). However there was a significant difference in the deviances of models with and without bird identity, indicating that individual birds tended to head in similar directions on consecutive foraging trips. There was a significant relationship between maximum range from the colony and trip duration in both years (2002; $F_{1,32} = 325.9$, $P < 0.001$: 2003: $F_{1,26} = 176.1$, $P < 0.001$), according to the following equations:

2002: Maximum range (km) = 7.1 (S.E. ± 0.4) x Trip duration (h)
2003: Maximum range (km) = 6.8 (S.E. ± 0.5) x Trip duration (h)

Therefore the average travel speed over complete foraging trips (calculated as twice the slope of each regression) was 14.2 (S.E. ± 0.8) and 13.6 kmh^{-1} (S.E. ± 1.0) in 2002 and 2003 respectively. Percentage time spent on trips did not vary between years (2002, mean ± S.D. = 59 ± 19.7%; 2003, mean = 50.9 ± 11.9%; $F_{1,22} = 0.635$, $P > 0.1$) or between sexes (male, mean ± SD = 57.7 ± 20.0%; female mean = 57.9 ± 12.4; $F_{1,22} = 0.90$, $P > 0.1$;). Nor was there a significant interaction between year and sex ($F_{1,22} = 0.23$, $P > 0.1$). Gannets made longer foraging trips and travelled further from the colony in 2002. This may indicate that birds experienced lower food availability in 2002, although there was no difference in diet between years. Both sexes spent >50% of the time at sea, which is consistent with previous data indicating that adults at this colony occasionally leave chicks unattended (Lewis et al. 2004). However the percentage time at sea did not differ between years, indicating that the longer trips in 2002 did not result in chicks being left unattended any more often than in 2003.

Locational data from the GPS-loggers and GPS-TDs were overlaid on a geographic co-ordinate system (GCS_WCS_1984) using ArcGIS. Distances to the Bass Rock were calculated from equations in Hamer et al. (2000). For each trip, the maximum distance from the colony was taken as a measure of foraging range. The mean foraging range estimated by GPS loggers in 2003 was 190.4 ± 12.7 km, which was similar to the estimate of 162.2 ± 15.1 km derived from PTTs. Mean trip duration, estimated from GPS loggers in 2003, was 23.3 ± 1.9 h, which was very similar to the estimate of 24.6 ± 1.7h derived from PTTs. Mean uplinks for the PTTs per day in 2002 were 5.1 d^{-1}(± 2.1 SD) and 7.1 d^{-1}(± 1.6 SD) compared to GPS which generated fixes as frequently as every 3 minutes. As such, a much more complete picture of foraging trips was obtained (see Figs 5.5.10 and 5.5.11).

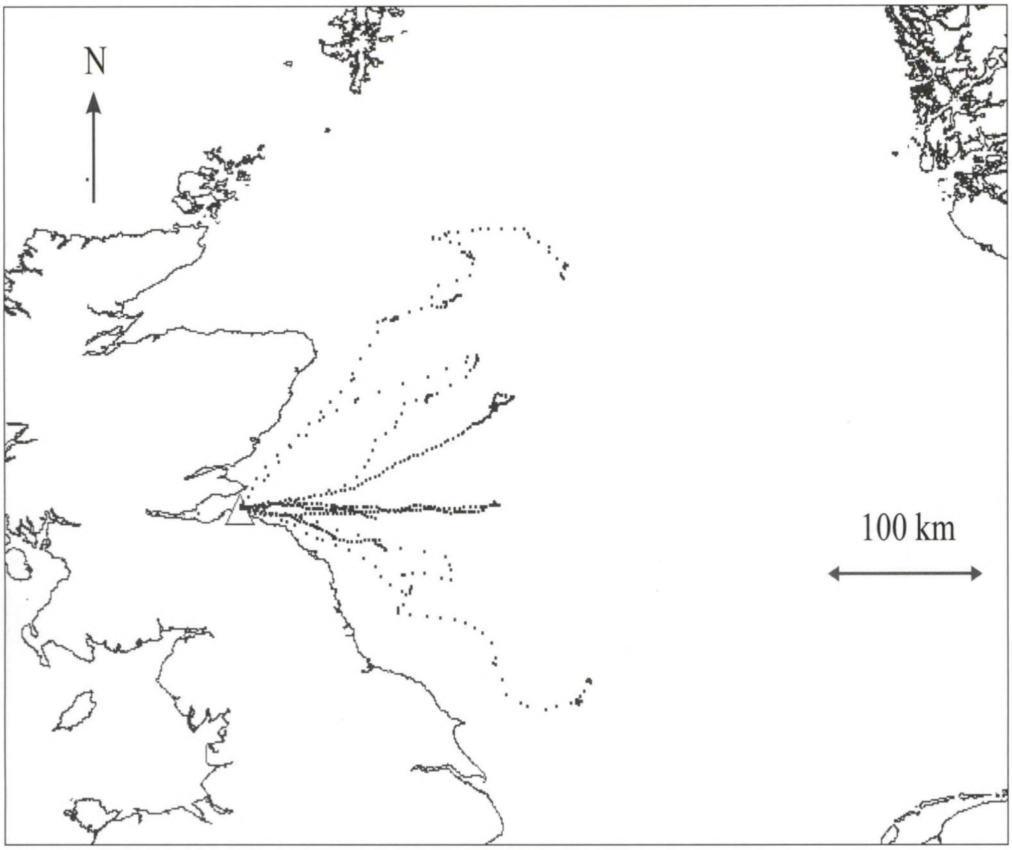


Figure 5.5.10. *All locations at sea of the Gannet from Bass Rock (white triangle) of all GPS locations (black circles) in 2002.*

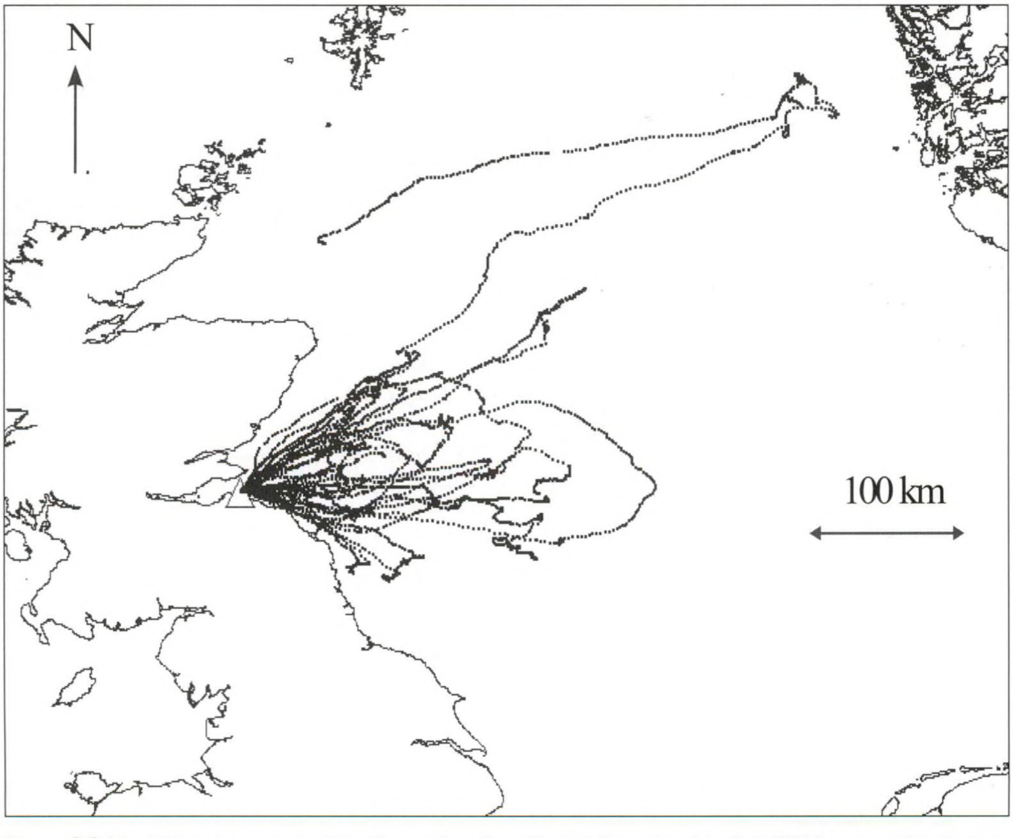


Figure 5.5.11. *All locations at sea of the Gannet from Bass Rock (white triangle) of all GPS locations (black circles) in 2003.*

Analysing depth utilisation

PreciTD temperature depth loggers were deployed on Shags, Guillemots and Gannets during chick-rearing. Bird capture and logger attachment and retrieval were achieved in a similar way to the locational loggers. Successful deployments were carried out on 29 Shags in 2001 (1st June to 7th July), of which 22 also carried Minitemp-xl stomach temperature loggers under UK Home Office licence, 48 in 2002 (28th May to 3rd July) of which 23 carried a compass logger and 25 carried a Minitemp-xl, and 8 in 2003 (1st to 12th June). PreciTD loggers were successfully deployed on 9 Guillemots in 2001 (21st June to 3rd July), on 8 in 2002 (18th to 29th June) and on 5 in 2003 (14th to 20th June). Data on Gannets were obtained in 2002 (1st July-14th August) and in 2003 (8th July – 2nd August). In 2002: 1) 5 birds had a PreciTD only; 2) 12 birds had a PreciTD and a Minitemp-xl stomach-temperature logger; 3) 5 birds had a PreciTD and a GPS-log. In 2003: 1) 4 birds were given a GPS-log, a PreciTD and a Minitemp-xl stomach-temperature logger; 2) 19 birds were deployed with a combined GPS-TDlog and a Minitemp-xl stomach-temperature logger logger. Upon recapture, devices were removed, and a blood sample of less than 0.1 ml was taken for determination of sex.

The data collected gave complete time series of depth and external temperature at 2 s intervals, providing detailed information on depth utilisation (summarised in this section), time activity budgets (section 5.4.3) and foraging habitat (chapter 7, Daunt et al. 2003). Depth data were analysed using specialist software (Multitrace-dive, Jensen Software Systems) that estimated the number of dives per foraging bout (bout definition after Sibly et al. 1990) or trip. For each dive we estimated the dive duration, surface duration, mean depth and diving efficiency (the ratio of dive duration to the dive plus following surface duration). Dives were typically U-shaped with a flat, bottom phase (bottom time) during which prey capture was assumed to take place (foraging time). Bottom efficiency was defined as the ratio of bottom time to dive duration and following surface duration. A small proportion of dives were V-shaped and hence lacked bottom time and had a bottom efficiency of zero. The loggers also recorded the duration and vertical speed of descent and ascent.

When comparing differences in normally distributed parameters (e.g. dive duration, swim speeds) between years, sexes and/or depths where there were repeated measurements for each individual, REML (Residual Maximum Likelihood) analyses were carried out in Genstat with bird identity as a random effect to account for pseudoreplication (Patterson & Thompson 1971; Genstat 1993). For Gannets, time of day was split into 01.01-07.00h, 07.01-13.00h, 13.01-19.00h and 19:01-01.00h, following Lewis et al. 2002). The number of dives per trip and per hour for 2003 were analysed by fitting a generalized linear mixed model (GLMM) with a Poisson error distribution and logarithmic link function, and bird identity as a random effect.

Depth utilisation and dive duration

PreciTD loggers were successfully deployed on 85 **European Shags**. An example of the dive depth and external temperature data collected is shown in Figure 5.5.12. In this case the Shag was diving to a depth of about 20 m and there was very little variation in water temperature with depth (integration of diving data and temperature data are dealt with in Chapter 7). Number of foraging trips per day varied from 3.15 in 2001 to 2.26 in 2003 (Table 5.5.4; no significant difference between years, GLM with poisson errors, effect of year: $F_{1,83} = 1.47$, ns). There was also no significant difference in the number of dives per trip between years (GLMM with poisson errors, effect of year: W = 1.49, ns). In all three years, the commonest foraging depth was between 21-30 m (Figure 5.5.13: 50% in 2001, 48% in 2002, 62% in 2003). However, mean dive depth was greater in 2003 than the other two years (Table 5.5.4; REML: year = 4.95, $P< 0.01$). There was significant annual variation in dive duration, which was significantly longer in 2003 than the other two years (REML, effect of year: W = 4.36, $p = 0.01$). However, the differences in dive depth and duration were not associated with significant annual differences in the other dive parameters (REML, effect of year: surface duration: W = 1.55, dive efficiency, W = 0.58; bottom duration: W = 1.00; bottom efficiency: W = 1.52; vertical descent speed: W = 0.84; vertical ascent speed: W = 2.28, all ns). Irrespective of year, dive durations were longer than succeeding surface durations (REML: W = 382.91, $P < 0.001$), and vertical ascent speeds were greater than descent speeds (REML: W = 3127.29, $P < 0.001$).

Table 5.5.4 also lists the parameter estimates for 1997 and 1998 (Wanless *et al.* 1999, Daunt 2000). Dive durations and surface durations in 2001 and 2002 were similar to those in 1997 while dive durations and foraging depths in 1998 were similar to those in 2003. However, surface durations in 1998 were considerably longer and hence diving efficiency was lower compared to 2003.

Foraging depth had a significant effect on all dive parameters (Figure 5.5.14). Dive duration increased linearly with depth, and surface duration increased exponentially. Dive efficiency declined linearly after an initial increase between 5 m and 10 m. Bottom duration initially increased linearly with depth, but flattened off at approximately 30 m, whilst bottom efficiency increased markedly between 5 m and 10 m but then declined linearly with depth. Vertical descent and ascent speed both initially increased with depth, before levelling off at approximately 30 m. For all parameters, the effect of depth was highly significant, there were no differences between years, but there were significant interactions between year and depth (REML: dive duration: depth: W = 12269.51, $P < 0.001$; year: W = 0.07, ns; interaction term: W = 61.93, $P < 0.001$; surface duration: depth: W = 1819.01, $P < 0.001$; year: W = 0.36, ns; interaction term: W = 27.79, $P < 0.001$; dive efficiency: depth: W = 343.37, $P < 0.001$; year: W = 0.69, ns; interaction term: W = 5.16, $P < 0.01$; bottom duration: depth: W = 1750.14, $P < 0.001$; year: W = 0.75, ns; interaction term: W = 25.06, $P < 0.001$; bottom efficiency: depth: W = 363.20, $P < 0.001$; year: W = 0.86, ns; interaction term: W = 7.41, $P < 0.001$; vertical descent speed: depth: W = 1930.89, $P < 0.001$; year: W = 2.54, ns; interaction term: W = 20.47, $P < 0.001$; vertical ascent speed: depth: W = 4441.21, $P < 0.001$; year: W = 0.91, ns; interaction term: W = 16.46, $P < 0.001$). The average dive parameters for the commonest dive depths (21-30 m) are highlighted in Figure 5.5.14.

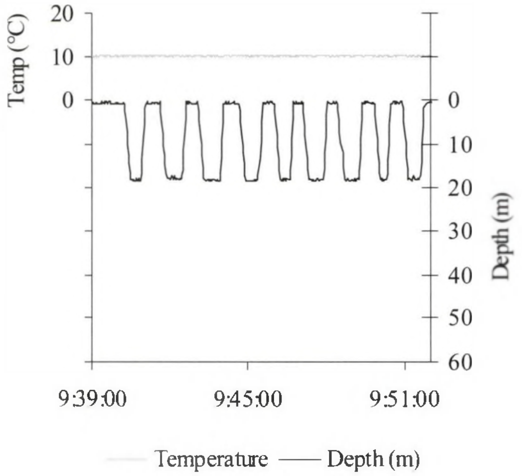


Figure 5.5.12. An example of water temperature and dive depth output from a PreciTD logger on European Shag. The data show nine dive cycles over a 12 minute period.

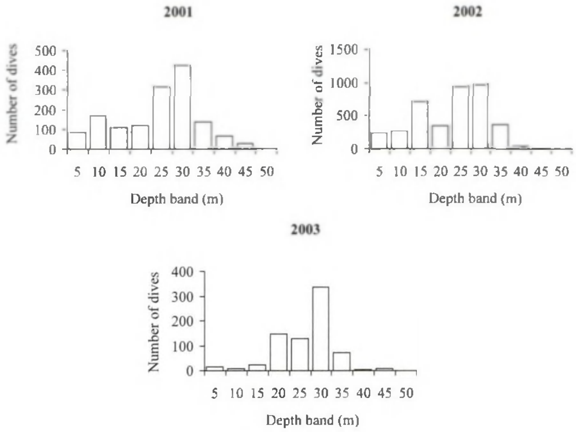


Figure 5.5.13. *Frequency distributions of dive depths of European Shags.*

PreciTD loggers were successfully deployed on 9 **Common Guillemots** in 2001, on 8 in 2002 and on 5 in 2003. An example of logger output showing dive and external temperature data is shown in Fig. 5.5.15. The interpretation of the relationship between dive depth and water temperature data is dealt with in Chapter 7.

The number of dives per bout varied from 12.2 in 2001 to 4.8 in 2003 (Table 5.5.5; no significant difference between years, REML, effect of year: $W = 0.68$, ns). In all three years, foraging depth varied considerably (Fig 5.5.16; 2001: 1.1 - 67.0 m; 2002: 0.5 – 68.9 m; 2003: 0.7 – 64.0 m). Depth distributions were similar in 2001 and 2002, with a peak between 41-60 m (2001: 48% of dives; 2002: 52%). However, the pattern was markedly different in 2003, when the majority of dives were less than 20 m deep (59% of dives; REML, effect of year, $W = 4.48$, $p = 0.01$). Associated with these differences in dive depth among years, there was significant annual variation in dive and bottom durations and vertical descent and ascent speeds, which were all significantly lower in 2003 (dive duration: REML, effect of year: $W = 5.41$, $P < 0.01$; bottom duration: REML, effect of year: $W = 7.14$, $P < 0.001$; vertical descent speed: REML, effect of year: $W = 8.89$, $P < 0.001$; vertical ascent speed: REML, effect of year: $W = 3.96$, $p = 0.02$). However, there were no differences among years in the other parameters (REML, effect of year: surface duration: $W = 2.77$, ns, dive efficiency, $W = 0.26$, ns; bottom efficiency: $W = 1.96$, ns). Mean dive duration was significantly longer than mean surface duration (REML: $W = 7750.02$, $P < 0.001$) and vertical ascent speed was significantly less than vertical descent speed (REML: $W = 124.52$, $P < 0.001$).

Comparing data for 2001-2003 with results from 1997 and 1998 indicated that dive durations were shorter, particularly in 2003, but surface times were longer, such that dive efficiency was generally lower in 2001-2003 (Table 5.5.5). However, data on dive depth were collected using different methods in 1997 and 1998 than in 2001-2003. The results suggested that mean foraging depth was between 39 m and 43 m in all years except 2003, in which depth was markedly shallower.

Table 5.5.4. Diving parameters for European Shags in 1997, 1998, 2001, 2002 and 2003. Values are means (± SE) of individual bird means. Dive durations, surface durations and dive efficiency were recorded using VHF telemetry in 1997 and 1998. Depths in 1998 were recorded with time-at-depth gauges.

	1997	1998	2001	2002	2003
Number of birds	40	19	29	48	8
Trips per day			2.70 ± 0.25	2.26 ± 0.09	3.25 ± 0.41
Dives per trip			27.7 ± 2.9	32.7 ± 2.3	26.6 ± 2.7
Dive duration (s)	63.3 ± 2.7	71.9 ± 2.9	62.4 ± 2.1	58.2 ± 1.3	68.8 ± 3.5
Surface duration (s)	59.5 ± 4.8	77.9 ± 7.4	53.8 ± 3.8	50.5 ± 2.3	62.5 ± 5.9
Dive efficiency	0.54 ± 0.01	0.50 ± 0.01	0.57 ± 0.01	0.57 ± 0.01	0.54 ± 0.01
Mean foraging depth (m)		27.2 ± 2.6	22.8 ± 1.1	20.6 ± 0.8	26.7 ± 2.2
Bottom duration (s)			33.9 ± 1.2	32.2 ± 0.7	
Bottom efficiency			0.31 ± 0.01	0.31 ± 0.01	
Vertical descent speed (ms^{-1})			1.38 ± 0.05	1.34 ± 0.02	1.29 ± 0.02
Vertical ascent speed (ms^{-1})			1.74 ± 0.05	1.64 ± 0.03	1.74 ± 0.03

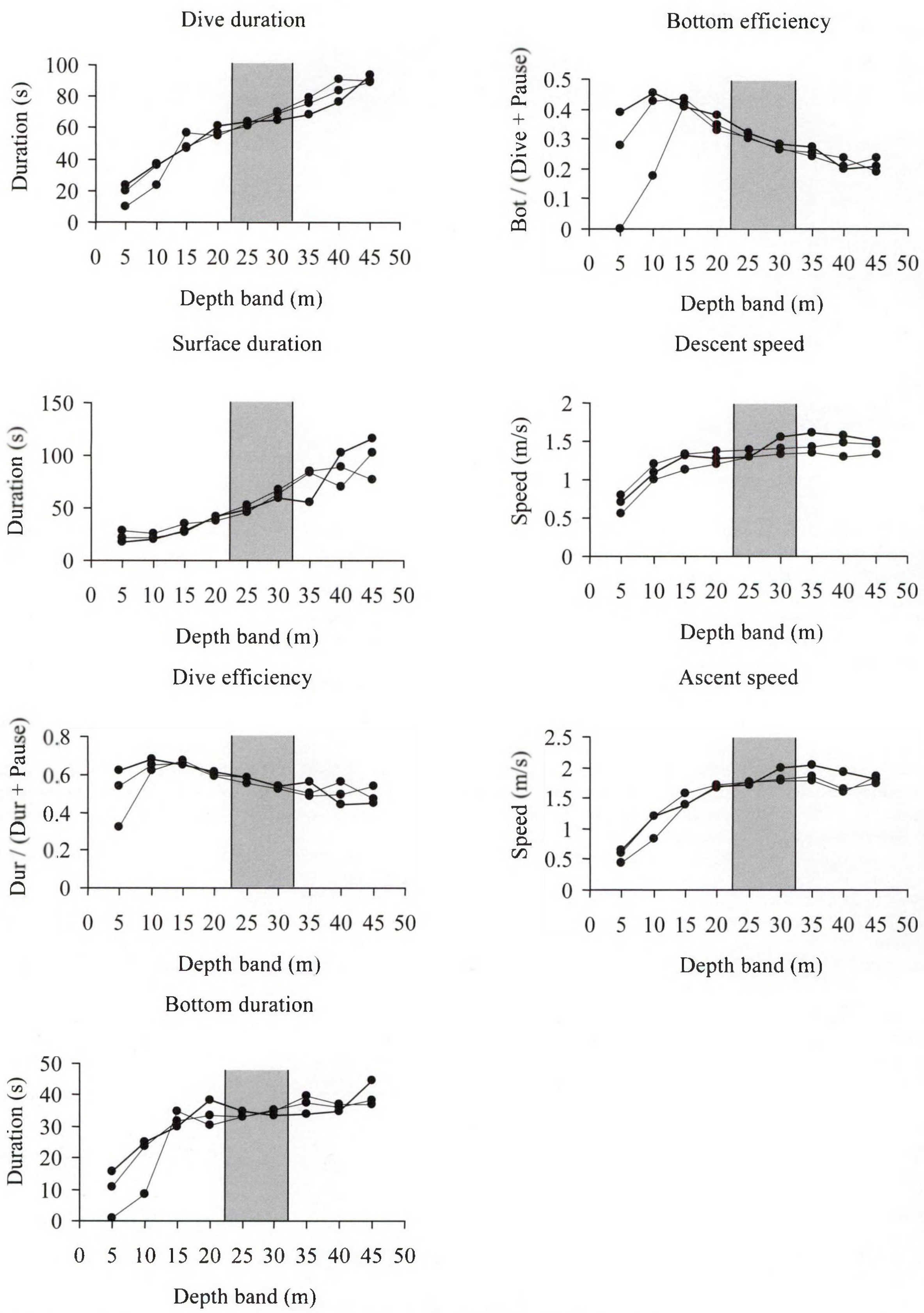


Fig. 5.5.12. Diving parameters of European Shags in relation to foraging depth in the three study years (solid line = 2001, long hatch = 2002 and short hatch = 2003).

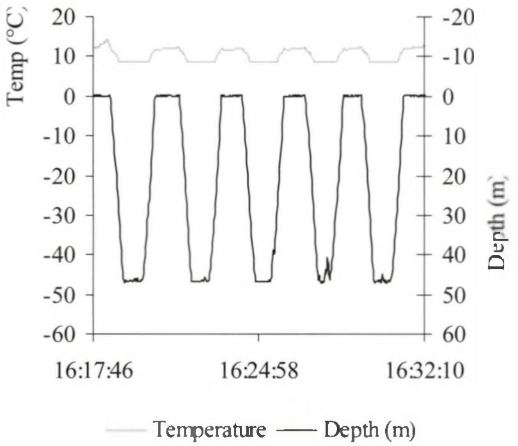


Figure 5.5.15. *Example of temperature and depth data recorded by a PreciTD deployed on a Guillemot.*

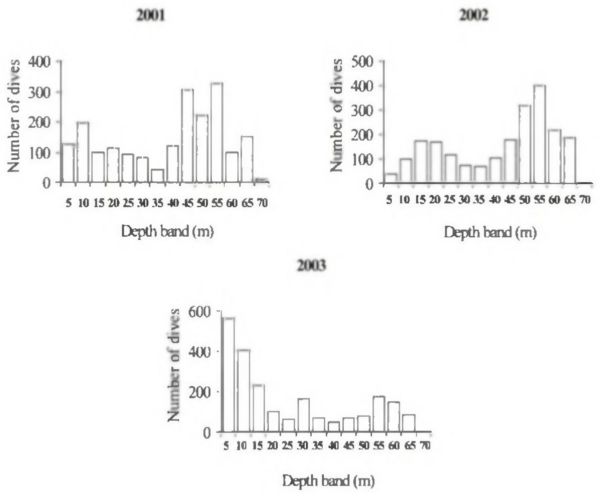


Figure 5.5.16. *Frequency distributions of dive depths of Guillemots in the three years.*

Foraging depth had a significant effect on all dive parameters (Figure 5.5.17). Dive duration increased linearly with depth up to about 50 m, when it started flatten off. Surface duration decreased between 5 m and 10 m but then increased linearly. Integrating these two relationships resulted in dive efficiency increasing between 5 m and 10 m and then showing a very slight decline up to 60 m. Bottom duration increased with depth up to about 45 m before flattening off (2002 and 2003) or decreasing (2001). Bottom efficiency increased between 5 m and approximately 20 m but then declined markedly. Vertical descent speed and ascent speed both initially increased with depth but flattened out at approximately 20-30 m. In all these cases, the effect of depth was highly significant. Bottom duration, bottom efficiency and vertical descent speed were significantly higher in 2001, independent of depth. There were significant interactions between year and depth for all parameters (REML: dive duration: depth: W = 28158.41, $P < 0.001$; year: W = 0.45, ns; interaction term: W = 16.35, $P < 0.001$; surface duration: depth: W = 937.33, $P < 0.001$; year: W = 0.10, ns; interaction term: W = 4.34, $P < 0.05$; dive efficiency: depth: W = 28.28, $P < 0.001$; year: W = 0.23, ns; interaction term: W = 35.39, $P < 0.001$; bottom duration: depth: W = 3135.17, $P < 0.001$; year: W = 3.37, $P < 0.05$; interaction term: W = 47.81, $P < 0.001$; bottom efficiency: depth: W = 29.60, $P < 0.001$; year: W = 3.29, $P < 0.05$; interaction term: W = 25.66, $P < 0.001$; vertical descent speed: depth: W = 3967.93, $P < 0.001$; year: W = 4.59, $p = 0.01$; interaction term: W = 73.04, $P < 0.001$; vertical ascent speed: depth: W = 1933.51, $P < 0.001$; year: W = 1.78, ns; interaction term: W = 17,74, $P < 0.001$). The average dive parameters for the commonest dive depths in 2001 and 2002 (41- 60 m) and 2003 (1-15 m) are highlighted in Figure 5.5.17.

Table 5.5.5. Dive parameters for Guillemots in 1997, 1998, 2001, 2002 and 2003. Values are means (± s.e.) of individual bird means, with 95% confidence intervals. Dive durations, surface durations and dive efficiency were recorded by VHF telemetry in 1997 and 1998.

	1997	1998	2001	2002	2003
Number of birds	7	7	9	8	18
Dives per bout			12.20 ± 4.69	7.30 ± 0.78	4.82 ± 1.17
Dive duration (s)	107.2	107.7	104.0 ± 8.4	100.0 ± 6.6	71.7 ± 7.1
95% CI	96.0 - 122.8	94.1 - 123.9	57.9 - 140.1	71.9 - 126.4	57.7-85.0
Surface duration (s)	51.8	41	67.1 ± 5.5	65.3 ± 7.7	51.2 ± 5.0
95% CI	45.5 - 72.4	33.0 - 48.1	32.2 - 91.4	45.6 - 97.4	41.4 - 61.5
Dive efficiency	0.66	0.73	0.62 ± 0.01	0.62 ± 0.02	0.61 ± 0.02
95% CI	0.64 - 0.70	0.69 - 0.74	0.58 - 0.66	0.54 - 0.69	0.58 - 0.64
Mean foraging depth (m)	38.7 ± 1.5	42.6 ± 3.0	39.4 ± 11.3	40.2 ± 8.5	22.1 ± 4.3
Bottom duration (s)			44.1 ± 0.7	38.0 ± 4.0	27.7 ± 3.8
Bottom efficiency			0.25 ± 0.01	0.25 ± 0.02	0.22 ± 0.02
Vertical descent speed ($m.s^{-1}$)			1.33 ± 0.09	1.24 ± 0.09	0.96 ± 0.01
Vertical ascent speed ($m.s^{-1}$)			1.21 ± 0.12	1.22 ± 0.07	0.89 ± 0.01

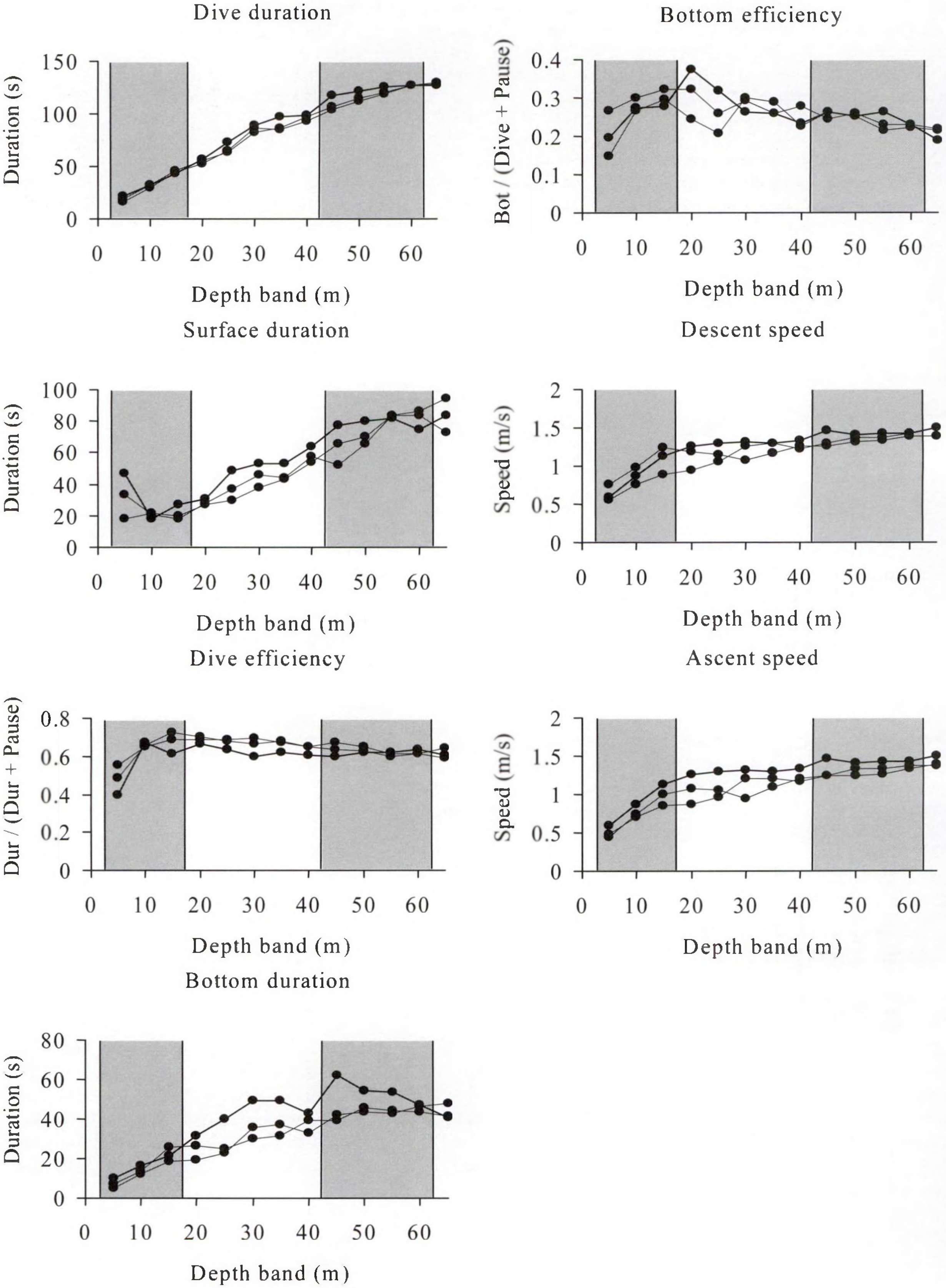


Fig. 5.5.17. Diving parameters of Guillemots in relation to foraging depth in the three study years (solid line = 2001, long hatch = 2002 and short hatch = 2003). Shaded areas indicate commonest dive depth bands (see text for details).

Data on diving behaviour of **Northern Gannets** were collected during early to mid chick-rearing. In 2002, only PreciTDs were used but, in 2003, both PreciTD loggers and combined GPS and temperature depth loggers (GPS-TD) were used. Apparent dives of less than 0.3 m were excluded from the analysis, based on calibration of the devices by the manufacturer and observations of Gannets foraging at sea (S. Garthe pers. obs.). Dive depth had a highly significant correlation with dive duration (Spearman correlation: $r = 0.71$, $n = 2252$, $P < 0.001$) so only dive depth was used in further statistical analyses. Totals of 1517 and 735 dives were recorded from 18 adults in 2002 and 2003 respectively. Dive depth did not differ between years (2002, mean = 2.50 ± 0.06 m; 2003, mean = 2.96 ± 0.10 m; REML: W = 1.1, $P > 0.1$; Fig 5.5.18) but females made significantly deeper dives than males (females, mean = 3.99 ± 0.10 m; males, mean = 1.96 ± 0.05 m; REML: W = 42.8, $P < 0.001$). There was a significant interaction between sex and time period (REML: W = 20.4, $P < 0.001$; Fig 5.5.19) with females diving much deeper than males in the middle of the day. There were no significant differences between sexes in 2003, for dives per trip (male, mean = 35.8 ± 6.6; female, mean = 30.9 ± 6.6; W = 0.14, $P > 0.1$;) or for dives per hour within trips (male, mean = 1.5 ± 0.4; female, mean = 1.3 ± 0.3; W = 0.04, $P > 0.1$).

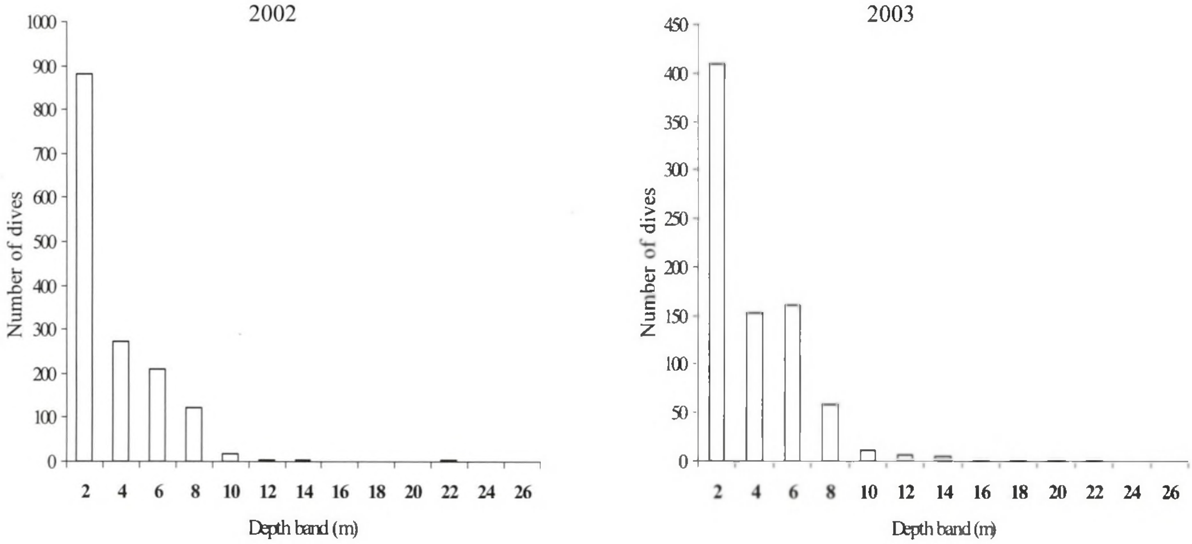


Fig 5.5.18. Frequency distribution of dive depths of Gannets in 2002 and 2003.

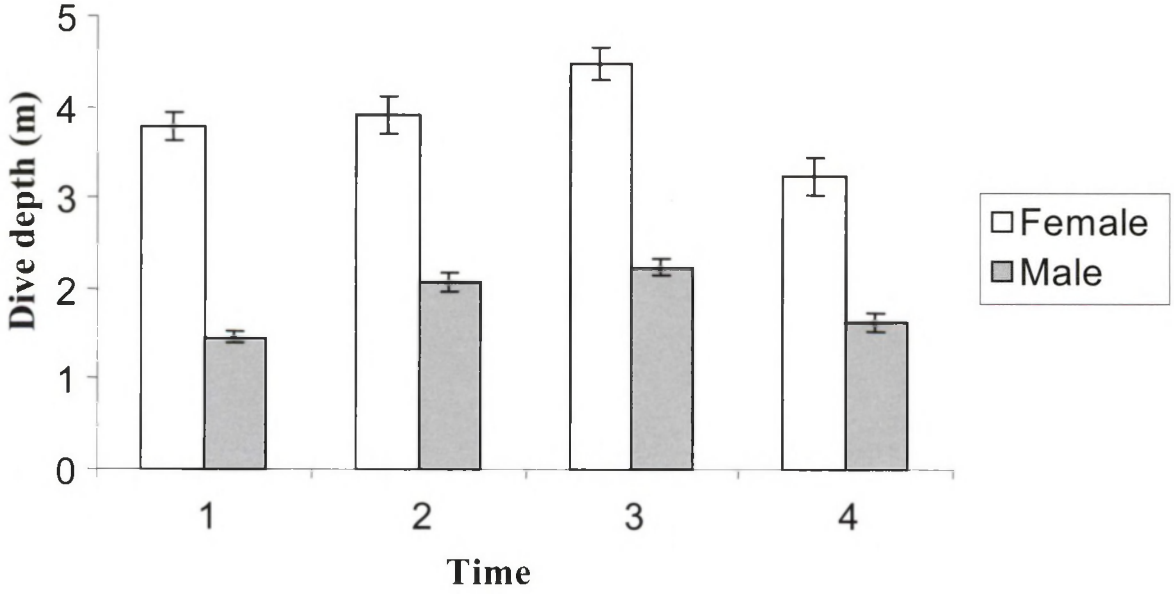


Figure 5.5.19. Mean dive depth (± 1 S.E.) of Gannets in relation to sex and time of day (period 1= 01.01 - 07.00h; period 2 = 07.01 - 13.00h; period 3 = 13.01 - 19.00h, period 4 = 19:01 - 01.50h).

5.6 Time activity budgets

Methods to assess activity

Time activity budgets were obtained for all four species during chick-rearing. For Shags, this was achieved using both PreciTDs and locational loggers. Output from PreciTDs identified the time spent by the bird on the sea and the component activities e.g. foraging (bottom) time, time spent travelling between the surface and the foraging depth and periods on the surface between dives. When output from the PreciTD was combined with data from locational loggers it was possible to distinguish when the bird was flying. In 2001, VHF transmitters were deployed in parallel with PreciTDs and confirmed that flight was reliably identified by the latter. In 2002, a sample of birds were deployed with both a PreciTD and a compass logger to measure time activity. The compass loggers unequivocally distinguished time spent on land, in flight and resting on the sea due to characteristic outputs from the compass and temperature traces. Hence, flight had a typically stable compass trace, but unstable temperature trace; periods on the sea when the bird was diving showed up as rhythmic changes in compass and temperature traces, with the temperature trace being very stable when viewed at a fine scale. Time ashore was denoted by unstable compass and temperature traces.

For Guillemots, time activity budgets were estimated using compass loggers in 2002 and 2003. Output from the loggers identified time spent at the colony, in flight and on the sea. Guillemots are too small to carry both PreciTD and compass loggers, but time on the sea could be subdivided into bottom time, travel time between the surface and the foraging depth and surface time using a sample of birds carrying PreciTD loggers. Kittiwake activity budgets were estimated using a flight activity sensor combined with a saltwater switch (Instituto di Elaborazione dell'Informazione, C.N.R., Pisa, Italy; details in Daunt *et al.* 2002) in 2001 and 2002. Output from the logger enabled travelling flight, foraging flight, time sitting on the sea and at the nest site to be determined. Fig. 5.6.1 shows an example of the data recorded and denotes the different activities. For Gannets, the total time spent at sea for each bird was derived by summing trip durations over the period of deployment of each PTT. Birds were equipped with PTTS for different time periods, and so the unit of sampling for statistical comparisons between birds was standardized to the first 5 days, which was the minimum time that a PTT was deployed on a bird.

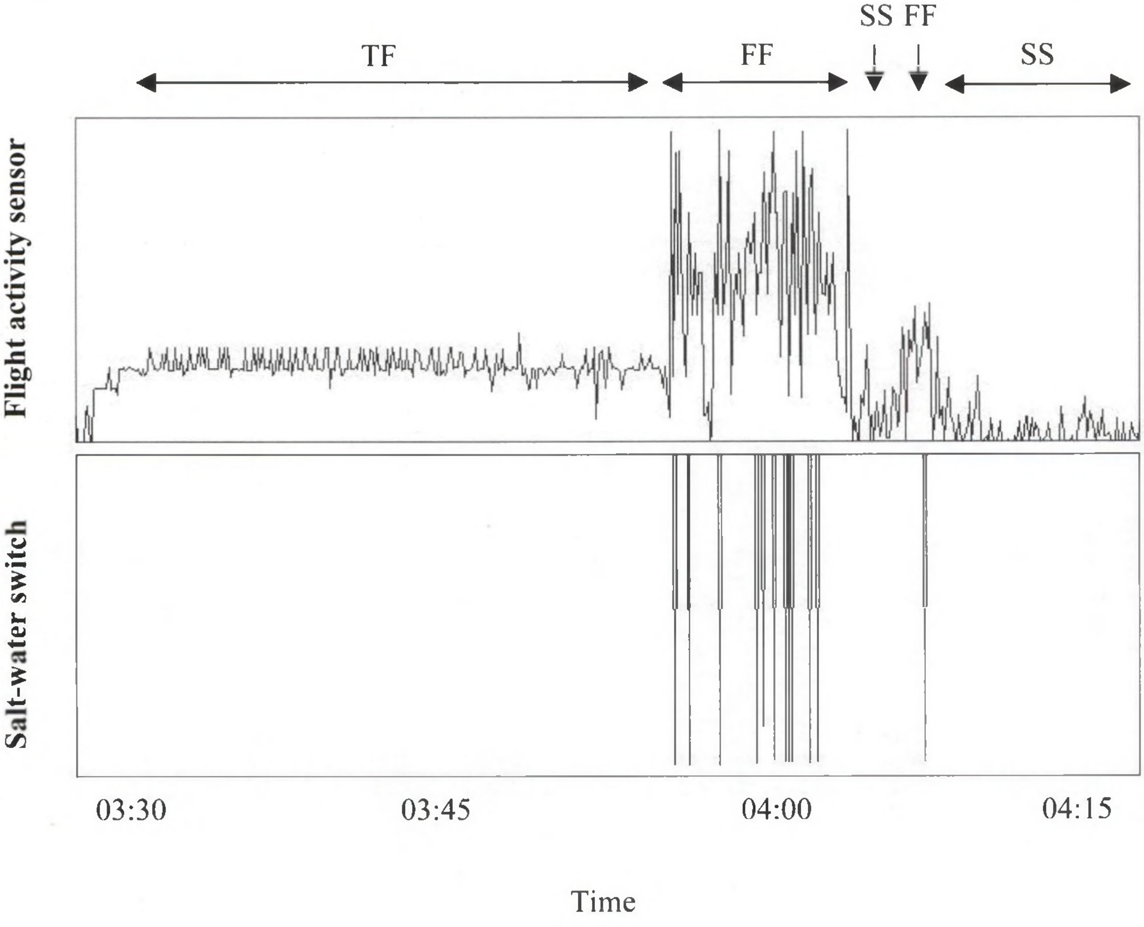


Figure 5.6.1. Example of output from a flight activity logger deployed on a Kittiwake showing the characteristic signals for three activities recorded during a foraging trip made on 22 June. Travelling flight (TF) consisted of high, stable signals; foraging flight (FF) consisted of strong signals of variable intensity and frequency, together with activation of the saltwater switch; presence on the sea surface (SS) consisted of weak, frequent signals (see Daunt et al. 2002 for details).

Time spent in different activities by Gannets (diving, flight and resting/swimming on water) during foraging trips was determined from temperature and pressure (converted to depth) data obtained from PreciTDs and GPS-TDs. The timing and duration of dives were analysed using Multitrace-Dive 4.0 (Jensen Software Systems, Laboe, Germany). Periods of more-or-less constant temperature during foraging trips were taken to indicate that the bird was either swimming or resting on the water. When these periods exceeded 3 minutes, we were then able to use locational data to confirm that the bird had not moved from its previous position. Flight was indicated by rapid changes in location, accompanied by sudden and rapid fluctuations in temperature. As with diving activity, the analysis of time-activity budgets within trips was only possible for 2003, because it was not possible to determine when trips ended from logger data collected in 2002.

Variation in the proportion of time spent in flight by Gannets (arcsine square root transformed) was analysed in linear mixed models using REML. Sex was included as a fixed factor and bird identity as a random factor to account for pseudoreplication. The percentage time spent at sea (arcsine transformed) was analysed in a general linear model assuming a normal distribution. Year, sex and the interaction between the two were included in the model. Stepwise deletions of variables from maximal models were carried out and the significance of terms in the final model are given as *F* values.

Table 5.6.1 *Number of foraging trips and daily time activity budgets (expressed as a proportion of 24 h) for Shags in 2001-2003.*

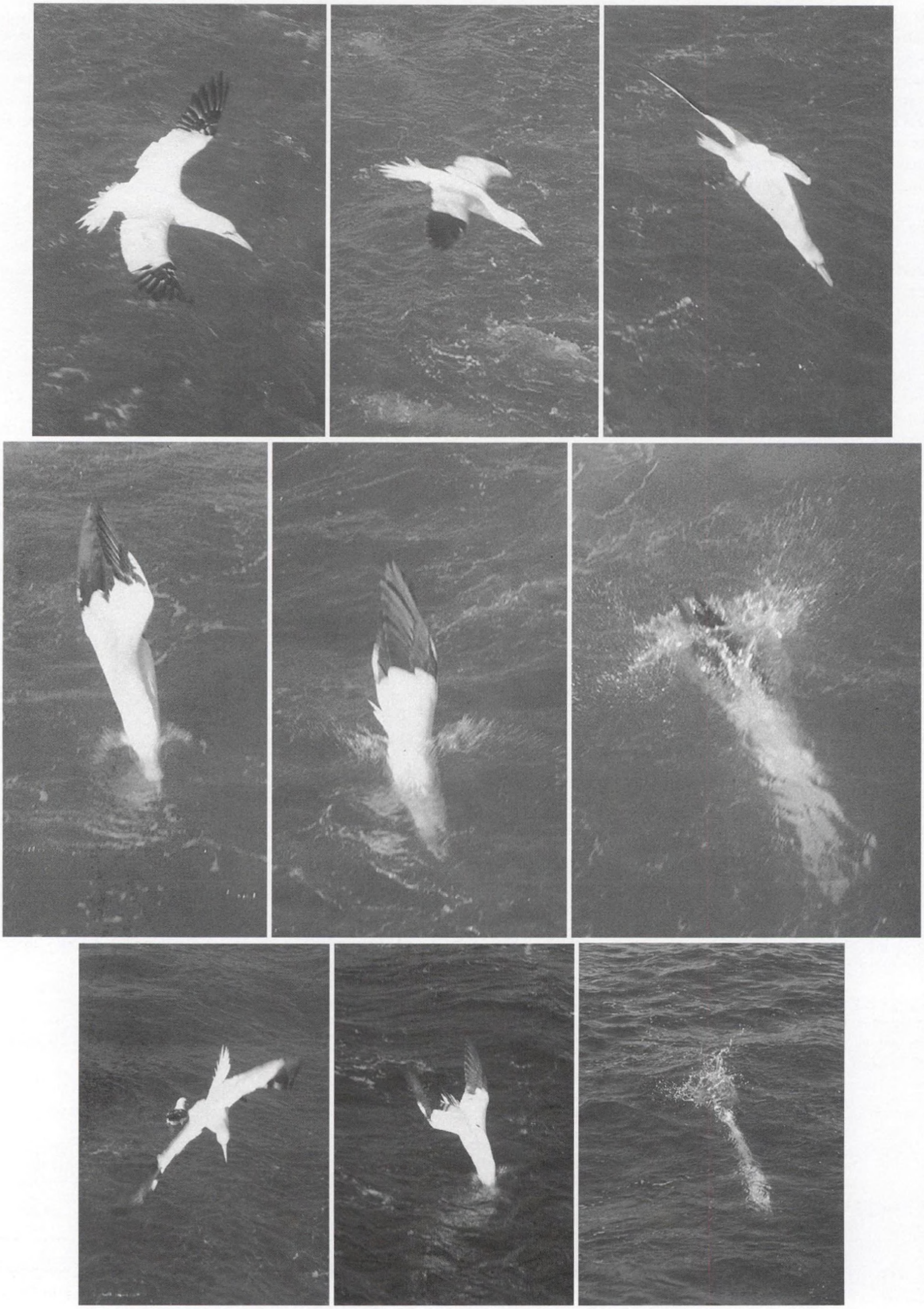
			Proportion of daily time spent in activity						
		Trips d^{-1}	Flight	Dive (travel)	Dive (forage)	Surface	Total dive	On water	On land
2001	Mean	2.46	0.031	0.018	0.015	0.027	0.061	0.019	0.89
	SD	0.88	0.012	0.011	0.007	0.014	0.03	0.014	0.041
	n	13							
2002	Mean	2.6	0.047	0.036	0.028	0.054	0.118	0.022	0.814
	SD	0.82	0.011	0.016	0.009	0.019	0.04	0.015	0.054
	n	15							
2003	Mean	3.25							
	SD	1.16							
	n	8							

Table 5.6.2. *Number of foraging trips and daily time activity budgets (expressed as a proportion of 24 h) for Guillemots in 2002 and 2003.*

			Proportion of daily time spent in activity						
		Trips d^{-1}	Flight	Dive (travel)	Dive (forage)	Surface	Total dive	On water	On land
2002	Mean	1.79	0.047	0.033	0.078	0.067	0.177	0.244	0.532
	SD	1.04	0.042	0.003	0.009	0.009	0.089	0.104	0.033
	n	11	11	9	9	9	11	11	11
2003	Mean	2.48	0.076	0.049	0.087	0.088	0.224	0.181	0.519
	SD	1.98	0.063	0.017	0.018	0.015	0.081	0.092	0.013
	n	8	8	8	8	8	8	8	8

Table 5.6.3. *Number of foraging trips and daily time activity budgets (expressed as a proportion of 24 h) for Kittiwakes in 2001, 2002 and 2003. Time spent on land was not recorded in 2002 or 2003. Proportions of time spent on at-sea activities is based on 50% of time spent in the colony, following observations that mates spent negligible time together at the nest but did not leave chicks unattended during deployment periods.*

			Proportion of daily time spent in activity			
		Trips d^{-1}	Flight	Foraging	On water	On land
2001	Mean	1.34	0.148	0.095	0.253	0.503
	SD	0.34	0.064	0.056	0.079	0.203
	n	6				
2002	Mean	2.49	0.192	0.134	0.174	
	SD	1.3	0.048	0.059	0.055	
	n	12				
2003	Mean	4.3	0.176	0.168	0.156	
	SD	1.81	0.055	0.064	0.071	
	n	13				



Deep plunge-diving Northern Gannets Morus bassanus (C.J. Camphuysen)

Recorded activity

Table 5.6.1 summarises the number of trips made per day and daily time activity budgets of **European Shags**. Shags made similar numbers of trips per day in 2001 and 2002, but the proportion of time spent foraging was greater in 2002, and accordingly less time was spent on land (arcsine transformed: $t_{26} = 4.30$, $P < 0.001$). However, this between year difference was not apparent in the larger data set obtained on diving behaviour, which indicated few significant differences (see previous section). The sub-sample of birds for which time activity budgets were measured in 2002, were foraging during a period in which overall foraging effort appeared to be higher than for the season as a whole. The number of foraging trips per day was greater in 2003 than in 2002 or 2001, although the difference was not significant (GLM: $F_{1,26} = 0.18$, ns). Detailed time activity budgets for 2003 were not available for comparison with the previous two years.

There was no difference in the number of trips by **Common Guillemots** made per day between 2002 and 2003 (Table 5.6.2; $t_{17} = 1.55$, ns). In 2003, birds tended to spend more time flying and diving and less time resting on the sea compared with 2002, but the difference was not significant (arcsine transformed: $t_{17} = 1.15$, ns). **Black-legged Kittiwakes** made more trips per day in 2003 than in 2002 or 2001 (Generalized Linear Model with poisson errors: $F_{1,28} = 5.34$, $P < 0.01$), and birds spent a higher proportion of time in foraging flight (General Linear Model: $F_{1,28} = 3.60$; $P < 0.05$) and consequently less time on the water (Table 5.6.3).

A total of 21 complete trips was recorded from 18 Gannets in 2003. Percentage time spent at sea did not vary between years (2002, mean ± S.D. = 59 ± 19.7%; 2003, mean = 50.9 ± 11.9%; $F_{1,22} = 0.635$, $P > 0.1$) or between sexes (male, mean ± SD = 57.7 ± 20.0%; female mean = 57.9 ± 12.4; $F_{1,22} = 0.90$, $P > 0.1$;), nor was there a significant interaction between year and sex ($F_{1,22} = 0.23$, $P > 0.1$). There was a significant positive correlation between time spent in flight and overall trip duration (Spearman correlation: $r = 0.78$, $n = 21$, $P < 0.001$), according to the following equation:

$$\text{Trip duration (h)} = 1.51\ (\text{S.E.} \pm 0.25) \times \text{flight time (h)}$$

Whilst on a trip, Gannets spent 0.3% (± 0.05), 43.1% (± 2.61) and 56.6% (± 2.62) of time respectively diving, flying and resting/swimming on the surface of the water, with no difference between sexes (REML: $W = 0.41$, $P > 0.1$). These values are very similar to those reported by Garthe *et al.* (2003) and Hamer *et al.* (2001), indicating a similar pattern of behaviour within foraging trips at different colonies.

Interspecific comparisons

Comparison of results indicated that all species, except Shags, spent about 50% of their time at the colony and 50% at sea. In contrast, Shags spent only about 15% of their time away on feeding trips, and were present at the colony for the remaining 85% of the time. The situation was reversed in terms of the time spent at sea, when Kittiwakes, Gannets and Guillemots spent 15-30% of their time resting whereas Shags spent most of the time diving. The two pursuit-diving species (Shag and Guillemot) spent a much smaller proportion of their time flying than the surface-feeder and plunge-pursuit diver (Kittiwake and Gannets) reflecting their greater use of prey patches closer to the colony.

5.7 Prey capture rates

Assessing prey capture rates

Gastric temperature loggers (Minitemp, Earth & Ocean Technologies, Kiel) were used to measure prey capture rates in all four study species, under UK Home Office licence. The technique assumes that precipitous drops in gastric temperature are associated with the ingestion of cold prey such as fish. The method had previously been used successfully on Gannets (Garthe *et al.* 1999) and Shags (Grémillet *et al.* 1998), but never for Kittiwakes or Guillemots. The main technical difficulty is usually ensuring that the logger stays in the stomach. Details of the number and outcome of deployments per year for the four species are shown in Table 5.7.1.

Table 5.7.1. Sample sizes of gastric logger deployments in the four species in 2001-2003.

Species	Year	Deployed	Recaptured	Logger retrieved	Lost	Logger retrieved (%)	Lost (%)
Shag	2001	43	43	36	7	84	16
	2002	27	27	24	3	89	11
Guillemot	2002	4	4	1	3	25	75
	2003	11	9	9	0	100	0
Kittiwake	2001	8	8	1	7	13	88
	2002	5	5	0	5	0	100
Gannet	2002	19	19	19	0	100	0
	2003	23	23	23	0	100	0

As expected, retrieval rate was high for Gannets and Shags. However, major methodological problems were encountered with Kittiwakes. Gastric loggers were deployed in eight birds in 2001. Seven of these were regurgitated, in most cases within a few hours of ingestion. In an attempt to overcome this problem, in 2002 the loggers were made considerably lighter, by replacing the titanium housing with a plastic housing, and the spring crowns, that reduce the chances of regurgitation, were made slightly larger. However, even after these adjustments, all five of the study birds regurgitated their gastric loggers before they were recaptured (Table 5.7.1). At the end of 2002 we therefore concluded that this was not an appropriate method for this species and no further attempts were made to collect prey capture data.

A pilot study to investigate the use of gastric loggers in Guillemots was carried out in 2002. The period of deployment coincided with a spell of bad weather and the interval between deployment and recapture of the study birds was longer than planned. Thus, by the time the birds could be re-caught, four out of the five had regurgitated their loggers. The work was repeated in 2003, this time using gastric loggers fitted with spring crowns. Birds were recaptured within 24-48 hours and seven usable sets of data were obtained.

Detecting feeding events

In order to calibrate the detection of feeding events and the calculation of prey mass, feeding experiments on captive Gannets were performed under license at the EcoMare educational centre (Texel, The Netherlands) from 19-23 May 2003. Six Gannets were equipped with gastric loggers (Minitemp-xl, Earth&Ocean Technologies, Kiel, Germany) and fed with fish of known mass and temperature. A total of 46 fishes (Mackerel and Sprat) weighing between 5.9 – 271.0 g (median 11.7 g) was fed to the birds in five feeding bouts. It was not possible to use sandeels or other small fish in the trials because the captive birds would not eat them.

Of 46 fish fed, 42 (91%) were successfully registered by the gastric loggers, while 4 (9%) fish were not detected. Thus, the detection of feeding events on a wide range of prey sizes was accurately recorded with only a small underestimation. However, several reasons made it impossible to refine the approach further and calculate the mass of the prey caught by a Gannet on a foraging trip. First since no very small fish (sandeel) could be fed in the feeding trials, the signal strength of these prey in the stomach temperature could not be assessed. Second, it is not known if, and how, Gannets feed on sandeel during a dive. However, the available evidence suggests that sandeels are important in the diet and that birds take several fish, one after the other, during a single dive. However, there was no way to quantify this behaviour nor to identify drops in stomach temperature caused by it in the captive birds. Third, Gannets feed on sandeel by 'scooping': the bird sits on the water surface and scoops the fish from the upper layers of the water column into its bill, together with seawater (C.J. Camphuysen *pers. observ.*, Chapter 5.4, Chapter 7). Under these conditions, stomach temperature drops will not be associated with dives. Thus while scooping will lead to a drop in stomach temperature, estimating the number of fish swallowed and the error due to the ingestion of seawater currently make it impossible to calculate sandeel intake during scooping.

As sandeels contributed more than 50% to the biomass of the diet of Gannets (Table 5.3.3), the resulting error in prey mass calculations is potentially immense. Therefore, we refrained from calculating the prey mass taken by Gannets during their foraging trips and quantitative conclusions on foraging success were not attempted. Given that all the species studied during the IMPRESS project fed to a large extent on sandeels, it was concluded that the problems encountered in the Gannet would also apply in these cases. Data from gastric loggers were therefore used only to indicate the timing and frequency of recorded feeding events. Note that the latter must be regarded as a minimum because the effectiveness of prey detection decreases as the stomach fills, because undigested food may cover the logger preventing direct contact with freshly ingested prey (full discussion in Wilson *et al.* 1995).

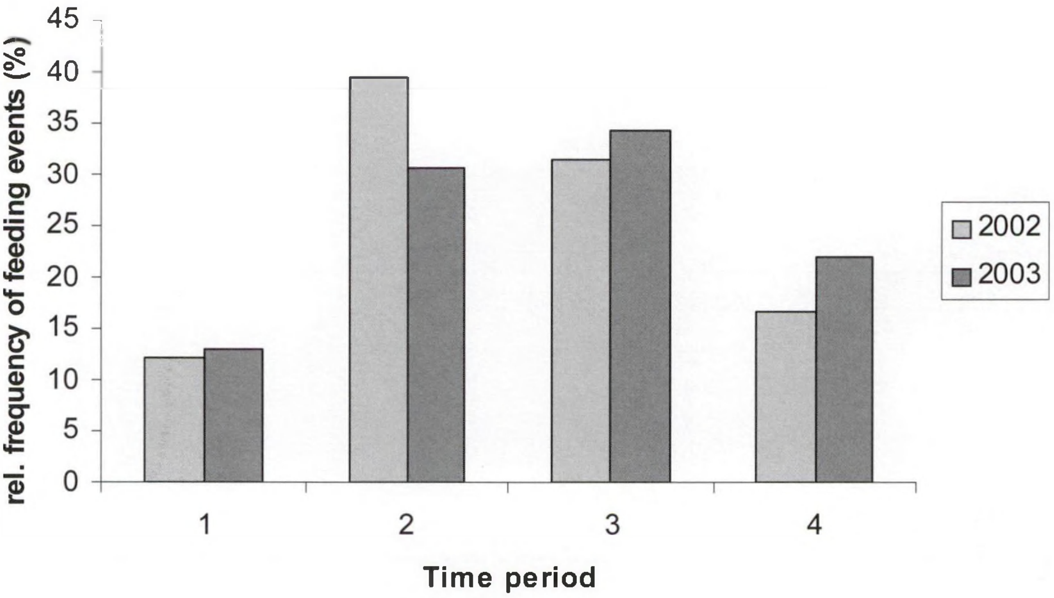


Figure 5.7.1. Relative frequencies of feeding events of Gannets in relation to time of day (period 1 = 01:01 – 07:00 h; period 2 = 07:01 – 13:00 h; period 3 = 13:01 – 19:00 h; period 4 = 19:01 – 01:00 h).

Feeding events and prey ingestion

In total, 449 feeding events by Gannets (of which 168 were covered by dive data) were detected for 25 birds in 2002 and 183 events (172 covered by dive data) were recorded from 21 birds in 2003. Most feeding events took place between 07:00 – 19:00h (Fig. 5.7.1) and there was no significant difference in this daily pattern between years ($\chi^2_3 = 4.48$, $p > 0.1$). In 2002, a total of 67 feeding events (40.5%) were associated with a dive, comparable figures for 2003 were 94 events (54.6%). Since not all feeding events were detected using gastric loggers (see 5.4.4.2), these success rates were likely to be underestimates. However, since diet composition was similar in each season (Table 5.4), the relative numbers allow qualitative analyses. The frequency of successful dives was significantly higher in 2003 ($\chi^2_1 = 6.29$, $P < 0.05$, $n = 339$). This suggested that feeding conditions were more favourable and accorded well with the birds making shorter, closer trips (see Chapter 5.5). The depths of successful dives did not differ significantly between 2002 and 2003 (males: $U = 868.0$, $P > 0.1$, $n = 92$; females: $U = 376.5$, $P > 0.1$, $n = 69$), indicating that the vertical distribution of prey was similar in the two years.

The locations of diving and feeding events were derived by interpolation between the locations immediately preceding and following the feeding or diving event, assuming a constant flight velocity and a direct flight path between locational fixes. Distances between consecutive diving and feeding events were calculated using spherical trigonometry (arc distance formula, Robinson *et al.* 1978). A total of 81 dive locations was obtained from 4 birds in 2002, and 554 dive locations were obtained from 21 birds in 2003 (Fig 5.7.2). A total of 40 feeding locations was obtained from 4 birds in 2002 and 141 feed locations were obtained from 20 birds in 2003 (Fig 5.7.3). Distances between dives and feeding events were obtained from only 18 of 20 individuals in 2003.

Dives, as well as feeding events, occurred all along the foraging trips. The first dive of a trip was performed at a median distance from Bass Rock of 137.8 km (range 21.7 – 167.1 km) in 2002, and of 57.42 km (range 1.29 – 275.92 km) in 2003. The first feeding events occurred at distances of 43.9 km (range 6.7 – 64.0 km) and 46.0 km (SD ± 16.2) respectively. The distances of the first dive and feeding event from the colony did not differ significantly between years (dives: $U = 24.0$, $p > 0.1$, $n = 24$, feeding events: $U = 36.0$, $p > 0.1$, $n = 24$). Thus, prey was not distributed further away from the colony in one of the seasons. In 2002, the median distance between consecutive dives was 2.95 km (range 1.28 – 4.96 km) and between consecutive feeding events 13.0 km (range 5.77 – 40.8 km). In 2003, the median distance between dives was 1.29 km (range 0.13 – 161.44 km), and the mean distance between feeding events 21.27 km (SD = 19.8). The differences between seasons were not significant (dives: $U = 21.0$, $p > 0.1$, $n = 22$; feeding: $U = 34$, $p > 0.1$, $n = 22$), indicating a similar small-scale spatial distribution of prey patches in 2002 and 2003.

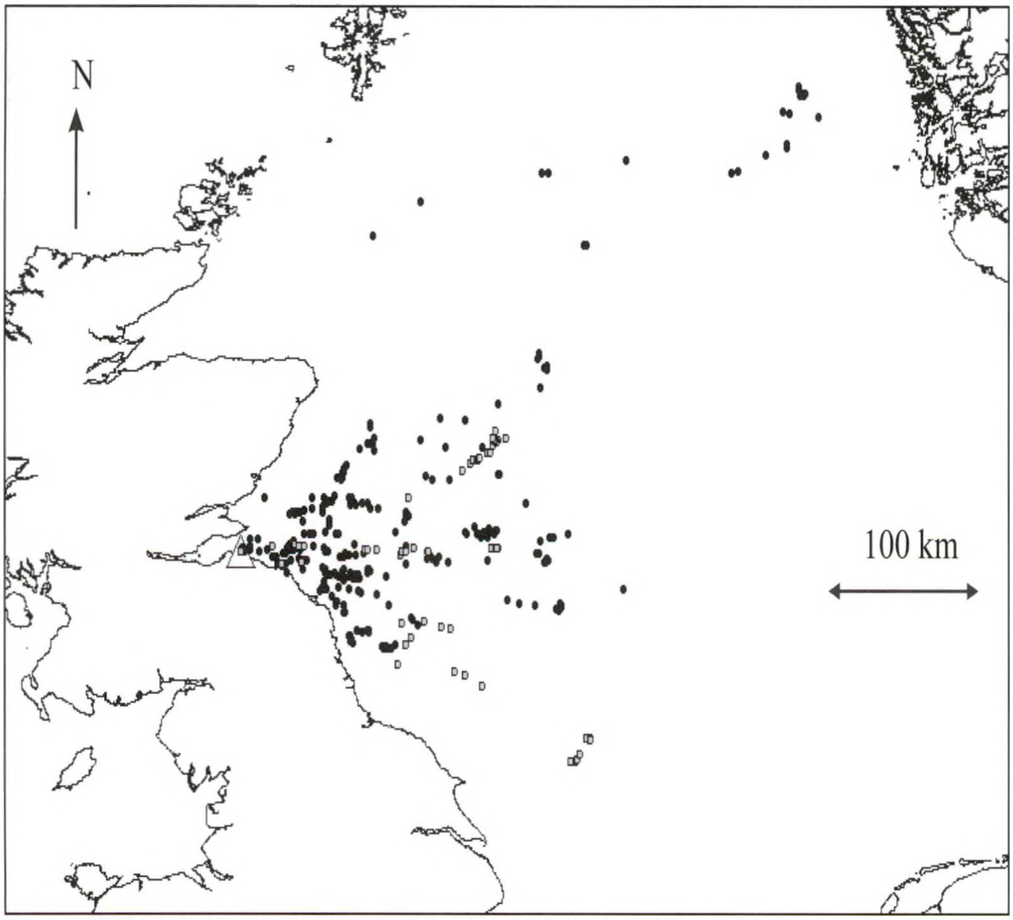


Figure 5.7.2. Locations of dives in 2002 (grey circles) and 2003 (black circles).

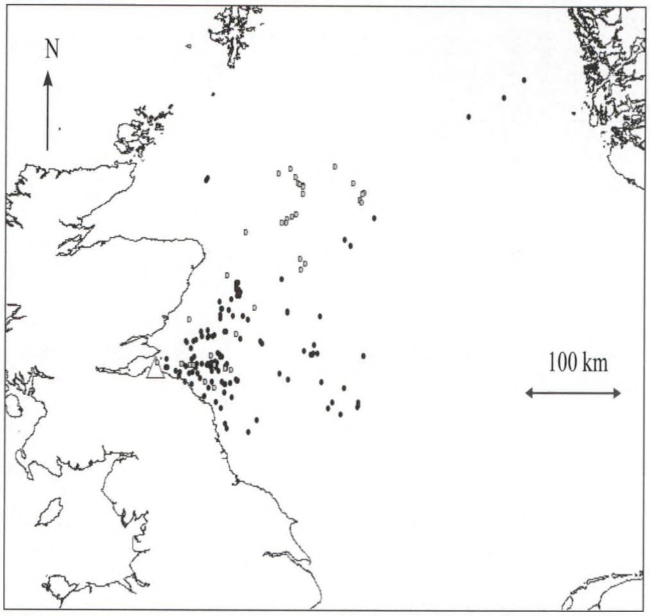


Figure 5.7.3. Locations of feeding events in 2002 (grey circles) and 2003 (black circles).

Gastric loggers were deployed in tandem with PreciTD loggers in **European Shags** in 2002 (n = 26) and 2003 (n = 23). Drops in gastric temperature were clearly associated with dives on all the deployments, indicating that prey ingestions were detected by the gastric logger. However, in some instances, prey ingestion could be attributed to an individual dive (see Figure 5.7.4a). This was usually the case during long, deep dives with long intervals on the surface between dives, when the logger had more time to equilibrate. In many other cases, particularly during bouts of short, shallow diving when surface intervals were short, it was only possible to associate an ingestion with a foraging bout (Figure 5.7.4b). There were no significant differences for either measure of ingestion rate between 2001 and 2002 (events per bout: t_{37} = 0.65, ns, events per dive: t_{37} = 0.83, ns). The results suggest that Shags were successful on approximately 10% of dives and in 55-65% of bouts (Table 5.7.2).

Seven successful deployments of Gastric loggers in tandem with Lotek LTD1110 loggers were achieved in 2003 on **Common Guillemots**. The analysis confirmed that drops in stomach temperature were always associated with diving bouts. As with Shags, ingestions could be associated with individual dives in some cases (Figure 5.7.5a), and bouts in other cases (Figure 5.7.5b). We were able to summarise the data in the same way as for Shags, and recorded a much higher success rate per dive (33%) but similar rate per bout. Prey captures for chick provisioning will not be measured by the logger, since chick prey are carried in the bill, so success rate is likely to be even greater than we could estimate.

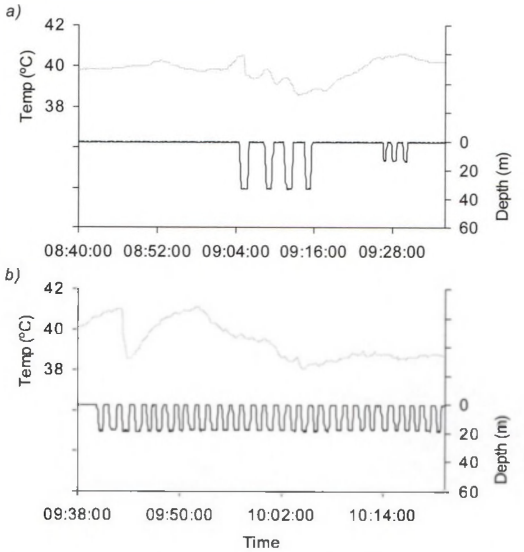


Figure 5.7.4. Gastric temperature and dive depth collected concurrently from a foraging Shag: a) example where prey ingestions can be associated with individual dives. The first bout contains three successful and one unsuccessful dive, and the second bout is completely unsuccessful; b) an example where prey ingestion can only be associated with the dive bout.

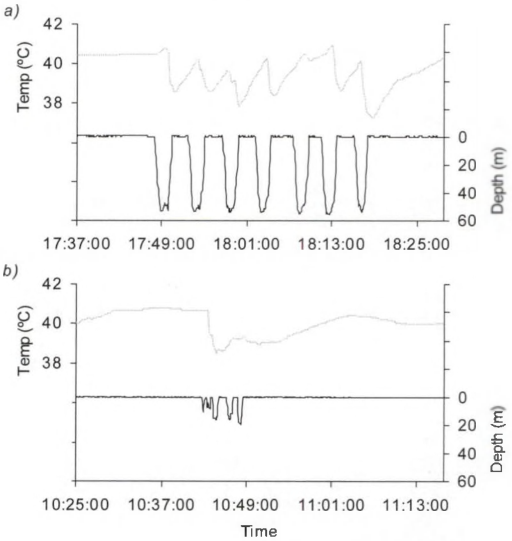


Figure 5.7.5. Gastric temperature and depth collected concurrently from common Guillemots: a) an example where prey ingestions can be associated with individual dives. The first bout contains six successful dives and one unsuccessful dive; b) an example where prey ingestion can be associated with the bout only.

Table 5.7.2 Number of prey ingestions recorded per bout and per dive for each Shag in 2001 and 2002.

Year	Bird	Bouts	Ingestions	Successful bouts	% Bouts successful	Ingestions/ bout	Dives	Ingestions/ dive
2001	1	6	5	4	67	0.83	34	0.15
	2	6	0	0	0	0.00	71	0.00
	3	4	2	2	50	0.50	35	0.06
	4	2	4	1	50	2.00	35	0.11
	5	9	5	2	22	0.56	79	0.06
	6	2	2	1	50	1.00	16	0.13
	7	3	3	2	67	1.00	42	0.07
	8	4	5	2	50	1.25	39	0.13
	9	2	3	2	100	1.50	33	0.09
	10	2	3	2	100	1.50	35	0.09
	11	5	8	4	80	1.60	52	0.15
	12	3	0	0	0	0.00	47	0.00
	13	5	4	4	80	0.80	53	0.08
	14	7	9	4	57	1.29	73	0.12
	15	7	4	2	29	0.57	42	0.10
	16	3	2	2	67	0.67	33	0.06
	Mean	**4.38**	**3.69**	**2.13**	**54**	**0.94**	**45**	**0.09**
2002	1	9	5	3	33	0.56	91	0.05
	2	2	3	2	100	1.50	19	0.16
	3	7	5	3	43	0.71	62	0.08
	4	3	4	3	100	1.33	60	0.07
	5	11	8	5	45	0.73	115	0.07
	6	5	8	3	60	1.60	87	0.09
	7	5	5	4	80	1.00	64	0.08
	8	2	3	2	100	1.50	23	0.13
	9	4	3	3	75	0.75	94	0.03
	10	6	6	3	50	1.00	68	0.09
	11	4	4	2	50	1.00	34	0.12
	12	3	5	3	100	1.67	97	0.05
	13	4	4	3	75	1.00	51	0.08
	14	8	6	5	63	0.75	88	0.07
	15	3	4	2	67	1.33	28	0.14
	16	4	3	2	50	0.75	15	0.20
	17	1	1	1	100	1.00	11	0.09
	18	2	0	0	0	0.00	3	0.00
	19	3	3	1	33	1.00	20	0.15
	20	4	3	1	25	0.75	22	0.14
	21	7	2	1	14	0.29	42	0.05
	22	3	2	2	67	0.67	17	0.12
	23	4	6	1	25	1.50	79	0.08
	Mean	**4.52**	**4.04**	**2.39**	**59**	**0.97**	**52**	**0.09**

Table 5.7.3. Number of prey ingestions recorded per bout and per dive for each common Guillemot in 2003.

Bird	Bouts	Ingestions	Successful bouts	% Bouts successful	Ingestions/ bout	Dives	Ingestions/ dive
1	6	28	6	100	4.67	34	0.83
2	10	11	7	70	1.10	32	0.43
3	23	16	9	39	0.70	55	0.36
4	8	6	3	38	0.75	32	0.15
5	8	5	5	63	0.63	19	0.22
6	13	11	9	69	0.85	117	0.23
7	40	39	17	43	0.98	350	0.07
Mean	**15**	**17**	**8**	**60**	**1.38**		**0.33**

Black-legged Kittiwakes Rissa tridactyla (C.J. Camphuysen)

Chapter 6 Experimentation and strategic modelling

6.1 Experimental studies: foraging performance under controlled conditions

Manfred Enstipp & David Gremillet

The objective of experimental studies was to explore the behavioural and physiological responses of diving seabirds to abiotic and biotic parameters in a controlled laboratory environment. The studies were designed to provide the modelling work with novel, accurate input data. Seabirds are important top predators in marine ecosystems. To understand the role of these predators in the nutrient fluxes of marine food chains it is important to study their energetic requirements. The first part of the study investigated the energetic costs associated with diving in two pursuit divers, the Guillemot and the Shag. Energy requirements (e.g. daily energy expenditure) can be estimated by linking the knowledge of activity specific metabolic rates measured in the lab with time-activity data collected from birds in the wild (time-energy budget; e.g. Chapter 6.4; Enstipp *et al.* 2006). Hence, the experiments were designed to provide detailed information on the activity specific metabolic rates of two pursuit divers in the North Sea with contrasting morphological and physiological adaptations to diving. The results provide the essential and basic input data for bio-energetic modelling. In detail, we determined the energetic costs of diving in relation to water temperature, dive depth, digestive phase, and bird condition. The second part of the study was to look at the prey capture behaviour of these two seabird species, investigating prey capture techniques and prey capture rates in relation to water temperature, dive depth, light regimes, bird condition, prey type, and prey availability. The aim was to get a better understanding of how a decline in prey availability might potentially affect the fine scale foraging behaviour of seabirds. If prey availability decreases, seabirds may have to spend an increased amount of time and energy to locate and capture their prey. A threshold fish density might exist, below which seabird foraging might be no longer sustainable in terms of time and energy expended. Field observations on the fine scale foraging behaviour of top predators in marine ecosystems are hindered by many practical difficulties and, consequently are rare. Apart from logistic problems associated with carrying out such observations, there are biotic and abiotic factors that might have an impact on predator behaviour but which often are unknown and cannot be controlled for. In a controlled captive setting, however, logistic problems can be overcome and it is furthermore possible, to control a variety of factors that might alter predator behaviour. We observed the fine scale foraging behaviour of the Double-crested Cormorant *Phalacrocorax auritus albociliatus* foraging within a deep dive tank on live Rainbow Trout *Oncorhynchus mykiss*.

During the first season (in Norway, 2001) adult guillemots and shags were caught from the Runde breeding colony off the west coast of central Norway and these were studied in a captive setting. We focused on the energetics part of our study and recorded metabolic rates during shallow diving in Shags, altering water temperature and digestive status, but dive experiments with the guillemots failed because of their poor health. As a direct consequence of this experience, we decided against catching adult birds from the wild to continue our experimentation but to rather make use of animals raised in captivity. In the absence of the desired species, it was decided to use captive raised Double-crested Cormorants as a substitute for the Shags and to catch Guillemot chicks and raise them in captivity. While all energetics and foraging behaviour experiments with the cormorants were completed successfully, health problems with the guillemot juveniles prevented any experimentation with them. Hence, we succeeded to investigate all aspects of diving energetics for the shags (except depth) and cormorants, while prey capture behaviour was investigated for the cormorants only. In the following we will limit our report to these completed aspects. Material and methods have been described in Chapter 1.6.

Foraging energetics experiments

Cormorants and shags are foot-propelled pursuit divers that catch their prey near the bottom or within the water column of marine habitats. The purpose of this study was to gain detailed knowledge about the energetic costs associated with diving in Shags. To this end we investigated how biotic and abiotic factors influenced diving metabolic rates (water temperature, depth, digestive phase, bird condition). As outlined earlier, since it was not possible to investigate all aspects in the Shag, the experimentation was continued by using a closely related species, the Double-crested Cormorant. To investigate whether these divers might employ a strategy of regional hypothermia as an energy saving mechanism to prolong dive duration (Handrich *et al.* 1997), we recorded abdominal temperature patterns in parallel with the measurements of energy expenditure.

Basal metabolic rate (BMR) measured at night and during the day was not significantly different ($t = 0.71$; $P = 0.55$), hence the data were pooled. When resting in air (12–19°C) the BMR of Shags was 4.7 ± 0.3 $W\ kg^{-1}$ (Fig. 6.1.1). Repeated measure ANOVA comparisons of Shag metabolic rate during different activities and feeding status showed that resting in water, diving, and feeding significantly elevated metabolic rates above resting rates in air ($F = 58.98$, $P < 0.001$). Resting in water significantly elevated metabolic rate (when compared with resting in air) to 19.4 ± 0.7 $W\ kg^{-1}$ and 22.3 ± 3.2 $W\ kg^{-1}$ in the post-absorptive and absorptive state respectively. During shallow diving metabolic rate increased further to 22.6 ± 2.8 $W\ kg^{-1}$ in the post-absorptive state and 25.5 ± 3.6 $W\ kg^{-1}$ in the absorptive state (Fig. 6.1.1). Metabolic rate during shallow diving was not significantly different, however, from birds resting at the surface (water temperature 8 – 12°C in both cases). Feeding before a trial significantly increased the metabolic rate during diving ($t = -4.48$, $p = 0.046$) but not during resting on the water surface (comparing post-absorptive and absorptive trials). Diving metabolic rate remained elevated by an average of 10% for up to 5 hrs after feeding (the max period tested). 'Preening' (wing flapping in preparation for take off at the end of a dive bout) was the most costly activity averaging 39.4 ± 3.1 W kg^{-1} in one of the birds displaying this behaviour.

Water temperature had a significant effect on post-absorptive diving metabolic rate, so that metabolic rate increased with a decrease in water temperature (Fig. 6.1.2). The equation relating post-absorptive diving metabolic rate to water temperature was:

$$MR\ (W\ kg^{-1}) = 28.461 - 0.671\ (\text{water temperature } (°C));\ (P < 0.01;\ r^2 = 0.69).$$

However, during absorptive diving this relationship was not significant, most likely because of confounding factors. For the absorptive dive trials birds were fed different amounts of food at different times before diving, which could have masked the effect of water temperature on diving metabolic rate during these trials.

Shags swam with an average speed of 1.1 m s^{-1} and remained submerged for an average duration of 24s (max: 57s; Table 6.1.1). On average 53% of each dive cycle (dive and subsequent surface interval) was spent underwater. Mean stomach temperature when resting during the day was 40.6 ± 0.2°C which declined significantly during the night to 39.2 ± 0.1°C (Fig. 6.1.3). At the start of a dive trial temperature was significantly elevated from the day resting value and continued to rise during diving. After about 5–10 min of diving, however, a peak was reached after which temperature started to decline. Stomach temperature at the end of a dive trial was significantly lower than the peak value reached during diving but this drop was not significant when compared with the temperature at the start of a dive trial (Fig. 6.1.3). The average temperature increase early in a dive trial was about 0.3°C, while temperature at the end of a trial was on average about 0.6°C below the temperature at the start.

BMR of Double-crested Cormorants was 4.56 ± 0.56 W·kg^{-1} (Table 6.1.2). Repeated measure ANOVA comparisons revealed that resting in water, diving (shallow and deep) and feeding significantly increased the metabolic rate of Double-crested Cormorants above resting rates in air ($P < 0.001$; Fig. 6.1.4). When floating calmly in warm water the metabolic rate was significantly elevated by a factor of about 2.5 x BMR, while the increase during diving in warm water was even more significant to about 4.5 and 5.5 x BMR for shallow and deep diving respectively (Table 6.1.2).

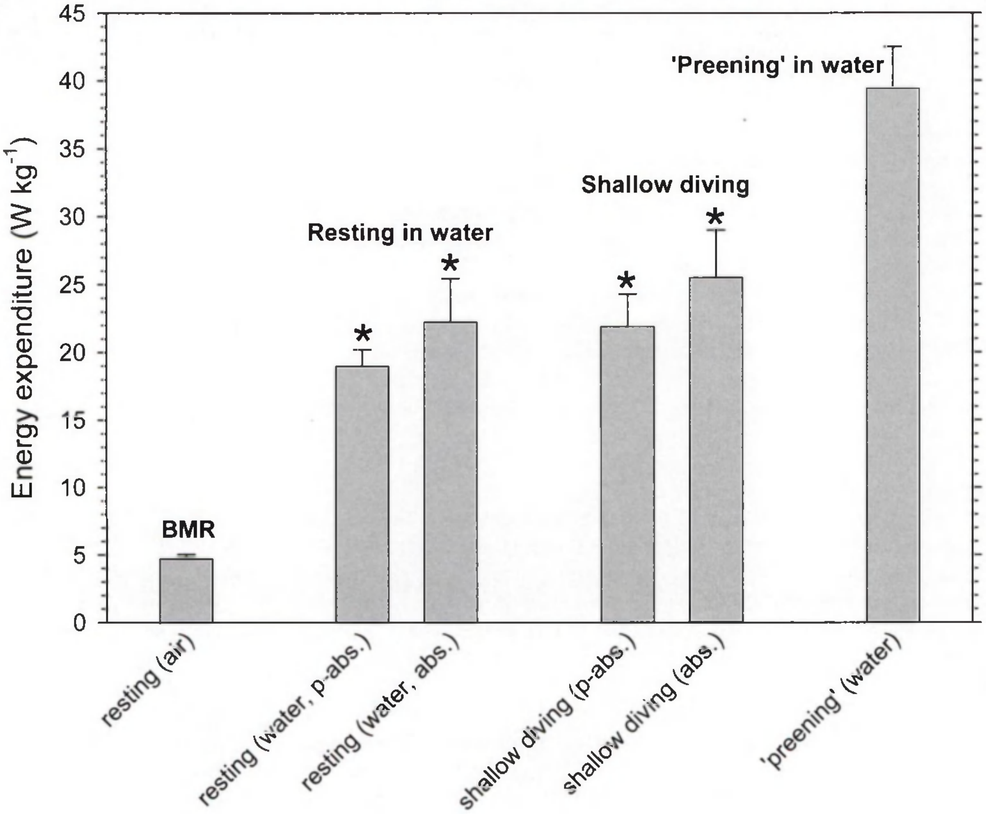


*Fig. 6.1.1. Energy expenditures (W·kg^{-1}) of European Shags during various activities. BMR was measured in air temperatures between 12 and 19 °C. All measurements in water were made at water temperatures between 8 an 12 °C. Values are grand means ± 1 S.D., which were established from individual bird means. N = 3 birds for all activities but 'preening' where N = 1 bird. * indicates a significant difference from BMR.*

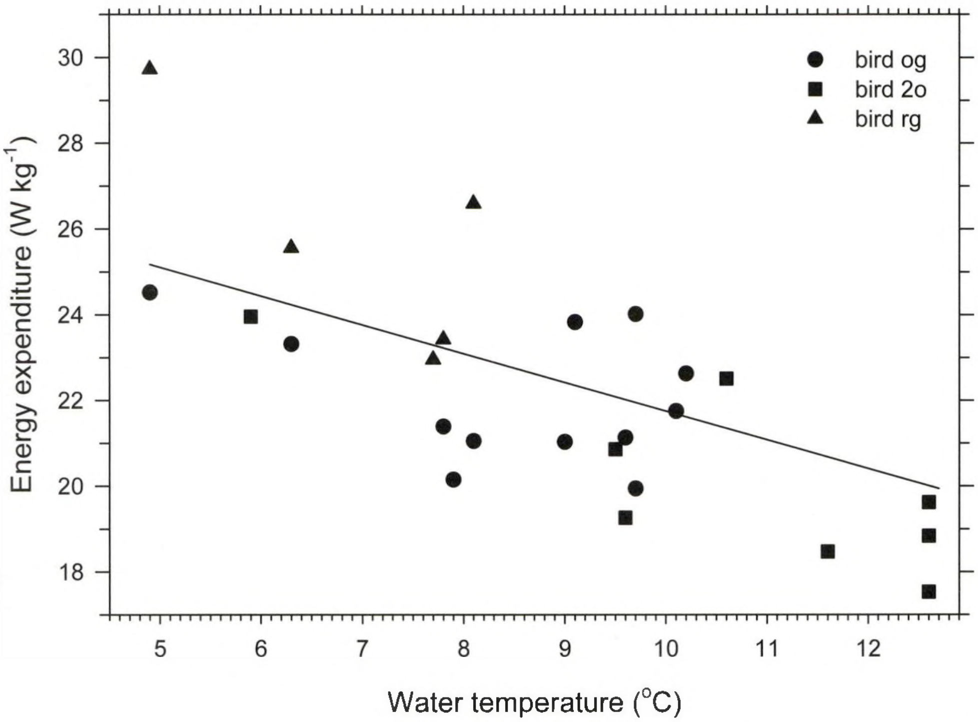


Fig. 6.1.2. Energy expenditure (W·kg^{-1}) of European Shags during shallow diving (post-absorptive) at various water temperatures (^{o}C). There was a significant negative relationship between energy expenditure and water temperature during diving. The regression line is the average relationship for all shags that takes into account variability between subjects and is described by $y = 28.461 - 0.671x$, where y is energy expenditure and x is water temperature ($r^2 = 0.69$). N = 3 birds, n = 25 trials.

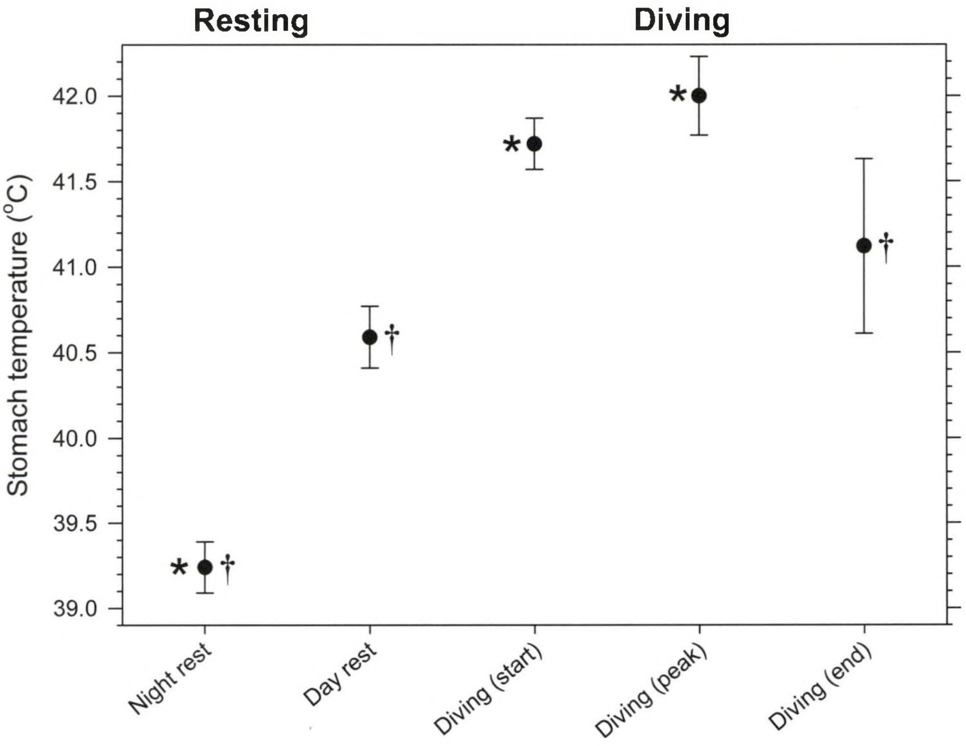


*Fig. 6.1.3. Stomach temperatures (^{o}C) of European Shags during rest at night and during the day, and during shallow diving. Values are grand means ±1 S.D., which were established from individual bird means. N = 3 birds. *Significantly different from day (rest) value. †Significantly different from diving (peak) value.*

Table 6.1.1. Summary of parameters measured during shallow diving in 3 Shags. Values are presented as means ± 1 S.D. (post-absorptive and absorptive trials combined). A grand mean is the mean of the individual bird means.

Bird	Body mass (kg)	Dive duration (s)	Dives per bout *n*	Trials *n*	Water temp (°C)	Swim speed (m s^{-1})	Energy expend. (W kg^{-1})	Respiratory exchange ratio
2O	1.56 ± 0.02	26.7 ± 6.2	5.6 ± 2.5	26	10.5 ± 1.6	1.2 ± 0.1	22.2 ± 2.8	0.82 ± 0.10
OG	1.97 ± 0.10	22.9 ± 3.3	12.3 ± 6.8	36	9.1 ± 1.0	1.1 ± 0.1	23.3 ± 2.4	0.74 ± 0.07
RG	1.44 ± 0.03	22.3 ± 5.7	5.2 ± 3.7	16	8.7 ± 0.8	1.1 ± 0.1	28.5 ± 4.0	0.74 ± 0.06
Grand mean	1.66 ± 0.28	24.0 ± 2.4	7.7 ± 4.0	26.0 ± 10.0	9.4 ± 0.9	1.1 ± 0.1	24.7 ± 3.4	0.77 ± 0.04

While metabolic rate was increased after feeding this increase was not significant when the effects of temperature and activity were accounted for. In other words, metabolic rates in absorptive and post-absorptive trials during a particular activity (e.g. shallow diving) and at a particular temperature (e.g. warm) were not significantly different from each other. However, metabolic rates during all absorptive trials were increased by about 5 - 8% above the post-absorptive level within 30 min after feeding and remained at this level, until slowly declining after about 2 hrs after feeding (Fig. 6.1.5).

Temperature had a significant effect on the metabolic rates of cormorants during all activities ($P < 0.001$). Resting in air at an air temperature below the lower critical temperature significantly elevated metabolic rate (Fig. 6.1.4; mean air temperature during cold air trials: 8.6 ± 1.1°C). When resting or diving in cold water the metabolic rate of cormorants was significantly increased when compared with the respective warm water trials (Table 6.1.2). In all cases there was a significant negative relationship between metabolic rates of Double-crested Cormorants during different activities and temperature, which allowed the calculation of linear regression equations (Table 6.1.3, Fig. 6.1.6).

Diving to depth was energetically more costly then performing shallow horizontal dives. Again this difference was significant, when comparing shallow and deep diving while accounting for water temperature and feeding status ($P< 0.001$).

Table 6.1.2. Dive patterns observed in Double-crested Cormorants and energy expenditures associated with different activities and feeding status. Values are grand means ± 1 S.D. which were established from individual bird means. Temperature refers to air temperature in case of 'BMR' and to water temperature in all other cases. 'Factor' is the energy expenditure of the respective activity expressed in multiples of BMR. All dive parameters given for 'deep diving' exclude individual shallow dives that birds might have performed during a deep dive trial. N gives the number of birds, while n refers to the number of trials.

		Temperature (°C)	Energy expenditure (W·kg^{-1})	Factor (x BMR)	Dive duration (s)	Surface duration (s)	Dive/pause ratio	N_0 dives per bout	*N*	*n*
BMR		22.1 ± 1.0	4.56 ± 0.56						10	27
Resting in water										
(post-absorptive)	warm	15.0 ± 0.7	10.65 ± 1.62	2.34					8	24
	cold	7.9 ± 0.0	14.76 ± 2.60	3.24					8	21
(absorptive)	warm	14.6 ± 1.1	11.13 ± 1.80	2.44					7	36
Shallow diving										
(post-absorptive)	warm	16.4 ± 1.1	20.16 ± 1.86	4.42	23.5 ± 2.6	20.0 ± 7.5	1.7 ± 0.6	17.3 ± 7.0	9	49
	cold	7.5 ± 0.1	23.23 ± 1.52	5.09	19.1 ± 3.2	21.3 ± 8.2	1.4 ± 0.3	9.7 ± 3.3	7	45
(absorptive)	warm	15.5 ± 1.2	20.58 ± 2.10	4.51	23.9 ± 2.9	24.9 ± 9.8	1.5 ± 0.6	14.9 ± 5.2	9	62
	cold	7.3 ± 0.1	24.88 ± 1.96	5.46	23.1 ± 0.9	26.8 ± 9.8	1.3 ± 0.5	8.9 ± 3.4	7	23
Deep diving										
(post-absorptive)	warm	13.9 ± 1.2	24.95 ± 0.94	5.47	21.2 ± 3.6	14.4 ± 4.3	1.7 ± 0.4	3.8 ± 0.7	7	55
	cold	7.6 ± 1.4	28.03 ± 1.37	6.15	19.1 ± 1.3	13.3 ± 2.7	1.7 ± 0.4	3.9 ± 0.4	7	77
(absorptive)	warm	13.9 ± 1.2	25.96 ± 1.10	5.69	21.4 ± 3.9	14.6 ± 3.8	1.7 ± 0.3	4.5 ± 1.3	7	61
	cold	7.7 ± 1.3	29.20 ± 2.04	6.40	19.3 ± 1.8	12.9 ± 2.8	1.7 ± 0.4	4.7 ± 0.6	7	68

Table 6.1.3. Linear equations for regressions of resting and diving metabolic rates (W kg^{-1}) of Double-crested Cormorants against temperature (°C). Regressions were determined by multiple linear regression that takes into account variability between subjects (Glantz & Slinker 1990). Values are means ± 1S.D. Temperature (mean and range) refers to air temperature in case of 'resting in air' and to water temperature in all other cases. N gives the number of birds, while n refers to the number of trials.

	Temperature (°C)	Intercept	Slope	*N*	*n*	r^2	*P*
Resting in air (post-absorptive)	16.6 (6.2 – 25.4)	6.994 ± 0.27	- 0.117 ± 0.015	10	62	0.73	< 0.001
Resting in water (post-absorptive)	11.7 (7.8 – 15.6)	19.880 ± 0.87	- 0.620 ± 0.072	9	45	0.78	< 0.001
Shallow diving (post-absorptive)	12.1 (7.1 – 17.5)	26.676 ± 0.46	- 0.401 ± 0.033	9	94	0.77	< 0.001
Shallow diving (absorptive)	13.1 (7.0 – 17.1)	28.953 ± 0.77	- 0.533 ± 0.054	9	85	0.70	< 0.001
Deep diving (post-absorptive)	10.2 (6.1 – 15.4)	30.920 ± 0.43	- 0.418 ± 0.038	8	132	0.60	< 0.001
Deep diving (absorptive)	10.7 (6.1 – 15.4)	32.409 ± 0.52	- 0.462 ± 0.045	8	129	0.62	< 0.001

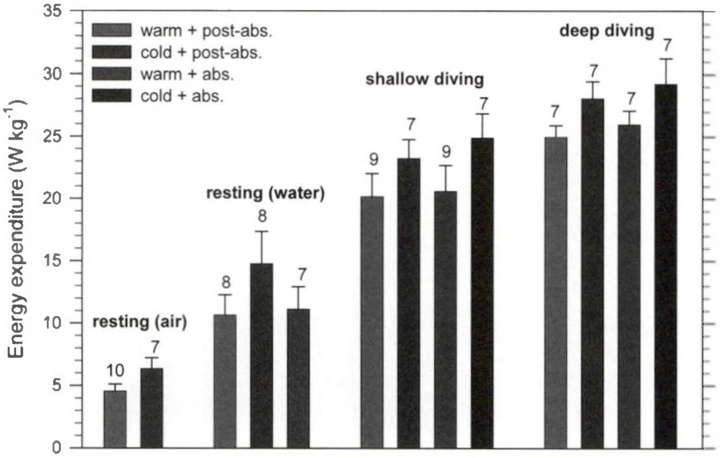


Fig. 6.1.4. Energy expenditure (W·kg^{-1}) of Double-crested Cormorants during various activities at different temperatures ('warm' and 'cold') and feeding status ('post-absorptive' and 'absorptive'). See Table 1 for the respective temperature values. Energy expenditure during resting in air (warm) was taken as BMR. Values are grand means ± 1 S.D. which were established from individual bird means. Values above the columns indicate the number of birds used.

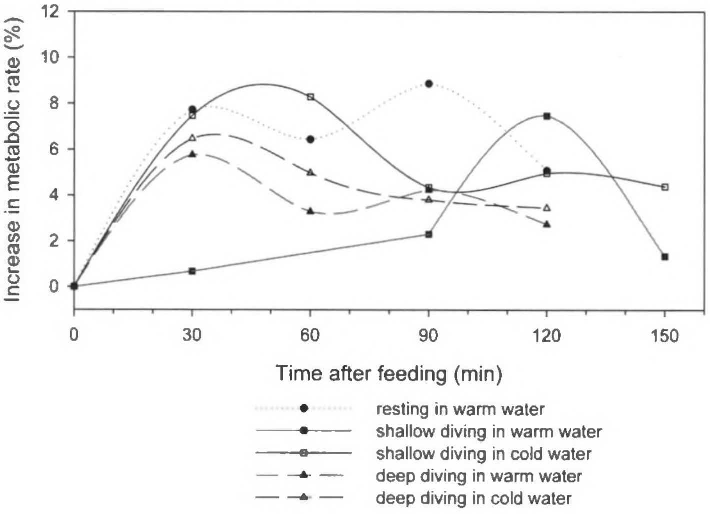


Fig. 6.1.5. Increase in metabolic rate (% above post-absorptive) during various activities at different water temperatures ('warm' and 'cold') when cormorants were fed 60 g of herring at various times before a trial. See Table 1 for details on the temperature values. Absorptive trials were conducted with birds being fed between 30 and 150 min before a trial.

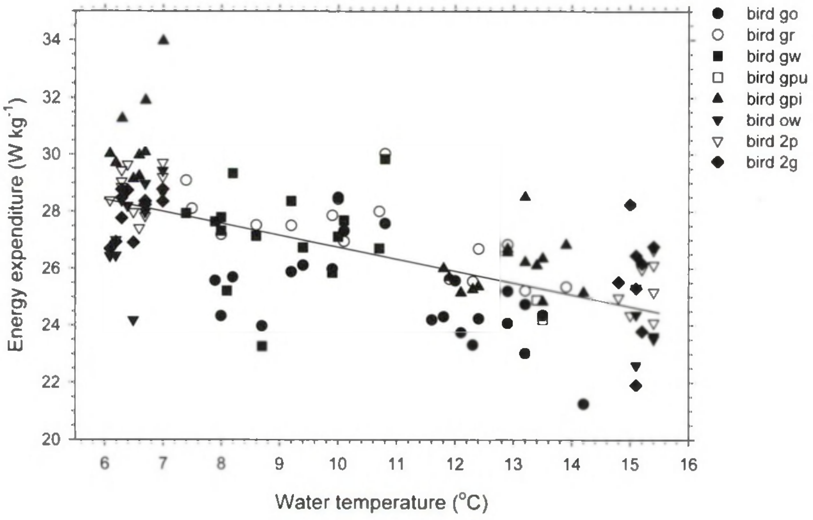


Fig. 6.1.6. Energy expenditure (W·kg^{-1}) of Double-crested Cormorants during deep diving (post-absorptive) at various water temperatures (°C). There was a significant negative relationship between energy expenditure and water temperature during diving. The regression line is the average relationship for all cormorants that takes into account variability between subjects and is described by $y = 30.920 - 0.418x$, where y is energy expenditure and x is water temperature ($r^2 = 0.60$). N = 8 birds, n = 132 trials

The various factors investigated during experimentation (activity, temperature, feeding status, depth) were interactive and additive. While diving was more costly than resting (in water and air), submerging to depth increased the energetic expenses even more. Ingesting food and decreasing water temperatures further increased the energy expenditure of cormorants. As can be seen in Table 6.1.2 and Fig. 6.1.4, the highest energy expenditure observed was during deep diving in cold water after food ingestion (absorptive), when metabolic rate increased by a factor of 6.4 x BMR.

Dive durations of birds were similar for shallow and deep diving but tended to be shorter when diving to depth. Surface duration, however, was significantly shorter during deep diving ($p < 0.001$) resulting in a higher dive pause ratio during deep diving (Table 6.1.2). A higher dive pause ratio would indicate that birds were working harder during deep diving and dived more efficient in that setting. Similarly, the fraction of the dive cycle (dive and succeeding surface interval) spent underwater was significantly higher during deep diving (60.4%), when compared with shallow diving (53.2%).

Foraging behaviour experiments

We experimentally investigated the effect on cormorant prey capture behaviour of prey availability (fish density), prey size, light conditions, fish behaviour, bird condition (body mass), water temperature, and dive depth.

Between late August and early November 2003 we conducted a total of 100 foraging trials with 9 birds of which 82 trials were included in the current analysis. During these 82 trials birds conducted a total of 660 dives, ranging from a few seconds to about 1 minute in duration. During a trial a bird would typically start diving within 30 s of introduction into the dive tank. If prey was encountered, the bird usually started a pursuit which ended either with the capture of the trout, a switch to attacking/pursuing another trout, or with the return to the surface, when the bird 'gave up'. A bird typically dived until either satiated (after multiple prey ingestions) or 'frustrated' (if no prey was encountered or caught) and left the water afterwards to wingspread. In the first situation a bird typically started another dive bout towards the end of the 30 min trial. In the latter situation a bird would usually reassess the situation frequently during the first half of a trial by performing a few exploratory dives, before finally giving up (and remaining outside the water), if no prey was encountered or caught.

We observed 518 prey pursuits of which 275 ended in the successful capture and ingestion of a trout. Mean success rate of all initiated pursuits by 9 birds was 58.3 ± 21.0% (range: 31.0 – 92.9%). Since birds often initiated more than one prey pursuit per dive, success rate was higher when expressed on a per dive basis, with a mean of 77.7 ± 14.5% of all dives during which prey was encountered and pursued being successful. Mean duration of pursuits that ended with prey capture was 6.77 ± 1.48 s (range: 1 – 28 s). After prey capture, birds typically surfaced with the fish and manipulated it so as to swallow it headfirst. Double-crested Cormorants are certainly capable of swallowing 'small' fish underwater (Enstipp, pers. observ.). In the current study, however, this was only observed in 9 cases (out of 275 prey captures) and mostly concerned the two largest birds. Handling times at the surface (from surfacing to prey ingestion) were short (mean: 3.8 ± 1.5 s, range: 1 – 12 s). If handling time was calculated as the time from prey capture to prey ingestion (hence, including the time underwater from capture to surfacing), it became largely a function of the depth at which prey was caught. ost fish that were attacked by a bird seemed to be well aware of the predator early on, as they were actively moving away from it. However, in 18% of all bird attacks a fish remained stationary until a very late stage and was captured in 73% of these attacks.

The total number of fish (**fish density**) inside the dive tank during a trial ranged from 1 to 23, which corresponded to a density of 0.18 to 7.26 g m^{-3} (0.01 to 0.12 fish m^{-3}). Fish density within the dive tank had a strong effect on the various aspects of cormorant prey capture behaviour investigated (Fig. 6.1.7-10). The total amount of time that cormorants spent searching during a foraging trial increased with a decline in fish density (Fig. 6.1.7). Similarly, the time that birds spent submerged before encountering a fish increased with a decline in fish density (Fig. 6.1.8), while the percentage of dives during which prey was encountered declined with a reduction in fish density (Fig 6.1.9). In all cases the relationship between fish density and the variable of bird foraging behaviour was not simply linear. It was rather characterised by a threshold fish density (around 2 g m^{-3}) below which the change was exponential. There was, however, a significant linear relationship relating fish density to prey capture rate (CPUE). As fish density increased, so did the prey capture rate of cormorants (Fig. 6.1.10).

The **prey size** (body mass and length) of the introduced trout ranged from 23 to 108 g and 15.5 to 25 cm respectively. Within the size range of trout that we investigated, there was no significant effect of fish size on cormorant predatory performance. The likelihood of getting caught was similar for large (≥ 18.5 cm) and small fish (< 18.5 cm). In trials with a similar mean fish density (0.06 fish m^{-3}) prey capture rates achieved by the birds were identical for small fish (1.6 g fish s^{-1} submerged or 0.03 fish s^{-1} submerged) and large fish (1.7 g fish s^{-1} submerged or 0.03 fish s^{-1} submerged). While individual pursuits tended to be more successful in trials with small fish (67% versus 57% for large fish), this difference was not significant ($P = 0.58$, $t = 0.58$). Similarly, foraging effort, as indicated by the duration of successful pursuits, was similar for both size classes (6.3 s versus 6.8 s for small and large fish respectively).

Light conditions did not limit the predatory performance of cormorants within the illumination range tested (1.8 – 120 lux). Cormorants achieved high prey capture rates even under low light conditions (Fig. 6.1.11). While we recorded some low CPUE values at the lower end of the illumination scale, these were also trials with a low fish density. Removing trials with a fish density below 2 g m^{-3} from the plot, also removed most of these data points.

Regarding **fish** behaviour, fish often started to form shoals, which was especially true, when the overall number of fish within the dive tank was large. This shoaling behaviour had consequences for the predatory performance of the cormorants. In 55.8% of all pursuits birds targeted individual fish that were not part of a shoal. 70.8 ± 22.1% of these pursuits were successful. 44.2% of all pursuits recorded were directed towards a shoal or an individual that was part of a shoal. However, the success rate of these pursuits was significantly lower, with only 40.5 ± 14.5% of pursuits culminating in prey capture ($P = 0.002$, $t = -4.43$). A similar picture emerged when we compared the success rate of dives where a pursuit was initiated (Fig. 6.1.12). Besides reducing predator success rate, on the level of a single pursuit and on a dive level, shoaling also significantly increased the amount of time birds had to spent in prey pursuit in order to succeed. When successfully attacking a non-shoaling fish, birds spent on average 5.2 ± 1.4 s in prey pursuit. In contrast a bird spent on average 10.2 ± 2.9 s in prey pursuit when it attacked and captured a fish that was part of a shoal ($P < 0.001$, $t = -5.78$). In a few cases we observed birds seemingly ignoring a shoal close to the surface, diving to the bottom of the 10 m dive tank instead, where a few non-shoaling fish were present.

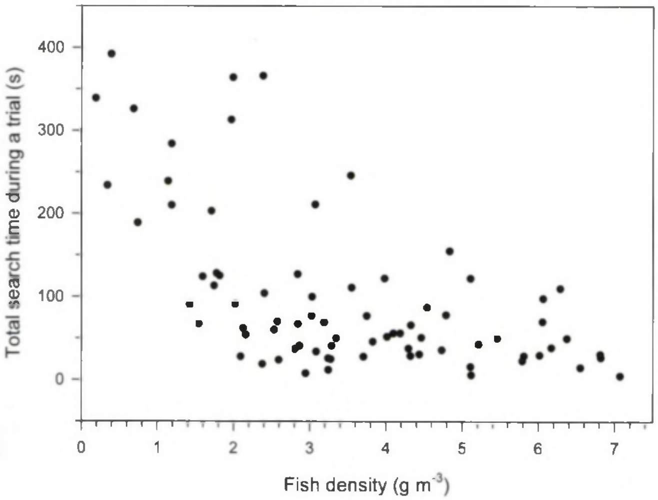


Fig. 6.1.7. Time spent searching during a trial (s) against fish density within the dive tank (g m^{-3}). A threshold fish density seems to exist at about 2 g m^{-3} below which the amount of time a cormorant spent searching during a trial increased drastically. N = 9 birds, n = 77 trials.

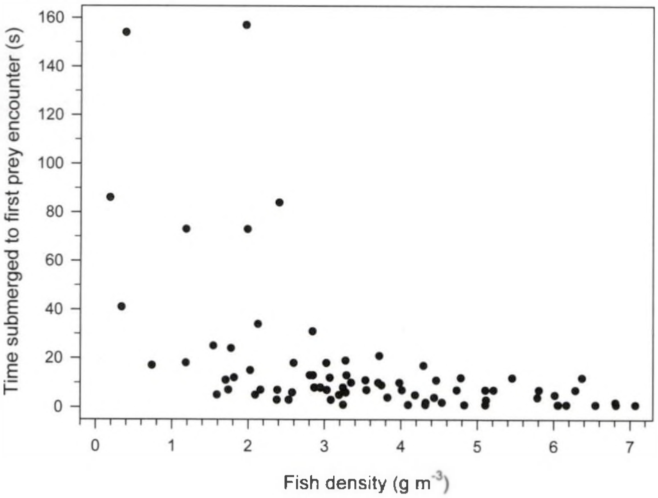


Fig. 6.1.8. Time spent submerged (s) before a cormorant first encountered a fish against fish density within the tank (g m^{-3}). A threshold fish density seems to exist at about 2 g m^{-3} below which a bird has to spend an increased amount of time underwater (i.e. searching) before encountering a fish. N = 9 birds, n = 76 trials.

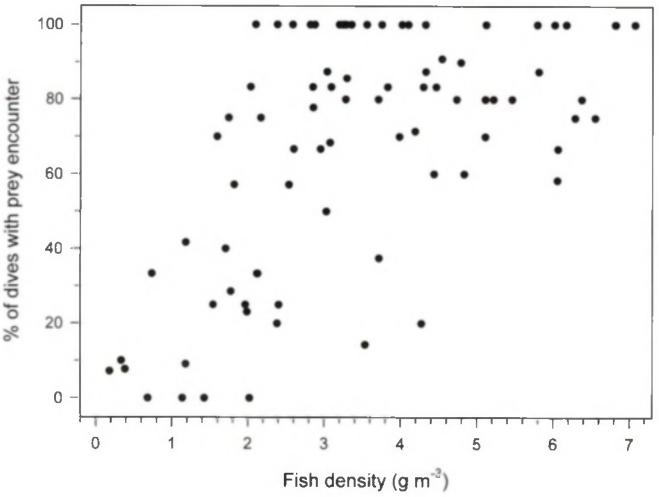


Fig. 6.1.9. Percentage of dives performed in a foraging trial during which a fish was encountered against fish density within the tank (g m^{-3}). A threshold fish density seems to exist at about 2 g m^{-3} below which the likelihood of a bird to encounter a fish during a dive decreases drastically. N = 9 birds, n = 82 trials.

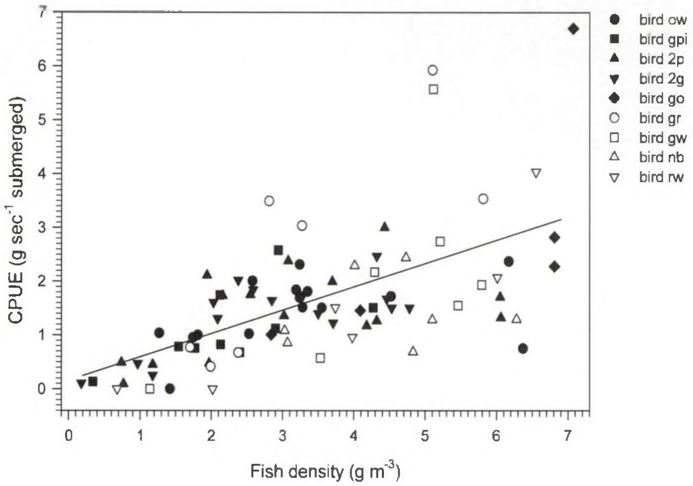


Fig. 6.1.10. Prey capture rate (CPUE in g s^{-1} submerged) of Double-crested Cormorants versus fish density (g m^{-3}) within the tank. The 'catch per unit effort' increased significantly with an increase in fish density. The regression line is the average relationship for all cormorants that takes into account variability between subjects and is described by $y = 0.160 + 0.434x$, where y is the catch per unit effort and x is fish density ($r^2 = 0.45$). N = 9 birds, n = 86 trials.

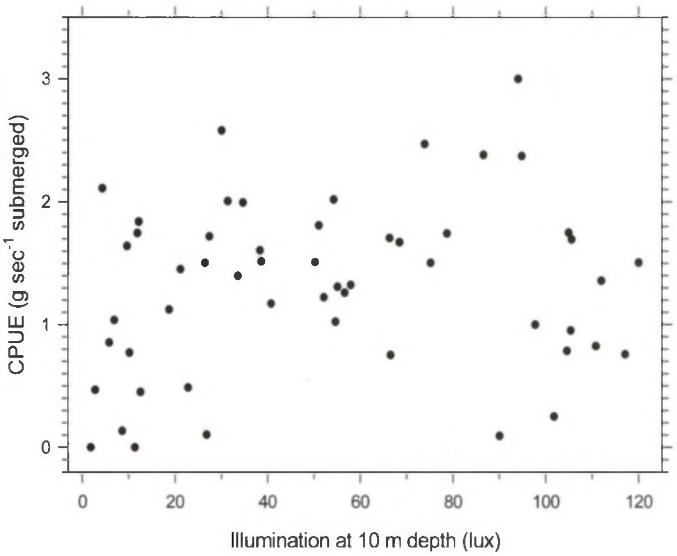


Fig. 6.1.11. Prey capture rate (CPUE in g s^{-1} submerged) against illumination (lux) measured at the bottom of the deep dive tank. Light conditions were varied by conducting trials either around midday (higher values) or in the late afternoon (low values). No clear trend is apparent, indicating that light conditions encountered did not limit the prey capture capabilities of cormorants. N = 9 birds; n = 54 trials.

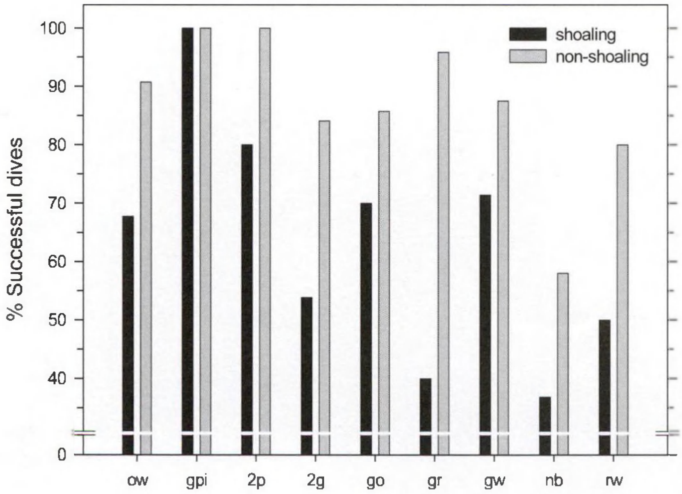


Fig. 6.1.12. Success rate (% of successful dives) of individual cormorants during foraging dives in which a prey pursuit was initiated, contrasting a situation in which fish form a shoal or not. In a non-shoaling situation the bird targeted an individual fish that was not part of a shoal (n = 209 observations), while in a shoaling situation the bird targeted a shoal or an individual that was part of a shoal (n = 148 observations). There was a significant difference between the two situations encountered, with a much higher success rate when birds targeted individual fish that were not part of a shoal ($p = 0.002$; $t = -4.69$). N = 9 birds; n = 82 trials.

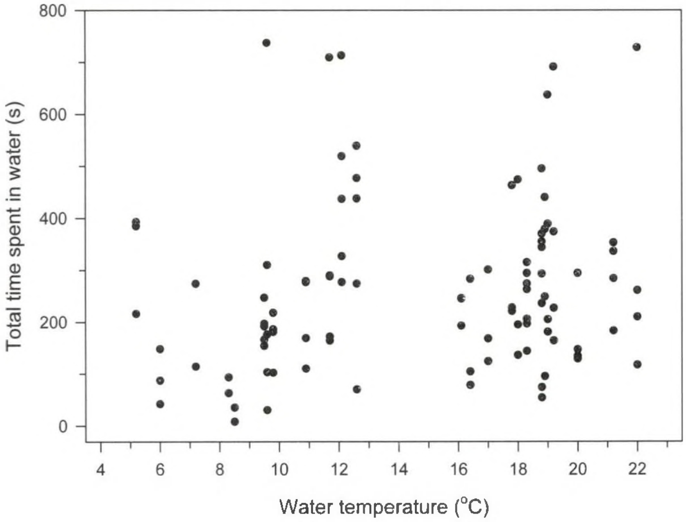


Fig. 6.1.13. Amount of time spent in water during a 30 min trial (s) against water temperature within the dive tank (°C). Birds seemed to spent less time in water when water temperature declined but this trend was not significant within the range of temperatures tested (5 – 22 °C). N = 9 birds, n = 100 trials.

There was no relationship between **bird condition** (body mass) and foraging success (CPUE) achieved by individual birds. Based on our observations some individuals seemed to be consistently more successful than others and this was most likely related to individual strategy and experience rather than body mass. One bird for example discovered that trout would often hide within a piece of the tank outflow pipe, which was accessible to the birds. From this point on the bird always checked this particular spot for fish and often succeeded in catching at trout by extending its long neck into the pipe.

Water temperature within the dive tank did not affect cormorant foraging behaviour within the range of temperatures tested (5 – 22 °C). While birds seemed to spent less time in water when water temperature declined, this trend was not significant (Fig. 6.1.13). This trend might have become significant, however, if water temperatures had been fallen to lower levels. There were a few observations that might support the idea of birds reducing the amount of time spent in cold and especially deep water to a minimum. One strategy of some birds, which seemed to be more exploited as water temperatures dropped, was to 'monitor' fish from a platform outside the water and start a pursuit when fish were close to the surface. Another strategy, more prevalent in cold temperatures was to leave the water after each dive.

Regarding **dive** depth, dive duration was significantly shorter in shallow dives ($\leq$ 3 m, 12.1 ± 1.7 s) than in deep dives (> 3 m, 27.2 ± 2.4 s; $p < 0.001$, $t = -12.56$). The duration of the succeeding surface interval, however, was not significantly different between shallow and deep dives (18.0 ± 9.6 s versus 25.9 ± 5.6 s), which was true also for the resulting dive to pause ratio (1.11 ± 0.37 versus 1.36 ± 0.33). 73.7 ± 14.6% of all shallow dives during which prey was encountered and pursued were successful, compared with 81.0 ± 17.9% of deep dives. While this difference was not significant, the difference in success rate of individual pursuits during shallow and deep diving was. 68.2 ± 15.8% of all initiated pursuits were successful during shallow diving, compared with 53.5 ± 21.1% during deep diving ($p = 0.015$, $t = 3.09$). This could indicate that birds in the deep diving situation were more willing to end a so far unsuccessful pursuit in order to initiate another (i.e. switch fish) than in the shallow dive situation.

Despite the problems we encountered with respect to the health status of our Guillemots, this study produced very valuable data concerning the foraging energetics and foraging behaviour of Shags and Double-crested Cormorants. This is especially true for the latter species, where all required experimental work was completed successfully.

We showed that water temperature, dive depth, and digestive phase are important factors that strongly affect the amount of energy which cormorants have to expend during foraging (dive depth not investigated in Shags). We also quantified the effect of these factors on bird energy expenditure during diving by establishing equations relating energy expenditure during shallow and deep diving to water temperature and digestive phase. Abdominal temperatures remained fairly stable during shallow diving in European shags, which would indicate that they did not employ a strategy of regional hypothermia to prolong dive duration. Foraging success of Double-crested Cormorants foraging on live Rainbow Trout depended to a large degree on prey availability (fish density), while fish behaviour (shoaling or not) had important consequences for predator performance. Prey size, light conditions, bird condition (body mass) and water temperature had little impact on cormorant foraging behaviour within the range tested. Dive depth greatly affected dive duration of cormorants but had little effect on the overall success rate of dives.

6.2 Strategic dynamical modelling of the foraging process of diving predators

J. van der Meer and J.G. Ollason

In order to understand the relationship between the food intake rate of a group of piscivorous avian predators and the numbers of spatially heterogeneously distributed prey fish, we aimed to develop an individual-based model in which population properties should emerge from the decisions of the individual animals. We have chosen to build such model in a step by step approach, based on first principles regarding foraging decision rules and basic bio-energetics. Within the IMPRESS project a few, but not all, of these steps could be taken. First, a model of the foraging behaviour of an individual diving predator feeding underwater on a single food patch was developed. This model is an elaboration of a previously developed model of a general predator (Ollason & Yearsley 2001).

A general predator model

The general predator model is based on only a few assumptions. Basically, they imply that feeding rate of the predator is a function of the standing crop of food, and that feeding stops when the feeding rate is less than the maintenance rate, which itself is proportional to the mass of the animal. In its most basic form the model contains three types of state variables. The first is the body mass of the animal, which increases as a result of feeding and decreases as a result of maintenance costs. The second refers to the behaviour of the predator, and has a finite number of states, e.g. feeding or waiting. The last one is the standing crop of food, which decreases as a result of feeding and may increase as a result of replenishment.

The model has been applied to a patchy environment, in which patches differ in the replenishment rate and in which animals will move to another patch only if feeding stops (i.e. when the feeding rate is less than the maintenance rate). The model predicts slight undermatching of the ideal free distribution (Ollason & Yearsley 2001). It should be recalled that the model does not make any assumption about the animals being "ideal" (ideal means that animals are omniscient and behave optimally). Animals only leave a patch when the feeding rate is less than the maintenance rate. All patterns emerge from this single rule.

Two versions of this general predator model exist. In one version feeding is continuous, whereas in the other version the predator feeds on particles. In the version in which feeding is on particles, the maintenance rate cannot continuously be compared to the feeding rate. Instead, the waiting time (which could also be interpreted as searching time) to find the next particle is compared to a remembered waiting time. The rule, then, is to leave the patch when the waiting time exceeds the remembered waiting time. The remembered waiting time follows some slightly complicated dynamics. See Box 6.2.1 and Ollason & Yearsley (2001) or Ollason *et al.* (2006) for further details.

A diving predator model

The model of the diving predator takes into account that the animal has to travel between a patch (near the seafloor) of particles of food and a patch (at the sea surface) in which the animal continuously replenishes oxygen used in diving. Again, two versions exist. The replenishment of oxygen is always a continuous process, but feeding can be described either as a continuous process or as a feeding on food particles process. The aim of the model is to predict the food intake rate as a function of food density and diving depth. The model also predicts the time budget of the diving predator in terms of time spent diving and feeding, and time spent at the surface replenishing oxygen used in diving.

Box 6.2.1. The general predator model: a version where multiple predators exploit a patchy environment in which feeding is continuous

State variables of this particular version of the model are $m_j(t)$, the body mass of predator j; $S_j(t)$ the behavioural state of predator j; and $F_k(t)$ the food density of patch k. The possible behavioural states are either feeding in a specified patch or travelling. The system can be represented by the following coupled equations:

$$\frac{dm_j(t)}{dt} = vF_k(t) - rm(t),$$

for predator j feeding in patch k, i.e. when $S_j(t)=k$;

$$\frac{dm_j(t)}{dt} = -rm(t),$$

for predator j travelling between patches, i.e. when $S_j(t)=0$;

$$\frac{dF_k(t)}{dt} = a_k - n_k(t)vF\ ,$$

for patch k, where n_k is the number of predators feeding in patch k. The value of n_k can be derived from the state variables S_j.
The parameter v is the rate of feeding (area of discovery of Hollings type I functional response), r is the specific metabolic rate, and a_k is the rate of replenishment in patch k.
The behavioural state of a predator changes from feeding in patch k to travelling for a period t_t towards another (neighbouring) patch, when

$$vF_k(t) < rm(t)$$

Box 6.2.2. The individual guillemot model when feeding is continuous

The most important state variables (units between brackets) of this version of the model are *g(t)* gut content (g), *m(t)* body mass (g), *O(t)* oxygen content in the body tissue (litre), and *S(t)* the behavioural state of the bird. The possible behavioural states discussed here are feeding, ascending, recovering and descending. Feeding rate is constant and only a single food patch is considered. When feeding the following three coupled equations hold:

$$\frac{dg(t)}{dt} = f - r_g g(t) \qquad (1)$$

which represents that the gut is filled with a feeding rate f (g s^{-1}) and emptied according to a first-order process, where r_g (s^{-1}) is the specific rate of clearance of the gut;

$$\frac{dm(t)}{dt} = \alpha r_g g(t) - \left[r_b m(t) + (r_f - r_b)(m(t) + g(t)) \right] \qquad (2)$$

which says that a fraction α (-), i.e. the assimilation efficiency, of the clearance rate of the gut enters the body, and that the metabolic rate is the sum of the basal metabolic rate (which is proportional to the body mass and with r_b (s^{-1}) as the specific metabolic rate) and a term (proportional to body mass plus gut content) expressing the extra costs of feeding, i.e. the extra transport costs; the parameter r_f (s^{-1}) is called the specific metabolic rate while feeding; and

$$\frac{dO(t)}{dt} = -\rho \left[r_b m(t) + (r_f - r_b)(m(t) + g(t)) \right] \qquad (3)$$

which simply shows that oxygen use is proportional to metabolic rate, with proportionality coefficient ρ (liter g^{-1}).
The equations for ascending and descending are basically the same, but there is no feeding ($f = 0$) and the parameter r_f, the specific metabolic rate while feeding, is replaced by r_a (s^{-1}) and r_d (s^{-1}), respectively. Similarly, while recovering there is no feeding and the parameter r_f is replaced by r_r (s^{-1}). The equation for the change of oxygen content now includes the replenishment of oxygen and becomes

$$\frac{dO(t)}{dt} = u(O_{max} m(t) - O(t)) - \rho \left[r_b m(t) + (r_r - r_b)(m(t) + g(t)) \right]$$

where O_{max} is the maximum oxygen concentration in the tissue (litre g^{-1}) and u is the specific replenishment rate (s^{-1}). Recall that it is assumed that the rate at which oxygen is replenished is proportional to the difference between the maximum oxygen content and the available content.

The model uses four state variables: behavioural state of the animal, body mass of the animal, mass of food in the gut, and the volume of oxygen contained in the body. The density of food particles is not depleted. The predator can show five or six different behavioural states: resting (at night), recovering at the sea surface, descending, feeding near the seafloor (in case of discrete particles this behavioural state is split in a waiting and a handling state), and ascending. The gut content is taken into account explicitly, because costs of travelling involve the total mass transported. A full gut can make a significant contribution to the total mass of the animal. As in the general predator model, decision rules about when to shift from one behavioural state to another, have been formulated. Feeding (on discrete particles), for example, stops when either the waiting time exceeds the remembered waiting time (as in the general predator model), or the oxygen is running out, or the gut is full, or the body mass has reached a certain maximum level. The chosen time is the earliest of all of these. Further description of the model structure is provided in Ollason and Ren (2002 b) and Ollason *et al.* (2006).

Table 6.2.1. Parameter values of the diving predator model for the guillemot. See Liu et al. (2002) and Ollason et al (2003) for details.

Parameter	Symbol	Unit	Value
Specific rate of clearance of the gut	r_g	s^{-1}	$1.0\ 10^{-3}$
Assimilation efficiency	*alpha*	-	0.8
Specific basal metabolic rate	r_b	s^{-1}	$1.8\ 10^{-7}$
Specific metabolic rate while feeding	r_f	s^{-1}	$2.448\ 10^{-7}$
Specific metabolic rate while ascending	r_a	s^{-1}	$3.267\ 10^{-7}$
Specific metabolic rate while descending	r_d	s^{-1}	$3.267\ 10^{-7}$
Specific metabolic rate while recovering	r_r	s^{-1}	$3.267\ 10^{-7}$
Stoichiometric equivalent of oxygen	*rho*	litre g^{-1}	0.1275
Specific rate of re-oxygenation	u	s^{-1}	0.1
Maximum oxygen concentration	O_{max}	µl g^{-1}	55
Minimum oxygen concentration	O_{min}	µl g^{-1}	13.75
Maximum gut content	g_{max}	g	10
Minimum gut content	g_{min}	g	200
Ascending speed		m s^{-1}	1.6
Descending speed		m s^{-1}	1.6

The individual guillemot model

The discrete food particle version of the diving predator model has been parameterised for the guillemot *Uria aalge*, one of the key species in the IMPRESS project. Additional processes, like provisioning of the chicks have been incorporated as well. Ollason *et al.* (2003) give all the equations, including analytical solutions, the simulation programs including documentation, and sample runs of the individual guillemot feeding on sandeels at depth. See further Box 6.2.2 and Table 6.2.1. Simulations have been run with the model varying, among other things, depth and feeding rate. See, as an example, figure 6.2.1 in which the frequency distribution of simulated search times is compared to one based on observed values in the field using tagged birds. Initial values that have been used in the simulations were 1000 g for body mass, 100 g for gut content and 50 µl g^{-1} for oxygen concentration. Hence 50 ml for oxygen content. Feeding rate and depth have been varied in the simulations.

Decisions have to be made about when to stop feeding and when to resume feeding while recovering. Ascending and descending are events that are always completed once initiated and involve no decisions. Hence, the only extra information required is the time these events last, which is given by diving depth and ascending/descending speed. The birds stops feeding when oxygen is running out, that is when $O/m = O_{min}$, or when the gut is full, that is when $g = g_{max}$. Resuming feeding occurs when the gut is almost empty, $g = g_{min}$, or when oxygen has been (almost) completely replenished.

Behavioural interactions between the diving predator and its prey

The diving predator model culminating in the individual guillemot model, treated the prey items more or less as inert particles. Hence the feeding process was represented in an extremely simplified form. Two strategic model exercises have been performed to simulate the spatial movements, including shoaling/grouping behaviour of (one or more) predator(s) and a group of prey. The first approach takes a short time perspective, which means that focus is on the shoaling behaviour of the prey in the absence of the predator, the escape behaviour of the prey in the presence of the predator and on the behaviour of the predator as it pursues individual items of prey. The model is described in detail in Ollason and Ren (2002 a). The second approach takes an even more general approach and aims to answer the question why prey would form groups at all and in what way the benefits of grouping behaviour depends on the cognitive abilities of the predator. For that reason a game-theoretical model has been developed (van der Meer 2004).

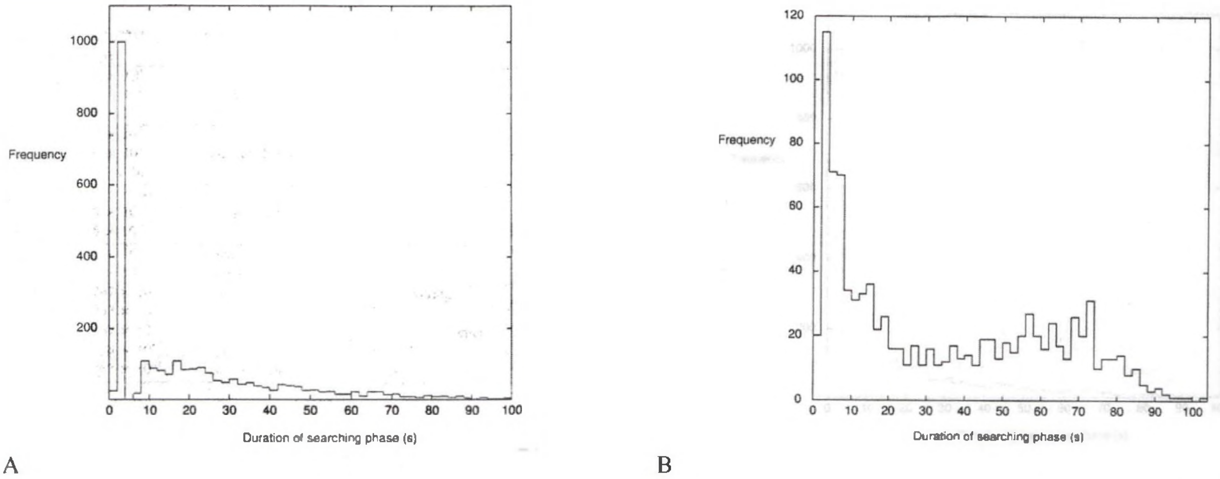


Figure 6.2.1. Frequency distribution of (a) simulated search times using the feeding for particles version (depth 60 m, feeding rate 1 g/s, t_w 20 s and t_h 5 s; see Ollason et al (2003) for explanation of these last two parameters and further details), and (b) observed search times in the field using tagged birds.

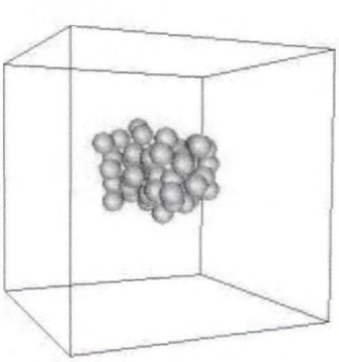


Figure 6.2.2. The conformation of a shoal of prey after 2000 iterations, showing a clear packing of near minimal shoal volume.

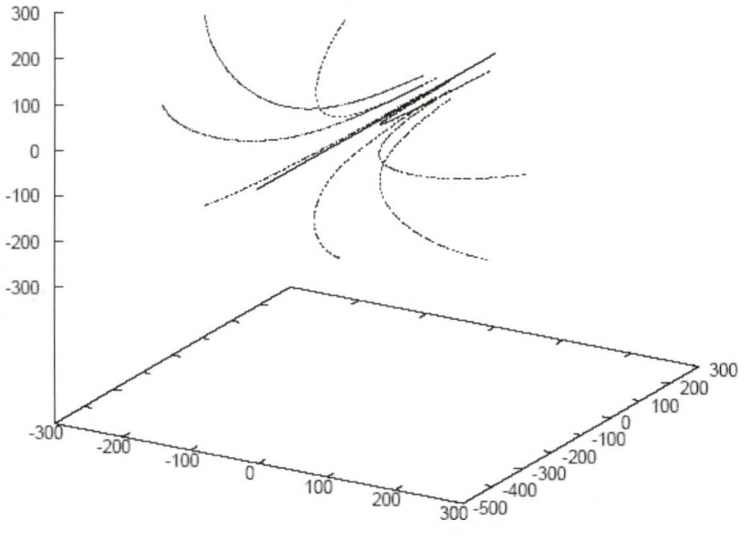


Figure 6.2.3. Example of typical escape trajectories of prey fleeing from a predator. The solid line represents the path of the redator, the dotted lines the paths of the prey.

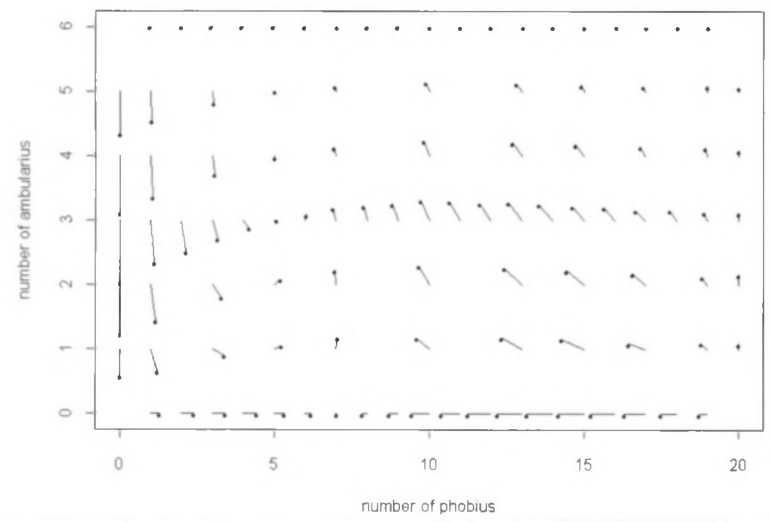


Figure 6.2.4. Number of the solitary prey type, called Phobion, versus the number of the random searching predator, called Ambularius. As the total numbers of prey and predators were fixed (20 prey and 6 predators) the graph shows (average) changes in the state of the model system in response to initial state. Vectors indicate the number of births minus deaths for Phobion (for positive values vectors are pointing to the right, for negative values they point to the left) and for Ambularius (for positive values vectors are pointing upwards) at a large number of fixed prey-predator compositions. The longer the vector, the higher the value. It can be seen that all vectors circle around an equilibrium near 5 Phobion and 3 Ambularius.

The behavioural model by Ollason and Ren (2002 a) first makes an analogy between shoaling behaviour and the cooling and solidifying of a melted solid. This means that in the absence of a predator a shoal will tend to a close packing, where the minimal shoal volume is determined by a minimum individual distance at which a prey individual can tolerate other items of prey (Figure 6.2.2). If a model predator attacks, it will move directly towards one individual and it will eventually capture it, since it is assumed that a predator can travel faster than its prey. When they perceive the predator all prey will move directly away from the current position of the predator. The resulting typical escape trajectories of prey fleeing from a predator are presented in Figure 6.2.3. A start has been made with incorporating this foraging behaviour in the diving predator model, described above.

The game-theoretical model by van der Meer (2004) has two prey types (one group-forming and the other solitary) and two predator types (one random searcher and the other re-visiting a site after an attack). They are allowed to play games in a one-dimensional and strictly uniform environment in order to see how the benefits of some prey strategy will depend on the presence of a specific type of predator, and vice versa. Both prey and predators are able to move in a continuous environment. Prey and predator distributions only depend on simple behavioural rules. Prey animals only know the position of their two nearest neighbours. Predators remember only the site of attack in the previous time step. Response to this knowledge is reflected only in the movements. Predators may decide to return to the attack site in the next time step. Prey may either be attracted or repelled by other prey. Attraction leads to prey grouping, which may result in a lowered food intake rate for the prey. This negative effect, which could lead to higher chance of death by starvation and a reduced fecundity, should be balanced out by a possible lowered risk of predation, as a result of dilution of the predator's effect. However, groups may also attract predators, henceforth increasing killing rates if predators are able to stay in the group. Apparently, the cognitive abilities of both prey and predators are of utmost importance. This modelling study therefore aimed for a fuller appreciation of the subtle interplay of the various processes involved in determining spatial patterns in both prey and predator groups. It appeared that advantages that one prey (or predator) type may have over the other were strongly frequency dependent. An equilibrium solution, where the two prey types as well as the predator types were performing equally well, existed (Fig. 6.2.4). Although this study was of a very strategic nature, it points to the importance of focusing on the cognitive abilities of both prey and predator in order to fully understand the adaptive properties of shoaling in fish as an anti-predation strategy.

6.3 A statistical analysis of the formation of mixed species feeding associations (MSFAs)

J. van der Meer and C.J. Camphuysen

Foraging seabirds often forage in flocks containing individuals of more than one species (so-called multi-species feeding associations, MSFAs; Chapter 5.4). MSFAs are formed and dissolute again after a while and the notion has been put forward that the various bird species that take part in these flocks, play different roles with respect to the formation and dissolution. Species like Guillemots and Razorbills are believed to act as producers, driving up fish towards the surface. The larger gulls and Gannets, on the other hand, are thought to behave as scroungers who ruin the flock shortly after arrival, possibly by hindering the auks in such way that these latter give up their feeding activities. Although it seems unlikely that MSFAs are merely the result of birds independently being attracted to a temporary food bonanza, a proper quantitative analysis of the formation and dissolution of such flocks is still lacking. Part of the reason for this unawareness, is that observation over the full period of formation and dissolution of the flock are almost lacking. Shipboard observers usually pass by when the flock has already been formed and loose sight of the flock before dissolution. Hence, most data are just snapshots of a flock that is still being formed.

In this section we compare such snapshot observational data, with the results of a model, borrowed from probability theory, in which the formation and dissolution of the flock is entirely based on independent and random events. Possible deviations between data and model might further point to more complicated underlying mechanisms of flock formation and dissolution.

The model

The following assumptions form the basis of the model:

- A flock starts with one individual
- A flock grows through the independent arrival of single individuals
- Fixed probabilities pi exists that an arrival (the same holds for the start) is due to a specific species i.
- The sum over all species of the pi's equals 1.
- At each arrival a constant probability q exists that the flock stops growing and falls apart.

Note that, apart from flock composition, the ultimate size of a flock is random variable following a geometric distribution (Ross 1976). As flocks of size one were not recorded as such (MSFAs contained more than one species and therefore 2 individuals as an absolute minimum), we measure flock size as the number of birds in the flock minus one. The probability that the ultimate flock size Y (ignoring flocks of size one and hence counting flock size as the number of birds minus one) equals n is:

$$\Pr(Y = n) = (1-q)^{n-1}\, q \qquad 1.0$$

Due to the memory-less property of the geometric process, the size (again minus one) X of a randomly chosen flock (which might be still in the process of growing) follows the same distribution.

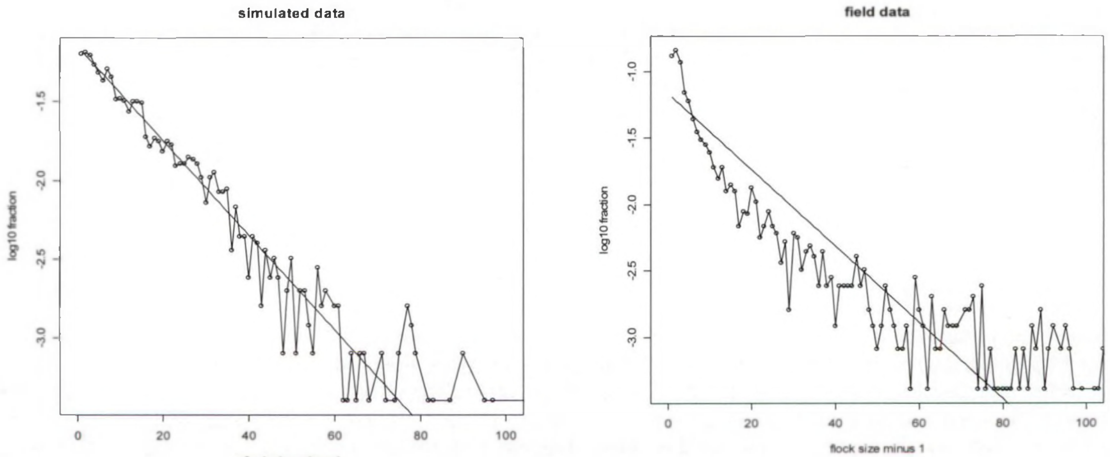


Figure 6.3.1a-b. Frequency distribution of flock size, plotted as log fraction versus flock size. Model predicts a straight line. Simulated dataset (a), field data (b).

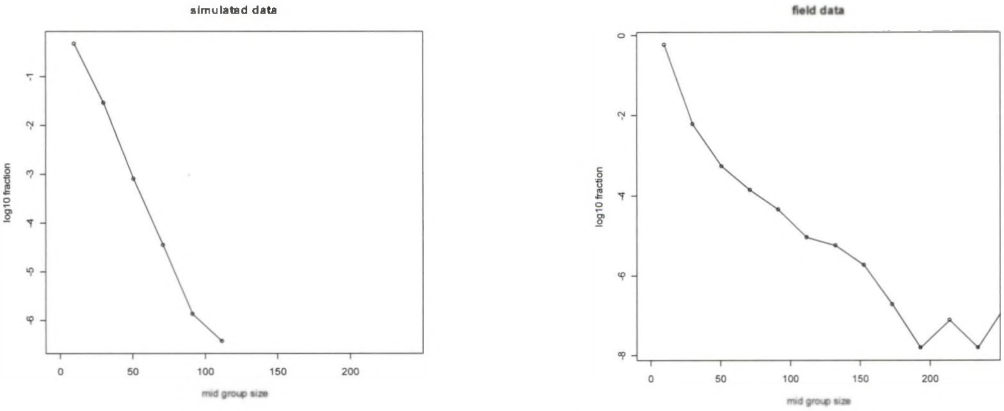


Figure 6.3.1c-d. Frequency distribution of flock size, plotted as log fraction versus flock size. Model predicts a straight line. Simulated dataset (c), field data (d). Flocks are grouped in classes of 20 flock sizes.

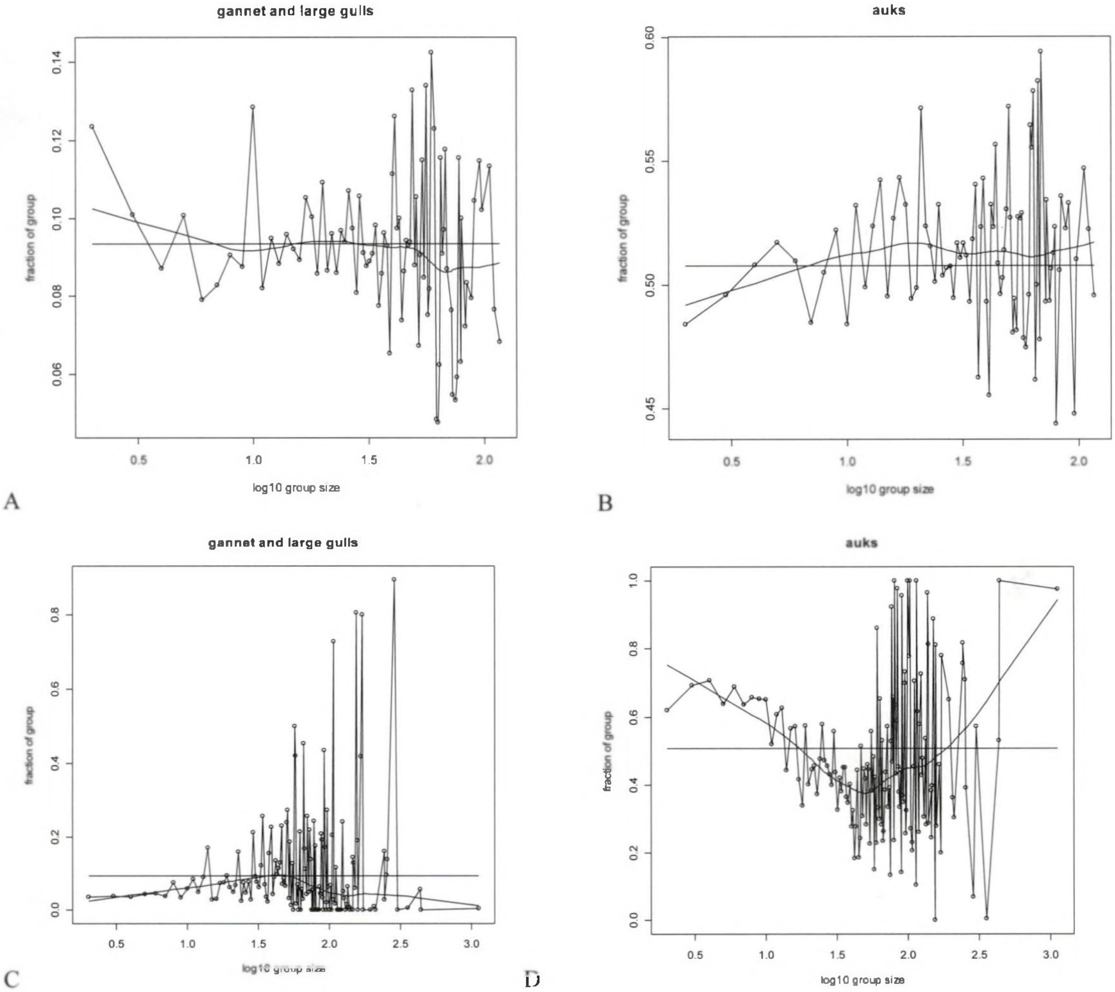


Figure 6.3.2. Average proportion of a species group versus flock size, including smoothed line and model prediction. Simulated data (A and B) and field data (C and D).

Observations on flock size and composition have been gathered during 9 cruises in the northwest North Sea over the years 1991-2003 on board FRV *Tridens* and on board RV *Pelagia* (Chapter 1.4-5; Camphuysen 2005). Ships of opportunity were used, so each observation is basically a snapshot. The six most important species (or species group) were used in the analysis: Gannet, larger Larus gulls (mainly Lesser Black-backed Gull, Herring Gull, and Great Black-backed Gull), Kittiwake, Guillemot, Razorbill, and Atlantic Puffin. Other birds were ignored. Flocks that were associated with marine mammals or human fishing activities were excluded from the analysis (Chapter 5.4). In total 2426 flocks were included.

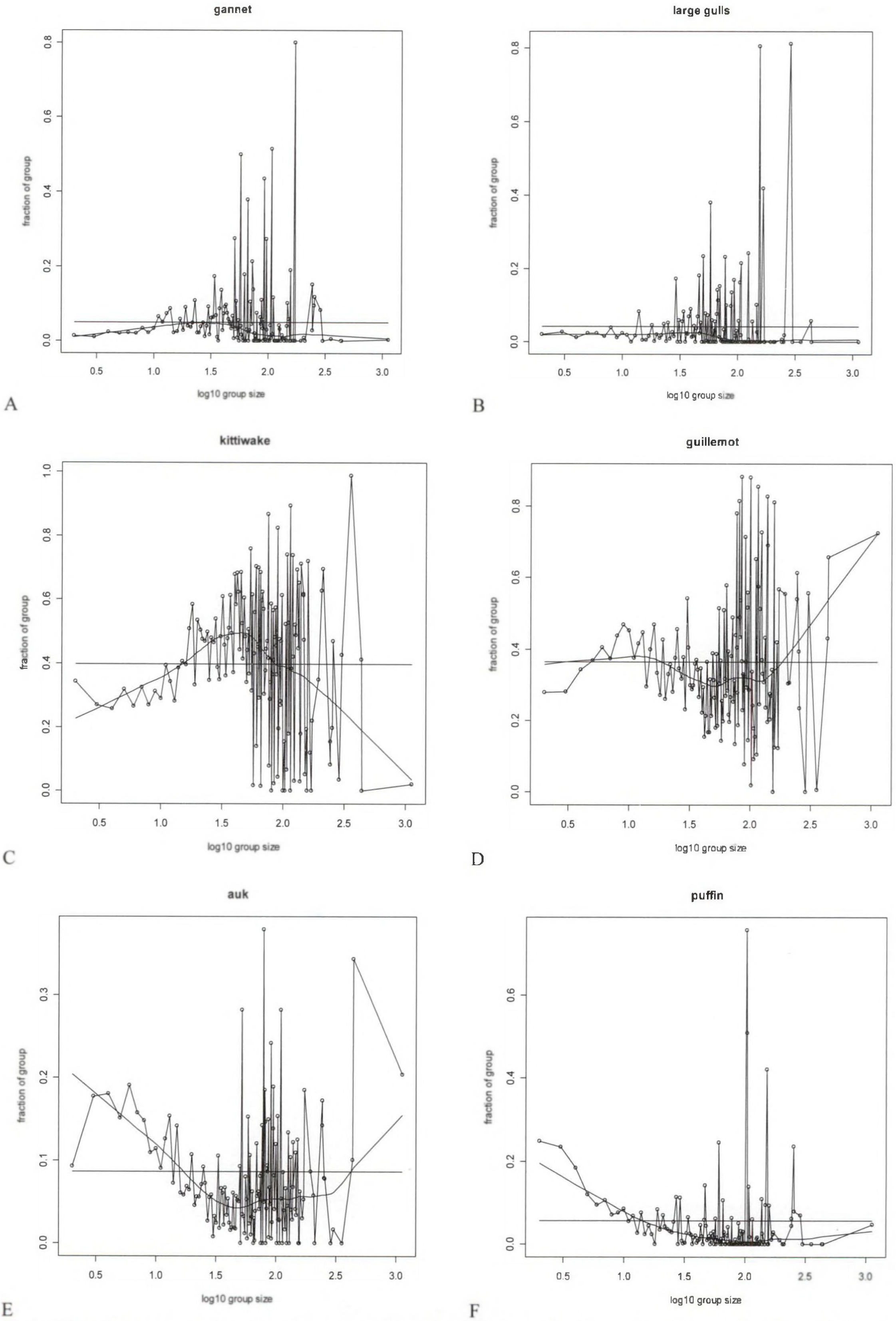


Figure 6.3.3. Average proportion of a species versus flock size, including smoothed line and model prediction. Field data for (A) Gannet, (B) large Larus-gulls, (C) Kittiwake, (D) Guillemot, (E) Razorbill (auk), and (F) Puffin.

Table 6.3.1. Average density in the study area, observed numbers in flocks. Percentage of total between brackets.

Species	Density at sea	%	Individuals obs. in flocks	%
Gannet	0.83	6%	2071	5%
Larger gull	0.19	1%	1783	4%
Kittiwake	2.53	18%	16469	40%
Guillemot	7.94	56%	15012	36%
Razorbill	1.04	7%	3591	9%
Atlantic Puffin	1.57	11%	2365	6%

Results

The average flock size equalled 16.6 ± 0.75 (SE). In total 41291 individual birds were observed in flocks, with Guillemot and Kittiwake as by far the most abundant ones (Table 1). The proportions in the flocks were not accordance with the relative densities at sea (G_{adj}= 15.8, df= 5, $P<$ 0.01; Table 6.3.1, see also Table 5.4.8). It appears that the most aerial species, surface feeding gulls (both Kittiwakes and larger species), had a greater tendency to become recorded as flock participants than expected on the basis of their overall abundance at sea.

The model predicts a negative linear relationship between the log probability of observing a flock of a specific size and size itself:

$$\log[\Pr(Y = n)] = (n-1)\log(1-q) + \log q$$

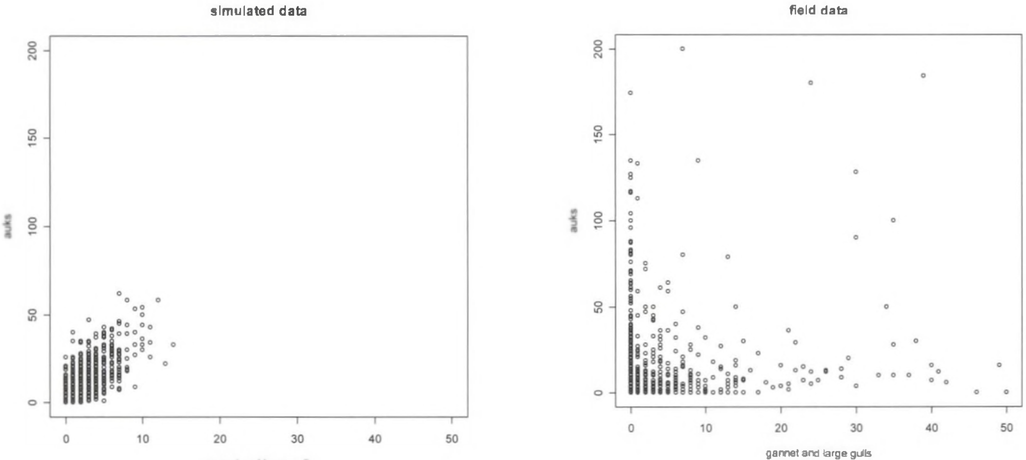


Figure 6.3.4. A-B, see next page

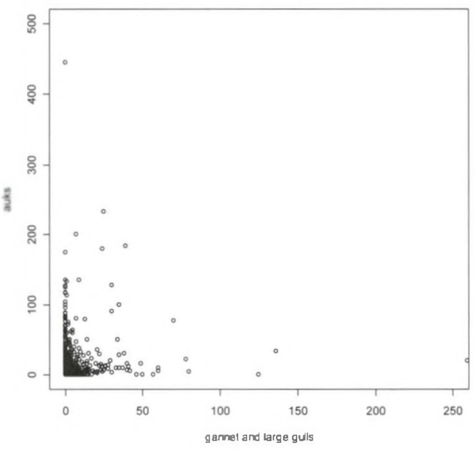


Figure 6.3.4. Number of Gannets and large gulls versus number of auks. Simulated data (a) and field data (b and c, where b gives a fraction of the data range only).

The expected average flock size (minus one) equals one over q. The observed average flock size (minus one) of 15.6 birds would thus have been predicted if q equals 0.064, which means that the model holds if at each arrival of a bird the chance that the flock falls apart would have been about 6.4%. The observed relationship, the expected relationship and one realization of the stochastic process, using the same number of flocks as observed, are presented in Fig. 6.3.1. The frequency distribution of flock size based on the field data clearly deviates from the model expectations. For small flock sizes the decrease in (log) frequency with increasing flock size is much faster than expected, whereas for large flock sizes it is much slower: the relationship between log fraction and flock size is not linear. This implies that small groups dissolute relatively easily (measured in terms of arrivals; Recall that no information is available on dissolution rates in terms of real time).

The relative proportion of the different bird species depended on flock size, which is also in contrast to the model predictions (Fig. 6.3.2). The model predicts that this proportion should be independent of flock size. Small flocks contain relative many auks, especially Puffins and Razorbills. Small flocks contain relatively few Gannets, larger gulls and Kittiwakes. The variability in the proportion of the various bird species was also much larger than predicted (cf. Figures 6.3.3a-b versus 6.3.3c-d). This points to individual birds not behaving independently, but suggests that groups of individuals from the same species act together. A plot of two major bird groups versus each other (Gannets and large gulls versus auks) shows that the field data lack the positive relationship that the model predicts (Fig. 6.3.4). In the field, there seem to be mostly Gannet and gulls groups or auk groups. This could point to the fact auks are attracted by auks and gulls by gulls.

The analysis of the frequency distribution and species composition of almost 2500 observed 'natural' MSFAs in the northwest North Sea showed that these associations could not be entirely the result of a simple stochastic process, in which both in the formation and in the dissolution of the flocks all individual birds behave similarly irrespective of species

6.4 Foraging energetics of North Sea birds confronted with fluctuating prey availability

M.R. Enstipp, F. Daunt, S. Wanless, E.M. Humphreys, K.C. Hamer, S. Benvenuti and D. Grémillet

Sandeel populations show strong spatial and temporal variability. A marked decline in sandeels around Shetland in the mid 1980s had adverse effects on many seabird species, like several surface feeders, while others were able to compensate for the reduction in sandeel availability to some extent by increasing their foraging effort (Monaghan 1992; Monaghan *et al.* 1996). Furness & Tasker (2000) found that small seabirds with high energetic costs during foraging and a limited ability to switch diet (e.g. many surface feeders) were most sensitive to a reduction in sandeel abundance. Larger species with less costly foraging modes and a greater ability to switch diet (e.g. many pursuit-diving species) were less sensitive. Furness & Tasker were uncertain about the relative importance of some factors, such as foraging energetics. In this chapter, the hypothesis is tested that the impacts of reduced sandeel availability on seabirds depend on energetic and behavioural constraints during foraging. We calculated the daily food intake (DFI) of four North Sea seabird species from knowledge of time-activity budgets, energy expenditures and diet (Chapter 1.6.3), allowing the estimation of required feeding rates (catch per unit effort, CPUE) under a number of scenarios that investigated the capacity of the four species to compensate for a reduction in sandeel availability by altering their foraging behaviour.

Table 6.4.1. Daily energy expenditure (DEE), Field metabolic rate (FMR expressed as xBMR), daily food intake (DFI) and feeding rate (catch per unit effort, CPUE) for 4 North Sea seabirds ('baseline situation'). CPUE values are based on the time spent underwater for Shags and Guillemots, the time spent in forage-flight for Kittiwakes and the total time spent at sea for Gannets. To allow comparison across species a CPUE value based on the active time spent at sea (excluding periods of rest at sea) is included in brackets.

		Kittiwake	Shag	Gannet	Guillemot
Adult					
	DEE (kJ d^{-1})	786.74	2249.25	4856.01	1641.01
	FMR (xBMR)	2.9	3.1	3.9	2.8
	DFI (g fish d^{-1})	211	514	1114	415
Chick					
	DEE (kJ d^{-1})	525.71	1203.98	1593.30	221.71
	DFI (g fish d^{-1})	131	275	366	56
	Chicks fledged pair^{-1}	0.71	1.51	0.67	0.69
	DFI (g fish d^{-1}, portion/adult	47	208	122	19
Total					
	DFI (g fish d^{-1})	258	722	1237	434
	CPUE g fish min^{-1}	1.35 (0.50)	10.10 (3.84)	1.63 (3.89)	2.45 (1.18)

Time-activity/energy budgets

The daily time-activity budget indicated that all species except Shags spent about 50% of their time at the colony and 50% at sea. Shags on the other hand allocated only about 15% of their time towards food acquisition, and stayed at the colony for the remainder of the time. Kittiwakes, Gannets and Guillemots spent a considerable amount of their time at sea resting (15-30%), but resting at sea was negligible in Shags. Shags and Guillemots spent a much smaller proportion of their time flying than Kittiwakes and Gannets, reflecting the use of prey patches closer to the colony. Daily energy expenditures (DEE) calculated for the four species considered (Table 6.4.1) compared well with reported energy expenditures measured in the field using doubly-labelled water (DLW), where available. The time-energy budget emphasised the relative importance of energetically expensive activities, especially flight, on the overall daily energy expenditure. While birds spent only between 13-34% of their day active at sea, this period accounted for 39-60% of their daily energy expenditure. Gannets worked the hardest with a field metabolic rate (FMR) of 3.9 x BMR (basal metabolic rate), while all other species worked at a level of around 3 x BMR (Table 2). CPUE values (based on active time spent at sea; see Table 6.4.1) for Shags and Gannets were high compared to the other species, with Shags foraging most efficiently (Table 6.4.2; foraging efficiency is defined as the ratio of metabolizable energy gained during foraging to energy used during foraging).

Sensitivity analysis

A sensitivity analysis was conducted to test the robustness of the algorithm (Grémillet *et al.* 2003). An assessment of the sensitivity of the calculation of prey requirements to each variable used in the calculation (Table 6.4.3) indicated that the time spent in each activity and the caloric density of the prey ingested had the strongest influence on the total energy expenditure. The calculations for Shags and Guillemots were particularly sensitive to variation of the amount of time spent flying per day. In contrast, Kittiwakes were most sensitive to time spent resting at the colony, whereas Gannets were equally sensitive to time spent flying, resting at sea and resting at the colony. These results emphasise the importance of measuring these variables as precisely and accurately as possible.

Table 6.4.2. Foraging efficiency (ratio of metabolizable energy gained during foraging to energy used during foraging) and foraging range of 4 North Sea seabirds.

	Energy acquired at sea day^{-1} to meet adult and chick requirements (kJ d^{-1})	Energy expenditure at sea day^{-1}		Foraging efficiency		Foraging range (km)	
		Total (kJ d^{-1})	Active* (kJ day^{-1})	At sea	Active*	Baseline situation	Potential increase
Kittiwake	972.07	534.44	473.59	1.82	2.05	49.6	+ 34.0
Shag	3158.25	932.76	879.27	3.39	3.59	10.4	+ 11.1
Gannet	5389.76	3484.77	2500.13	1.55	2.16	282.4	+ 26.8
Guillemot	1715.00	960.93	784.20	1.78	2.19	21.8	+ 41.5

*Excludes periods of rest at sea

Table 6.4.3. Sensitivity analysis for the time-energy budget of 4 North Sea seabirds. Minimum and maximum input values for each parameter were used (see Table 1) to compute the individual variation in mean DFI (%). Minimum and maximum values for all parameters[1] combined were computed for the most and least demanding situation, which indicates the maximum range of potential DFI values for the birds.

	Kittiwake		Shag		Gannet		Guillemot	
	Variation of mean DFI (%)	Range used	Variation of mean DFI (%)	Range used	Variation of mean DFI (%)	Range used	Variation of mean DFI (%)	Range used
Body mass (g)	± 8.1	SD	± 1.7	SD	± 5.2	SD	± 8.3	SD
Time resting at colony (min day^{-1})	± 10.8	SD	± 2.7	SD	± 9.9	SD	± 1.0	SD
Time resting at sea (min day^{-1})	± 2.3	SD	± 0.3	SD	± 9.4	SD	± 6.6	SD
Time spent flying (min day^{-1})	± 2.7	SD	± 5.3	SD	± 10.1	SD	± 18.5	SD
Time spent foraging (min day^{-1})	± 1.5	SD	± 2.0	SD	± 0.3	SD	± 5.9	SD
Assimilation efficiency (%)	± 1.5	SD	± 1.4	SD	± 5.9	SD	± 2.2	SD
Assimilation efficiency (%) chick	± 0.4	SD						
Calorific value of fish (kJ g^{-1} wet)	± 10.5	10%	± 9.6	10%	± 10.8	10%	± 10.4	10%
Water temperature at surface (°C)	± 0.4	SD	± 0.1	SD	± 0.5	SD	± 0.6	SD
Water temperature at bottom(°C)			± 0.1	SD			± 0.1	SD
Energy costs rest at colony (W kg^{-1})	± 1.9	SD	± 2.6	SD	± 4.2	SD	± 3.8	10%
Energy costs, rest at sea (W kg^{-1})	± 1.2	SD	± 0.2	SD	± 3.3	SD	± 1.0	10%
Energy costs, flying (W kg^{-1})	± 3.1	10%	± 1.9	10%	± 4.8	10%	± 2.4	10%
Energy costs, foraging (W kg^{-1})	± 1.9	10%	± 1.2	SD	± 0.1	10%	± 2.3	10%
Chick DEE (kJ day^{-1})	± 1.9	10%	± 2.9	10%	± 1.0	10%	± 0.5	10%
All parameters[1]								
Variation of mean DFI (%)	± 36.0		± 32.2		± 49.7		± 54.8	
Absolute range of DFI (g fish day^{-1})	179-365		527-992		750-1979		245-721	

Potential responses to decreased prey availability

Seabirds foraging in the North Sea are constrained by a delicate balance of the following three components: (a) the time they can allocate towards food acquisition; (b) the energy demands associated with their activities and (c) the food they are able to acquire. Confronted with a decline in availability of a particular prey species (e.g. sandeel), seabirds have a number of potential options to maintain their DFI at a sustainable level. For some it might be possible to switch to other prey species (e.g. clupeids, gadids) or to make greater use of fish discarded as bycatch in certain fisheries. Alternatively, they might be able to increase their foraging effort in a number of ways. In the following scenarios we explored the capacity of the four species to increase their foraging effort within the constraints imposed upon them by time, energy, and food. In all scenarios the increased amount of time allocated towards prey acquisition was balanced by reducing the time spent resting at sea and at the colony. While decreasing resting time at sea to zero we decreased resting time at the colony only to a minimum of 50% of the daily total, assuming that chicks were not left unattended. We also took into consideration that all species were inactive for some part of the night, during which no foraging activity occurred (Shags: 8 h, Wanless *et al.* 1999; Guillemots: 1h, Daunt unpubl.; Kittiwakes: 3h, Daunt *et al.* 2002; Gannets: 5h, Humphreys unpubl.). Assuming that partners shared the available time equally, the total time that could potentially be allocated towards foraging activity by an adult per day ranged from 8 h for Shags to 11.5 h for Guillemots.

Energy expenditure of endotherms sustained over a longer time period is limited by physiological constraints (e.g. digestive capacities; Weiner 1992). Hence, if energy expenditure of animals in the wild approaches such a ceiling, fitness costs may be incurred (e.g. reduced survival). Here we assumed the metabolic ceiling of 4 x BMR as suggested by Drent and Daan (1980) for birds raising chicks. In scenario 1 birds increased their foraging time spent within a prey patch. In scenario 2 birds made use of a prey patch at a further distance from the colony, increasing the amount of time spent flying. Birds flew to a further prey patch and foraged for a longer time within the prey patch in scenario 3 (both variables raised equally). Finally, we investigated the effect that feeding on a diet of lower caloric density (4.0 kJ g^{-1} wet mass) had in combination with the above scenarios.

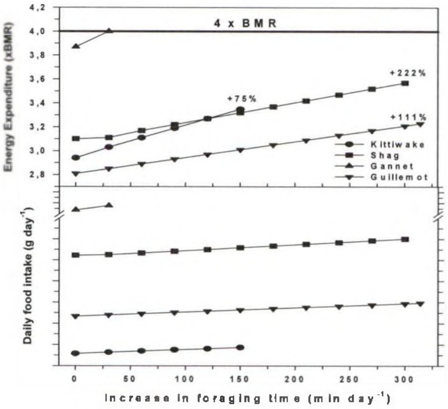


Fig. 6.4.1. Scenario 1 (increasing foraging time within a prey patch). Zero indicates the 'baseline situation' (i.e. before increasing foraging time).

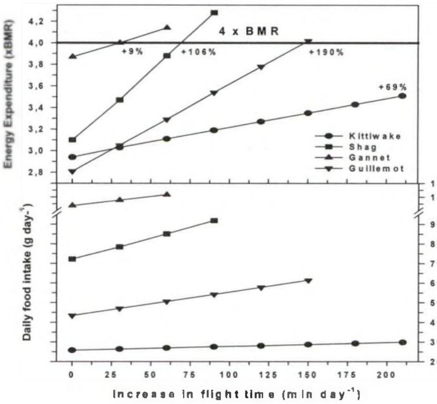


Fig. 6.4.2. Scenario 2 (foraging at a more distant prey patch). Zero indicates the 'baseline situation' (i.e. before increasing flight time).

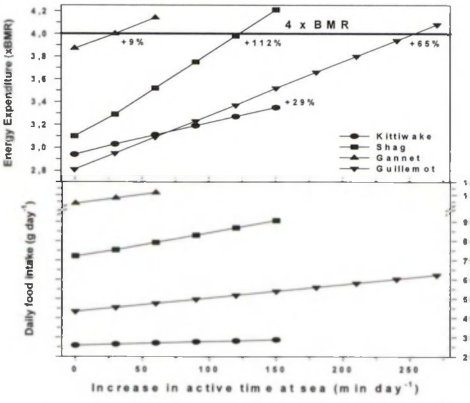


Fig. 6.4.3. Scenario 3 (foraging at a more distant prey patch and for a longer time within that prey patch). Zero indicates the 'baseline situation' (i.e. before increasing flight and foraging time).

The upper portion of Figs 6.4.1-3 plot the daily energy expenditure for the four species (as multiples of BMR) against the increase in foraging effort considered in scenarios 1 to 3. The solid upper line indicates the presumed metabolic ceiling of 4 x BMR. Increases in foraging effort that lead to an increase in energy expenditure beyond this ceiling are assumed to be unsustainable, indicating a physiological constraint. The *x*-axis indicates the scope that the bird may have to reallocate time towards an increase in foraging effort, with zero being the 'baseline situation' before increasing foraging effort. If the plot for an individual bird stops before reaching the physiological ceiling it indicates a time constraint because birds have no time left to increase their foraging effort. The percentages given indicate the relative increase in foraging effort that is possible before a constraint is reached. The lower portion of Figs 6.4.1-3 indicate changes in the required DFI (g day^{-1}) which accompany the increase in foraging effort considered in scenarios 1 to 3.

Time and energy

If seabirds are to increase their foraging effort in response to a reduction in sandeel availability, the first constraint encountered is likely to be the availability of spare time. Time-activity budget analysis illustrated that, with the exception of the Shag, no species could reduce their resting time at the colony much further, unless they left their chicks unattended. Doing so could potentially reduce their breeding success drastically, especially when the chicks are small. While non-attendance of chicks has been recorded in all four species (Harris & Wanless 1997; Daunt 2000; Lewis *et al.* 2004), we assumed that birds normally avoided this. All species except the Shag, however, spent a considerable amount of time resting at sea. In a first step then, birds are predicted to reduce their resting time at sea to a minimum before starting to reduce their resting time at the colony. Based on the time-activity budgets birds could potentially reallocate between 10% (Kittiwake) and 22% (Guillemot) of their daily time towards an increase in foraging effort.

Increasing foraging effort in these scenarios led to an increase in the amount of required daily food (lower portion of Fig 1 to 3). This was especially drastic in scenario 2, where birds made use of a prey patch at a greater distance from the colony, requiring longer flight times. The exact relationship depended on the strategy being pursued (commuting to a further prey patch, foraging for longer in a particular prey patch or a combination of both) and on the specific costs of the associated activities (e.g. flight vs. diving). It also depended on the benefits accruing as a result of the increased effort. Figs 6.4.1-6.4.3 clearly underline the limited possibilities for Gannets to increase their foraging effort because of energetic constraints. Gannets spent about 30% of their daily time resting at sea, of which 17% could potentially be allocated towards increasing their foraging effort (taking into account the inactive period at night). Since Gannets already worked close to the presumed maximal energetic capacity, however, they could only do so in very small increments before reaching the assumed metabolic ceiling in any of the three scenarios. Birt-Friesen *et al.* (1989) also reported high metabolic rates for northern Gannets during chick rearing and attributed these to the high costs of thermoregulation and flapping flight. The Gannets in our study were already working at a much higher level than the other birds considered here, hence their physiological limitation to increase foraging effort was not surprising. One possible strategy for Gannets, which is not explored in this analysis, since it assumes a balanced energy budget, could be that they incur an energy debt over a short period that is paid off at a later time. In fact, Nelson (1978) suggested that body condition declines in Gannets over the course of the breeding season. A possible explanation for the high FMR values we calculated for the Gannets could be the large size of the colony from which our data were collected. Foraging trip duration and foraging range of Gannets nesting at the Bass Rock colony are high when compared to a colony of smaller size (see Hamer *et al.*, this volume), resulting in higher energy expenditures per foraging trip. Hence, Gannets breeding at a smaller colony might not experience the same energetic constraint as the Gannets in our study. The other three species had much more scope (in terms of time and energy) to increase their foraging effort. While in all three scenarios Kittiwakes were ultimately limited by the amount of time they could reallocate towards an increase in foraging effort (Fig. 1 to 3), Shags and Guillemots were mostly constrained by the energetic demand that accompanied such an increase. This difference can be attributed to the relatively high costs of flapping flight in the latter two species. However, the overall capacity to increase foraging effort in Shags and Guillemots was quite considerable. Shags could potentially increase their foraging time by about 222%, their flight time by about 106% and their total active time at sea by about 112%. Comparable values for Guillemots were 111%, 190% and 65% respectively. Increased flight times in scenario 2 potentially doubled the foraging range of Shags while it tripled that of Guillemots (Table 3). A substantial increase in foraging range was prevented by time and energetic constraints in the case of Kittiwakes (69%) and Gannets (9%) respectively.

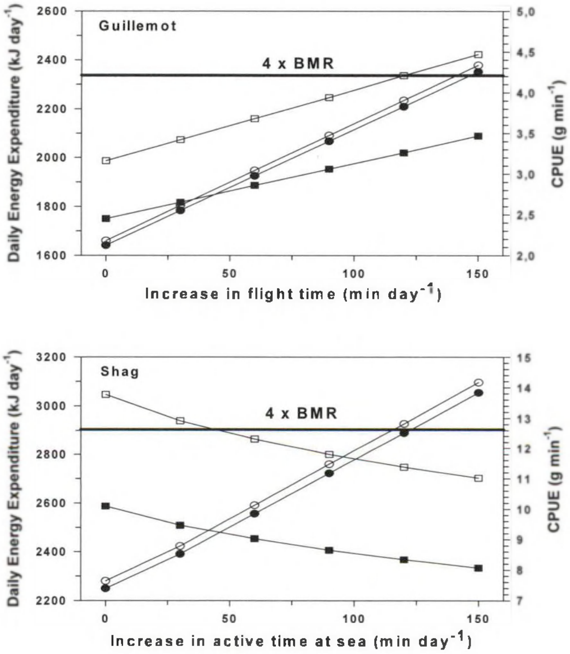


Fig. 6.4.4. (a) Scenario 2 (foraging at a more distant prey patch), and combined with feeding on prey of reduced caloric density for the Guillemot. (b) Scenario 3 (foraging at a more distant prey patch and for a longer time within that prey patch), and combined with feeding on prey of reduced caloric density for the Shag. Circles indicate DEE, while squares indicate CPUE. Filled symbols indicate scenario 2 and 3, while open symbols indicate combination of the respective scenario with feeding on less profitable prey. CPUE values are based on the time spent underwater.

Available food

Birds are constrained by the amount of food available and by the rates at which they can acquire food. In many cases we know little about sandeel abundance in the North Sea but we know even less about the prey capture capacities of seabirds and the fish densities they require to forage effectively. Under conditions of reduced prey availability birds presumably have difficulties finding sufficient food to meet their energy requirements and those of their chicks. Any additional increase in foraging effort, as suggested by our scenarios, will lead to an even higher requirement for food. Foraging effort has to be even greater when birds are forced to feed on prey of lower energy density. Combining the above scenarios with a diet switch to prey of lower calorific value (4.0 kJ g^{-1} wet mass; Fig. 6.4.4) did not change the basic outcome of our calculations in terms of time and energy constraints. However, it drastically increased the food requirement and the associated feeding rates for all species. Fig 6.4.4a illustrates this for scenario 2 in the Guillemot (foraging at a distant prey patch) and Fig 6.4.4b shows scenario 3 in the Shag (foraging at a distant prey patch for a longer period).

How steep the increase in foraging effort will need to be depends on how energetically expensive the associated activities are. Making use of a prey patch at a greater distance from the colony, requiring longer flight times, greatly increased daily food requirements for most species considered here (Fig. 6.4.2). There will be a limit, imposed by the food availability, at which a further increase in foraging effort becomes unsustainable. Feeding rates reported in the literature (6-12g fish min^{-1} underwater for Shags, Wanless *et al.* 1998; 0.5-1.3g fish min^{-1} at sea for Gannets, Garthe *et al.* 1999) are typically within the range or slightly lower than our estimates for the 'baseline situation' (before increasing foraging effort). The same holds true for DFI values reported for Kittiwakes and Guillemots. This could indicate that birds might not be able to achieve feeding rates that would be required in the above scenarios when foraging effort is drastically increased.

Further potential responses

An alternative strategy to increasing foraging effort might be to switch to exploiting other prey types. Unlike the situation in Shetland where sandeels are the only small, shoaling forage fish, other prey species are present in the Firth of Forth area that are potentially available to seabirds (Daan *et al.* 1990). Dietary information suggests that Kittiwakes and Shags may be less able to switch to alternative prey compared to Guillemots and Gannets. In the case of Kittiwakes this might be exacerbated by its surface feeding habit that limits its foraging abilities to prey items at, or close to, the surface (Lewis *et al.* 2001).

In addition to switching to other live prey species, seabirds can also potentially exploit fishery discards. Most fisheries in the North Sea produce bycatch that is discarded and can be consumed by seabirds. While most pursuit-diving species tend to ignore these discards, many surface feeders readily feed on them. Of the four species considered here only the Kittiwake and Gannet are observed in substantial numbers at fishing boats (Garthe *et al.* 1996). However, with the volume of fishery discards in the North Sea potentially declining (see Votier *et al.* 2004), this might not be a sustainable option.

This chapter has highlighted the interactions between physiological and behavioural constraints that condition the different responses of seabirds in the Firth of Forth area to reduced sandeel availability. While Shags and Guillemots may have sufficient time and energy to allow them to increase their foraging effort considerably, Kittiwakes and Gannets appear more constrained by time and energy respectively. Our analysis was relatively restricted in time and space. Clearly, including activity data from a larger geographical area and over a longer time period to establish the time-energy budgets ('baseline situation') would be desirable and would minimise any bias that years of high or low prey availability might introduce. As previously recognised by Furness & Tasker (2000), consideration of energetic constraints is essential to fully evaluate the capacity of species to cope with food, particularly sandeel, shortages. Gannets scored low for the criteria used by Furness & Tasker (2000) to establish vulnerability and sensitivity indices for seabirds in the North Sea and the authors concluded that this species was generally well buffered against change. In contrast, our study suggests that during chick-rearing Gannets are working at the highest metabolic level of all species considered and hence, have the least physiological capacity to increase foraging effort. This indicates that Gannets could potentially be very sensitive to a reduction in sandeel availability. To compensate for their energetically costly life, however, Gannets might make use of a highly profitable foraging niche.

6.5 Prey harvesting and predator conservation

Jaap van der Meer

Statistical approach

Traditionally, the term sustainable use of a population was interpreted as harvesting in such a way that future catches of the target population are guaranteed. Nowadays, however, ecosystem managers are not just interested in ensuring long-term harvesting of a target population, but they also may want to consider the impact on other components of the ecosystem (Murawski 2000). In particular, one might think of the impact that harvesting of one species may have on species directly linked to the harvested species, i.e. on its prey, its competitors or its predators. A special case is where those related species have conservation value. Examples are: fish and seabirds (Furness 2002), krill and seabirds and marine mammals (Constable *et al.* 2000; Boyd & Murray 2001), shellfish and waders (Goss-Custard *et al.* 2002), crops and geese or crops and songbirds (Pettifor *et al.* 2000; Stephens *et al.* 2003). Bio-economic models predicting optimal harvesting strategies have been developed, where optimality is not just defined in economic gain of the harvested species but also in terms of the conservation value of the non-harvested but affected species, usually the predator of the harvested species (Ragozin & Brown 1985; Stroebele & Wacker 1995). Most of these models, however, are based on the Lotka-Volterra predator-prey model, and are thus of a merely strategic character and do not have much practical relevance.

Alternatively, more tactical approaches have been used to advice on allowable catches of prey populations, while preserving the predator species. Three approaches are distinguished here: a statistical approach, an individual-based static approach and an individual-based dynamic approach. The various approaches will be discussed in general and suggestions will be made what way the results obtained within the *IMPRESS* project may contribute to the application of these approaches in the sandeel-seabird case. The statistical approach links empirical data (usually over years) on prey stocks with data on predator performance, e.g. breeding success or the rate of population change (Camphuysen *et al.* 2002; Furness 2002).

Box 6.5.1

Suppose that the energy requirements for an individual predator equal W' (watt), the length of the foraging period is t (seconds), the number of predators N_p, the energy content of an individual prey e (joule), then the **daily ration method** says that the number of prey items N_n' that should be left for the predator equals

$$N'_n = \frac{W'N_p t}{e}.$$

The **functional response method** (where a is the searching rate in m^2/s, and h is the handling time in s) adds that the prey density at the end of the period D_n' should at least enable a predator to acquire its energetic demands:

$$W' = \frac{eaD'_n}{1 + ahD'_n}$$

Hence the prey density at the end of the foraging period should not be lower than

$$D'_n = \frac{W'}{a(e - hW')}$$

And the number of prey items N_n' that should be left for the predator now equals

$$N'_n = \frac{W'N_p t}{e} + \frac{AW'}{a(e - hW')},$$

where A is the surface area.

The **generalized functional response method** takes into account the effects of interference. It considers the reduction in intake rate due to the presence of competitors. Various interference models have been proposed in the literature. Van der Meer and Ens reviewed a few of the simplest models. In case of, for example, the Beddington model, where q is the interference area (m^2) and D_p is the predator density, it is assumed that

$$W' = \frac{eaD'_n}{1 + ahD'_n + qD_p}.$$

The number of prey items N_n' that should be left for the predator now equals

$$N'_n = \frac{W'N_p t}{e} + \frac{AW'}{a(e - hW')}\left(1 + q\frac{N_p}{A}\right).$$

Individual-based static approach: minimum prey stock required to maintain the predator population at a fixed level

The individual-based approach is based on the food requirements of an individual predator. The simplest approach (called the daily ration method) considers the (seasonal) period after harvesting has ended until prey stock renewal or until the (seasonal) disappearance of the predators from the area. For this period the total food requirements of the (fixed) predator population are estimated by multiplying the required food intake rate per individual predator by the number of predators by the length of the period. Energetic costs of travelling (for central place foragers), searching (e.g. diving) and handling should be taken into account. Examples where this approach has been applied are the oystercatcher and the eider in the Dutch Wadden Sea.

This simple approach neglects the fact that predators may be time-constrained, as they have to search for their food. If prey densities are low and the total area is large the amount of food may be large enough, but the predators simply do not have the time to exploit it. Hence, a slightly more sophisticated approach is to combine the functional response (e.g. type II Holling curve) and the required food intake rate to obtain a second requirement, i.e. a threshold prey density which should not be exceeded at the end of the period.

A further complication is the presence of predator interference. In that case the so-called generalized functional response should replace the functional response. The most famous example here concerns the oystercatchers of the Exe estuary (Kacelnik *et al.* 1992; Goss-Custard *et al.* 2002). Recently, Goss-Custard and co-workers claimed that due to the interference effects the amout of food that should be left for the predator after harvesting has ended can be up to 8 times higher than calculated on the basis of the daily ration method. Prey is usually patchily distributed, and the heterogeneous distribution should be explicitly taken into account in the calculations. Boxes 6.5.1 and 6.5.2 present an example of the application of this static approach.

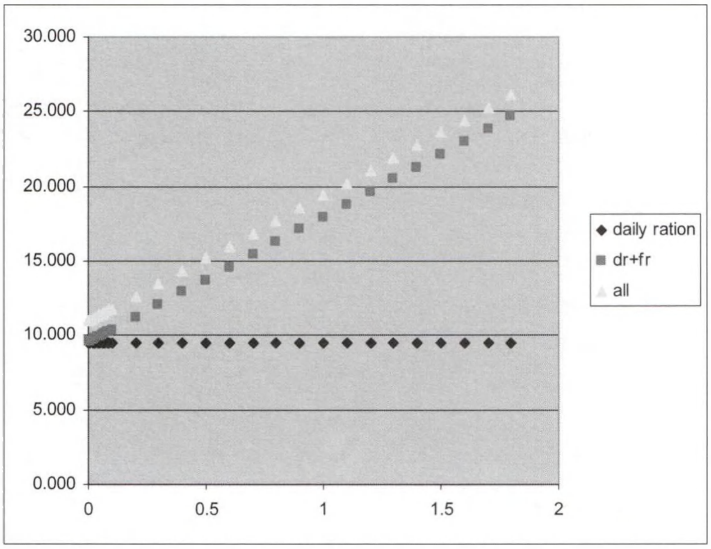
A final complication is the availability of prey. Of course, it is of crucial importance whether this availability is only temporarily (it will then only affect the area of discovery) or whether it is permanent. It should further be noted that the question whether or not the remaining prey (after the birds have left) are able to replenish the stock is not considered here.

Box 6.5.2

We have seen that the number of prey items N_n' that should be left for the predator should not be lower than

$$N'_n = \frac{W'N_p t}{e} + \frac{AW'}{a(e - hW')}\left(1 + q\frac{N_p}{A}\right)$$

It very much depends on the prey and predator densities what the relative importance is of the two terms in the equation. The same holds for the importance of the interference effect (indicated between brackets). In the Dutch Wadden Sea, the Dutch government used the daily ration method and reserved a biomass of shellfish which would satisfy 70% of the energy demands of the oystercatcher population. On the basis of somewhat complicated calculations (which, for example, accounted for the effect of ambient temperature on energy demands) the total food demands for the period 1 September until 31 May (273 days), were estimated as 9.5 10^9 g wet mass (WM). This figure can be approximated by assuming that each of 170 thousand birds eats 207 g wet mass per day. This intake rate is equivalent (assuming an absorption efficiency of 0.8, an ash-free dry mass / wet mass ratio of 0.21 and an energy density of 22 kJ g^{-1} AFDM) to an energy demand of 8.8 W. Goss-Custard *et al.* (2004)reported a food demand between 7.72 and 9.62 kg AFDM per individual over a 196-day period, which is in good agreement with our approximation of 8.47 kg. Using values of 7 cm^2 s^{-1} for the searching rate, 50 s for the handling time, 1000 m^2 for the interference area and 1.25 g for the WM per individual prey, it can be calculated with the equation given above that for the entire Dutch Wadden Sea (which intertidal surface area equals 1.8 10^9 m^2), the amount of shellfish that should be reserved for the oystercatcher equals 9.5 10^9 g WM (according to the daily ration method). The functional response approach states that when the prey are randomly distributed over the entire area, additionally 15.1 10^9 g WM should be reserved. If interference is taken into account this latter figure changes to 16.6 10^9 g WM (an additional 1.5 10^9 g WM or 9% only). Hence, the effect of interference is, contrary to the claims by Goss-Custard *et al.* rather small. If the food is more clustered, the 'functional response' amount decreases linearly, whereas the 'interference' amount is constant. The latter characteristic is related to the linearity in the (Beddington) aggregative response.



Required food reservation (in 10^9 g WM) according to (1) the daily ration method, (2) the functional response method and (3) the generalized functional response method versus the area (in 10^9 m^2) over which the food is randomly distributed. Hence, the more the food is clustered, the less difference between method (1) and (2). The difference between (2) and (3) is constant.

Dynamic approach: predator-prey models with prey harvesting

Although the days of Lotka and Volterra are since long gone, most models of predator-prey population dynamics are still of a highly idealized form. A central element in all predator-prey models is the predation rate, which usually is of the form $f(D) \times P$, where $f(D)$ is the functional response, and P is the predator density. This functional response gives the predation rate per predator as a function of the prey density D. In the original Lotka-Volterra model the per predator predation rate was simply a linear function of prey density (Holling type I). In more modern approaches this function levels off, as the predation process also involves handling prey (Holling type II). Usually, the predation rate is instantaneously coupled (through a fixed conversion factor) to the rate of increase of the predator population. Most of the assumptions underlying these models are, however, too unrealistic to be of any practical value. For example,

- true predators do not usually depend on a single prey species and a prey species is usually predated by more than one predator species;
- a captured prey is not instantaneously transformed into predator offspring, and such offspring is not immediately capable of producing new offspring themselves;
- prey and predator populations are not randomly distributed in space and encounter rates cannot simply be based on the rules of mass-action (i.e. proportional to the product PD);
- predators may interfere with each other, or, alternatively, they may facilitate each other;
- the abiotic environment is not constant, and abiotic variation may affect predation rates.

Box 6.5.3

Suppose that each bird has to spend a fraction t_0 of the total day at the colony. The rest of the day is divided in a fraction y flying, and the remaining fraction $1-t_0-y$ actively foraging (diving, recovering etc.). Suppose further that the energetic expenditure rates of these four activities (all expressed relative to BMR) are c_0, c_1, and c_2, respectively. Provisioning of the chicks requires an extra cost of c_3. The metabolic ceiling equals c'.

This metabolic ceiling sets the following constraint on the fraction of the day in flight:

$$t_0 c_0 + y c_1 + (1 - t_0 - y) c_2 < c',$$

or (when $c_1 \neq c_2$)

$$y < \frac{c' - t_0 c_0 - (1 - t_0) c_2}{c_1 - c_2}.$$

Note that when $c_1 = c_2$ the metabolic ceiling is reached at $t_0 = \dfrac{c' - c_1}{c_0 - c_1}$.

Suppose further that the rewards while foraging are equal to r (also expressed relative to BMR). The requirement of a positive net energy balance, which looks like

$$(1 - t_0 - y)(r - c_2) - t_0 c_0 - y c_1 - c_3 > 0$$

gives the required feeding rate as a function of flight time (and, if the flight speed is known the distance to the colony):

$$r > c_2 + \frac{t_0 c_0 + y c_1 + c_3}{(1 - t_0 - y)}.$$

This inequality should be evaluated for the range $0 < y < \dfrac{c' - t_0 c_0 - (1 - t_0) c_2}{c_1 - c_2}$. Additionally $0 < y < (1 - t_0)$, where t_0 might be determined by the metabolic ceiling (when $c_1 = c_2$).

At the metabolic ceiling of

$$y = \frac{c' - t_0 c_0 - (1 - t_0) c_2}{c_1 - c_2},$$

the required feeding rate equals

$$r > \frac{c' + c_3}{\left(1 - \dfrac{c' - c_2}{c_1 - c_2}\right) - \left(1 + \dfrac{c_2 - c_0}{c_1 - c_2}\right) t_0}.$$

The seabird-sandeel case

When we started to study the seabird-sandeel case within the IMPRESS project, most evidence of a negative relationship between sandeel stock and the performance of seabird populations was based on correlative analyses ('statistical approach'). Within the IMPRESS project, we aimed to come up with the 'individual-based static approach' and thus with, as far as possible, a description of true functional responses, while taking into account several of the complexities mentioned earlier. We further wanted to

- take into account the spatial aspects of the feeding process, that is we wanted to emphasize that colony-based seabirds are confronted with a non-random spatial distribution of their prey and that travelling costs will increase with increasing distance to the colony;
- restrict our case to short term aspects of the functional response, that is to feeding rates of the adults, provisioning rates of the chicks and possibly chick survival,
- acknowledge that our study system is a multi-predator and multi-prey system, and therefore pay attention to the presence of so-called MSFAs (multi-species feeding associations), in which some species may facilitate others; and
- know the effects of the hydrographical conditions on the foraging process.

Below we will discuss some aspects of these four issues in further detail, showing how our knowledge obtained on (1) energetics (maintenance costs, costs of provisioning, flight costs, foraging costs, diving costs,); (2) foraging behaviour (diet selection, searching rate, pursuit time, handling time; interference and facilitation); (3) fish abundance and distribution; and (4) effects of environmental factors on issues (1-3), might contribute to answering the question "how many fish should be left in the sea".

Energetics and foraging behaviour

The studies on avian energetics performed within IMPRESS have been summarized in chapters 6.1 and 6.4. Here we will provide some further simplifications in order to link these results to the ‘individual-based static approach’, discussed above. We aim to derive a function that describes the required food intake rate while foraging in relation to the distance to the colony. The food intake rate should be sufficient for the own energy expenditures of the adult bird and for provisioning food for an average number of chicks We assume that the birds have to stay a fixed time of the day at the colony (Chapter 6.4). For the rest of the day the birds may fly to the fish grounds and forage there. The birds further have to obey the constraint that the total energy expenditure per day should not exceed a certain level, the so-called metabolic ceiling. Boxes 6.5.3 to 6.5.5 present the relevant equations and example calculations for the shag and the gannet. It should be realized that at this stage these calculations are just back of the envelope ones.

In order to link this required feeding rate to fish abundance, we need information on the functional response, i.e. on the searching rate (in unit volume per unit time) and the handling time. Only data for double-crested cormorants feeding on trout are available. The experiments with the cormorants showed that the underwater part of the foraging process very much resembles a Holling type I process. Figure 6.1.10 shows that the feeding rate is almost a linear function through the origin of fish density. This might imply that there is no handling time underwater. The slope of this linear function equals 0.45 m^3 s^{-1}. This slope equals the searching rate. Hence about half a cubic meter of water is emptied of fish per second. Handling of the fish occurred at the water surface and took about 0.2 s per g fish (unpublished data Enstipp). The overall foraging process can thus described by the Holling type II curve, with a maximum intake rate of 5 gs^{-1} (which equals the reciproke of the handling time).

This maximum observed intake rate (while foraging) in the experiments of about 3 gram per second, or (using 4 kJ per gram wet weight) 12000 W, is equivalent to about 1450 BMR (note that BMR for the shag was estimated at 8.3 W, see Chapter 6.4). The required intake rate of about 8 BMR while foraging (Box 6.5.4), can thus be achieved at much lower fish densities than were used in the experiments.

Using the approach described in Box 6.5.2, we can derive the prey density at which this intake rate can be achieved:

$$D'_n = \frac{W'}{a(e - hW')},$$

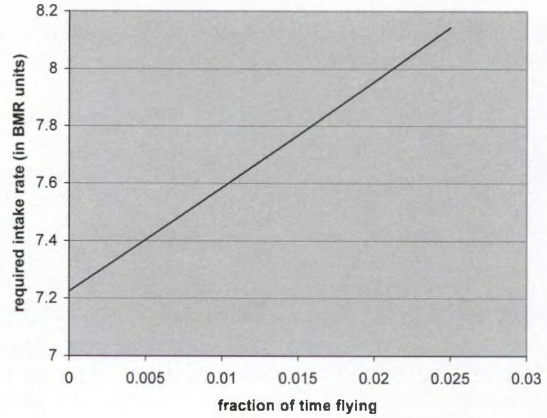
where W' equals 8 BMR, which is approximately 66 J s^{-1}, a is 0.45 m^3 s^{-1}, h is 0.2 s per g fish and e is 4 kJ per g fish. This gives a required prey density of about 40 mg m^{-3}, which is much lower than the minimum prey density of 180 mg m^{-3} in the experiment.

Box 6.5.4

For the shag, we used the following figures

t_0	1/3 (8 hours, see Chapter 6.4)
c_0	2 (based on unpublished data of Enstipp)
c_1	20.7 (based on Pennycuick model)
c_2	4.35 (based on unpublished data of Enstipp)
c_3	1.25 (based on 1.5 chicks $pair^{-1}$, a chick DEE of 1200 kJ and a BMR for the 1.76 kg parent using 4.73 W kg^{-1}, data Enstipp)
c'	4 (based on Drent & Daan 1980)

This gives the following relation between required feeding rate and flight time, where the metabolic ceiling is reached when the time spent flying is about 2.6%:



Fish abundance and distribution

How does this theoretically derived minimum prey density of 40 mg per m^3 compare with fish densities in the field? Acoustic surveys over the years 1997 until 2003 estimated the total biomass of sandeel in the IMPRESS study area to be on average 106 thousand tonnes (Table 4.2.1). The total numbers of sandeels were on average estimated at 58 billion in the study area. The study area is about 6000 km^2 large. Hence the estimated biomass was on average 18 g m^{-2} and the estimated density was about 10 m^{-2}. The grab surveys yielded higher estimates: on average 30 individuals per m^2. Since the average depth within the study are is about 60 m (Fig. 3.2.6), the estimated biomass density based on the acoustic surveys, when expressed per volume of water was about 300 mg per m^3. The grab surveys suggest a much higher number: about 900 mg per m3. This difference could be due to the fact that the acoustic surveys only measure the fish present in the water column, whereas the grab survey measures the total stock (see considerations in Chapter 4.2). Yet, both type of estimates are much higher then the required 40 mg per m3, that is the prey density at which the shag should be able to meet its energy requirements.

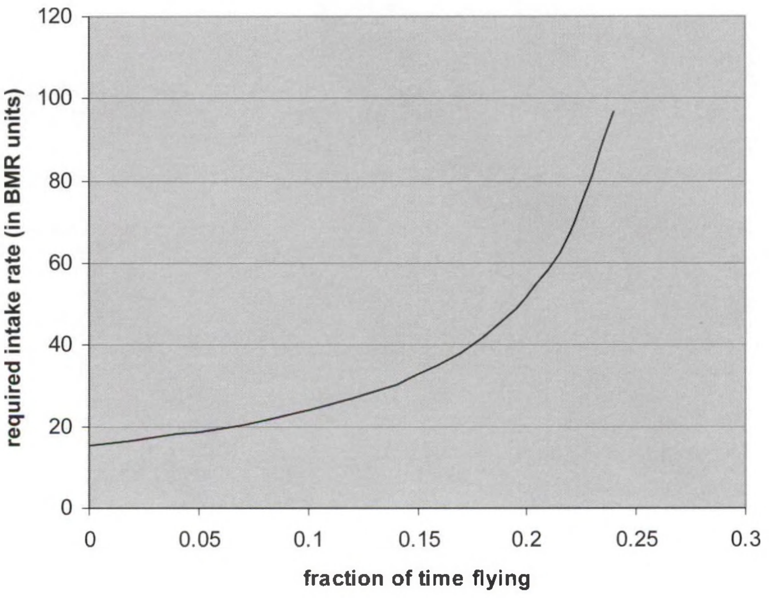
At this point at least four remarks should be made. First, the estimated biomass is an average over seven years. The lowest year (1999) revealed an estimate sandeel biomass of only 2.8 thousand ton, which is equivalent to only 8 mg m^{-3}: much lower than the required 40 mg m^{-3}. Second, the estimates are averages over the entire study area, and local densities could be much higher (or lower). The question what the relevant spatial scale actually is requires further attention. It should, for example, be noted that, since the Shag is, due to the metabolic ceiling constraint combined with the extremely high flight costs, only able to fly about 2.5% of the time, these densities must be available close to the coast. Third, the estimates are averages over the entire water column. Again, how do these compare with estimates over the appropriate depth range? Fourth, the reliability of the fish density estimates is perhaps not very large. Fifth, the estimate of the required fish density is partly based on laboratory experiment of the foraging process with another bird species (Double-crested Cormorant instead of Shag) and another fish species (trout instead of sandeel).

Box 6.6.5

For the gannet, we used the following figures

t_0	5/7*
c_0	2 (based on unpublished data of Enstipp)
c_1	9 (based on Pennycuick model)
c_2	9 (based on unpublished data of Enstipp)
c_3	0.43 (based on 0.67 chicks per pair, a DEE for the chick of 1600 kJ and a BMR for the 2.97 kilo parent using 4.85 W/kg, data Enstipp)
c'	4 (based on Drent and Daan 1980)

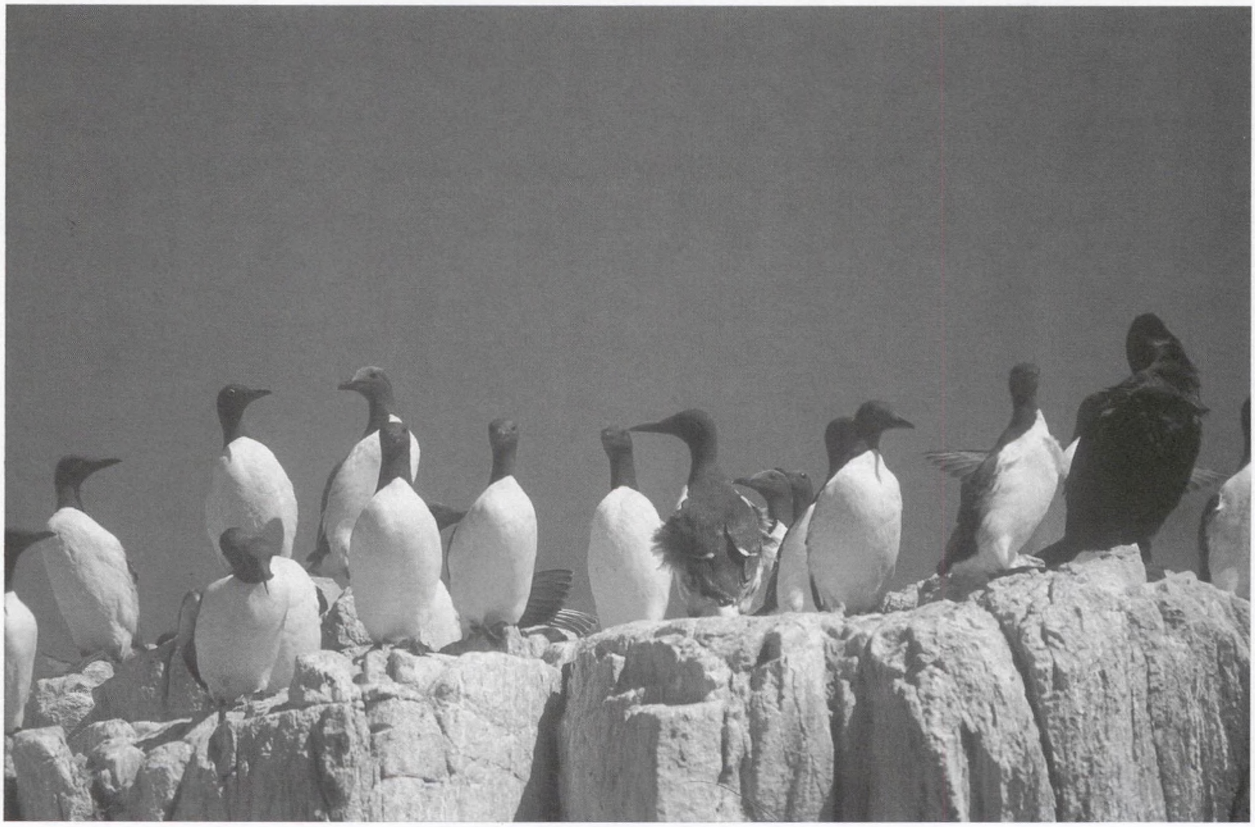
This gives the following relation between required feeding rate and flight time:



*The metabolic ceiling is reached at $t_0 = \dfrac{c' - c_1}{c_0 - c_1}$, i.e. at a time resting of 5/7. Indeed 9 BMR*2/7 + 2 BMR*5/7= 4 BMR.

Conclusions and way forward

The present model exercise still is rather sketchy. A more thorough analysis is at the moment not very helpful, as essential data are still lacking. This lack of knowledge merely refers to the foraging process itself, that is the functional response *sensu stricto*. Although, the energetic aspects of the various behaviours are now much better known, which is a major step forward, the link between fish densities and fish behaviour on the one hand and immediate foraging success of the seabirds on the other hand is only touched upon. In this project a start was made using an experimental approach with one type of species (the Double-crested Cormorant/Shag). This should be extended to other species and to more natural situations. We suggest that in future more emphasis should be put on these functional response aspects.



Common Guillemot Uria aalge and European Shag Phalacrocorax aristotelis (C.J. Camphuysen)

97585

Chapter 7 Local/daily scale hydrography, prey and seabird interactions

7.1 Impact of ocean physics on North Sea seabirds: combining logger data and at-sea surveys

Francis Daunt, Kees Camphuysen, Liz Humphrys, Keith Hamer, Sarah Wanless, Henrik Skov

Oceanography has a profound impact on the distribution of marine life (Miller 2004), and top predators frequently congregate in areas with a high prey biomass (Boyd & Arnbom 1991; Hunt *et al.* 1999). However, the impact of ocean physics on top predator foraging behaviour is poorly understood, largely because of the complex trophic linkages involved. In particular, a detailed understanding of the interaction between seabirds and their prey is lacking. The seasonal and daily patterns of ocean structure have been fully described in Chapter 3. In this chapter, we examine the fine scale local and daily impacts of oceanography on prey distributions and seabird foraging dynamics in our study area, combining the findings from many different workpackages collecting empirical data during 2001-2003.

All four seabird species are wholly or partly dependent on the Lesser Sandeel during the breeding season (see Chapter 5). For much of the summer, autumn and winter, adult sandeels are buried in the substrate, only entering the water column briefly in winter to spawn (Robards *et al.* 1999). In spring, adult sandeels are active in the water column during the daytime, returning to the sand at night (Winslade 1974). Within this diurnal pattern, distribution of sandeels in the water column is expected to be dependent on the vertical distribution of their principal prey, calanoid copepods. However, diurnal movements of calanoid copepods are highly flexible, diverging from the typical migration from shallow depths at night to deep depths during the day time depending on predation pressure (Frost & Bollens 1992). Because of this complex dynamic, the distribution of adult Lesser Sandeels in relation to ocean physics and primary production is poorly understood. Larval sandeels metamorphose in early spring into young of the year fish which have an extended pre-settled phase where they are present in the water column throughout the daily cycle (Jensen *et al.* 2003). These young fish are also preyed upon by seabirds, and are regularly aggregated in frontal zones (Camphuysen & Webb 1999), but the importance of other physical and of biological processes, including association with phytoplankton biomass at the thermocline, and the impact on other ages classes, is unknown.

Clupeids, and in particular Sprats *Sprattus Sprattus*, are important alternative prey for a number of seabird species in the North Sea. Like sandeels, clupeids feed primarily on zooplankton but have a very different diurnal distribution, foraging actively near the surface at night but being inactive at deep depths during the daytime (Blaxter & Hunter 1982). As such, they appear to match the typical vertical migration of their prey more closely, but the extent to which this ties in with frontal features and thermoclines is untested.

The temporal and spatial variation in hydrographic structure has been shown to impact on the distribution of top predators such as seabirds. An association between seabird distribution and horizontal fronts has been demonstrated repeatedly in shelf seas (reviewed in Hunt *et al.* 1999). In addition, stratified regions are known to be important to diving species (Russell *et al.* 1999), and preferences for the thermocline within stratified regions of shelf seas have been shown suggesting increased abundance at shallow pycnoclines of species with poor diving ability (Briggs *et al.* 1988, Hunt & Harrison 1990, Hunt *et al.* 1990, Haney 1991, Skov & Durinck 2000). Daily tidal advection influences the horizontal distribution of seabirds (Coyle *et al.* 1992). The interaction between bathymetry and daily tides may also drive seabird prey closer to the surface at certain times, affecting timing of seabird foraging (e.g. Irons 1998; Hunt *et al.* 1999).

The method by which a species obtains food is likely to have a profound impact on the role oceanography plays on its ecology. Here we consider the relationship between marine physics, prey availability and foraging dynamics in our four study species, representing four main foraging groups: surface feeders (Kittiwake), mid-water divers (Guillemot), benthic divers (Shag) and plunge divers (Gannet).

Kittiwake

Surface feeding seabirds require processes that bring prey to the sea surface (Garthe 1997; Camphuysen & Webb 1999). Horizontal frontal systems are predicted to provide such opportunities.

From **at-sea surveys** (1991-2004), it was demonstrated that Kittiwakes occupied a *c.* 100 km broad zone off the Scottish east coast during the breeding season (Figs. 5.4.2-3) and within that zone peak densities were often observed close to the shallow-sea front (i.e. the seaward side of the coastal zone). Kittiwakes were common and widespread, albeit in much lower densities, in the central North Sea, but the breeding status of these birds may be questioned. Between the coast (colonies) and the shallow sea front, rapidly moving flocks of Kittiwakes, travelling out to sea or towards the coast (interpreted as flocks moving to and from foraging areas), were a common sight, as well as more individually operating Kittiwakes with a meandering flight path (searching individuals). Plunge-diving or dipping Kittiwakes would immediately attract conspecifics, as a result of which small feeding flocks were formed. Such flocks disintegrated quickly when feeding success was low and the birds would either disperse and continue to search, or alight on the water and rest. Dipping, shallow plunge-diving, and surface pecking were typical forms of feeding behaviour observed in Kittiwakes within the coastal zone (i.e. coast to shallow sea front) and within the shallow sea front. Kittiwakes were seldom seen to disappear under water, meaning they were feeding at several centimetres depth at most.

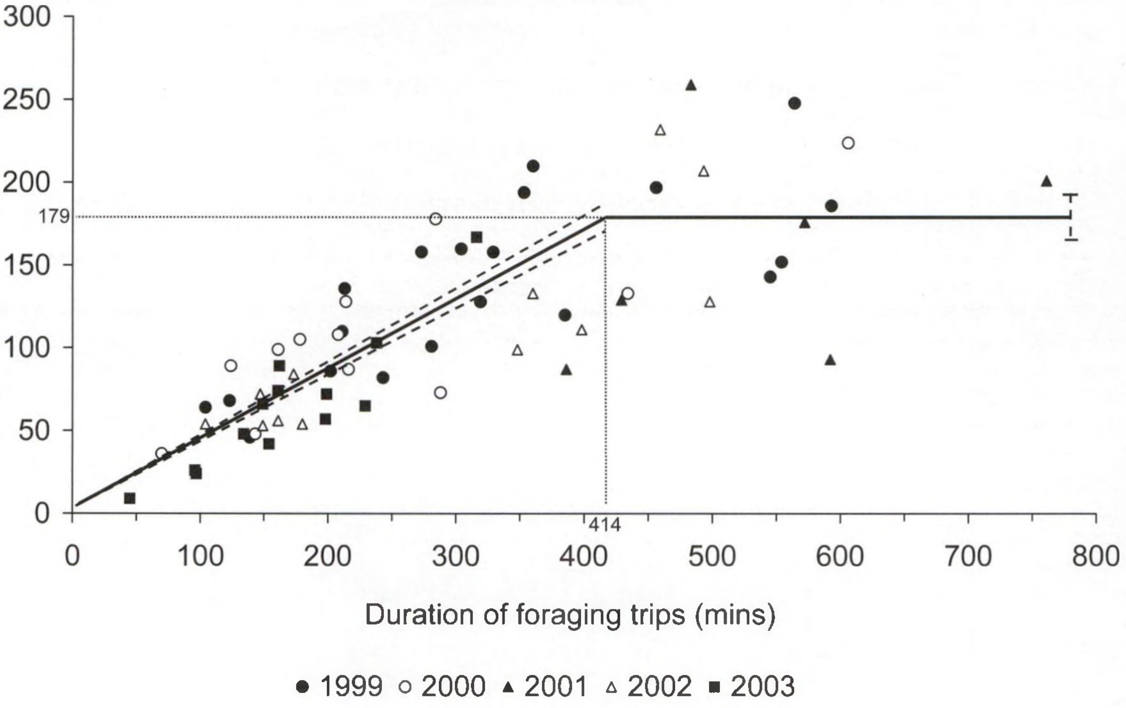


Fig 7.1.1. Relationship between travelling flight duration and trip duration during foraging trips of Kittiwakes in 1999-2003. A broken stick model with flat asymptote provided the best fit to the model (77.9% of the variation explained). The slope of the line is initially estimated at 0.43 ± 0.018, before flattening at a trip duration of 414 mins and flight duration of 179 mins. Thereafter, there is no increase in distance travelled with increasing trip duration.

From **behavioural** observations during ship-based surveys in the shallow-sea front zone, in the area between the front and the coast and within most of the principal study area (Fig. 5.4.4) were Kittiwakes commonly seen to join type 3 MSFAs (Chapter 5.4). Within the principal study area, it was clear that most Kittiwakes were feeding in freshwater-influenced coastal waters and over the banks (Fig. 5.4.13B); the latter area is characterised by numerous and often particularly large type 3 MSFAs (Fig. 5.4.10). Kittiwakes were seemingly constantly searching for social feeding large auks (Guillemots or Razorbills) that were driving fish balls towards the surface in a concerted effort. Feeding opportunities for Kittiwakes were most prominent when such auks were under water, and would cease as soon as the entire flock would resurface and rest. Nearby active feeding frenzies have been studied with particular attention and under good light conditions, a light brown fish mass could be seen only just subsurface (diameter several metres at most). Very close encounters of such fish balls and observations of successful plunge-divers revealed that these fish balls were usually (small) sandeels. Regurgitated material dropped on deck by Kittiwakes that had just left these frenzies confirmed that these were 0-group sandeels. The activity of the auks was seemingly important and three categories of 'attraction to auks' were observed: (1) feeding auks are ignored (feeding Kittiwakes in the same general area, but not associated with the auks, (2) attracted by flocks of feeding auks, but no immediate feeding opportunities for Kittiwakes, and (3) joint feeding frenzy. The first category has been interpreted as conditions where auks were simply feeding too deep to be of interest for the gulls. The second category is a situation where the auks were still to deep, but where feeding opportunities were (soon) expected. Compact swimming flocks of Kittiwakes were seen and these would suddenly take wing and start plunge diving in a small area where auks would soon become visible while surfacing to breath. In some of the areas with particularly high densities of seabirds, a majority of the dense flocks of Kittiwakes was observed to be inactive, even although in close association with feeding auks. Suggestions that these Kittiwakes were 'sitting out' phases of the tidal cycle during which the auks were not feeding in a for Kittiwakes profitable way were tested during so-called mini-surveys in June 2003 on board RV *Pelagia* (Chapter 7.3).

Results from this at-sea approach were compared with results from **colony-based studies** using information derived from birds of known status and origin. Chick-rearing Kittiwakes were equipped with activity loggers each June between 1999 and 2003, and recaptured after they had made a foraging trip (1999: n = 20 trips; 2000: n = 12; 2001, n = 6; 2002, n = 12, 2003, n = 13). Travelling flight is the only activity during which significant displacement occurs. During chick-rearing, Kittiwakes carry out trips with a direct or narrow eliptical flight path (Wanless *et al.* 1992; Humphreys 2002). Assuming travelling flight speeds of $13ms^{-1}$ (Pennycuick 1997), we estimated maximum foraging range from: max. range (km) = (travelling flight duration (s) * 13) / 2) /1000. We ran four models to describe the relationship between travelling flight duration and trip duration: constant, linear, exponential and broken stick (full details in Daunt *et al.* 2002). The best model was a broken stick model (Fig 7.1.1), with a maximum foraging range of 69 ± 6 km.

This distance accords well with the distance from the breeding colony to the shallow sea front, which runs parallel to the coast in the principal study area (Fig 3.2.5, 3.2.7). The front appears to form an outer barrier for breeding Kittiwakes, and foraging occurred throughout the zone between the colony and the front. Thus, the colony-based results from the activity loggers accord fairly well with at-sea surveys (Fig 7.1.2) and telemetry (Humphreys 2002; Fig 5.5.5) and demonstrate a consistent pattern of distribution of Kittiwakes and other surface feeders at, and westwards of, the front, with very few east of the front. However, the shallow sea front was not favoured by breeding Kittiwakes over other habitats within their foraging range. This result may reflect intrinsic constraints of breeding individuals. During the spring and summer the breeding component of the population is under two important constraints. First, individuals are restricted in their foraging range by the need to return repeatedly to the colony to feed the young. Thus, there may be a trade-off between habitat profitability and distance from the nest site, such that birds may not always prefer the highest quality areas (Davoren *et al.* 2003). The stronger preference for the shallow sea front demonstrated from at-sea surveys (Fig 5.4.2) compared with colony-based work, or at least the rather high densities of Kittiwakes in that area, may in part be due to the former comprising a large proportion of non-breeding (adult) individuals. Second, the elevated energetic costs associated with rearing offspring may force birds to forage at times that are sub-optimal. This constraint is compounded by the need to allocate a large proportion of available time to offspring attendance.

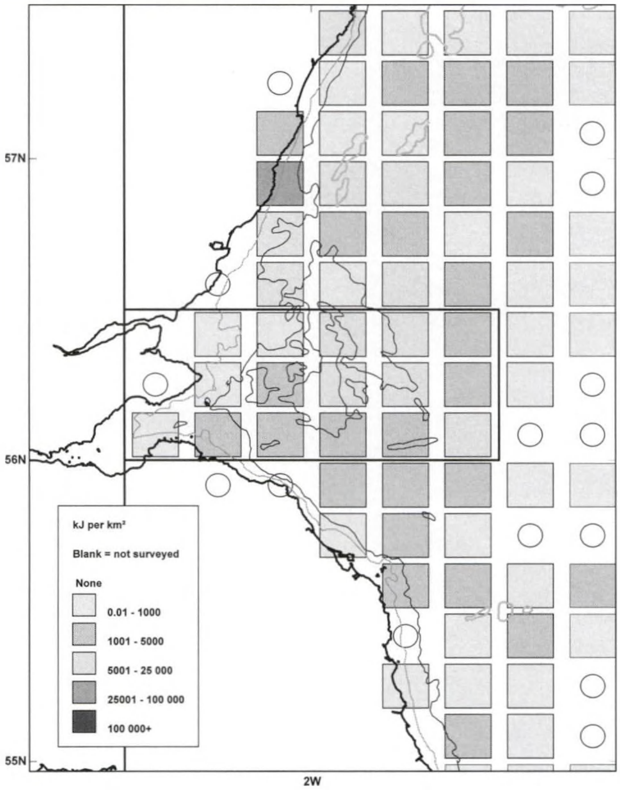


Figure 7.1.2. Daily energy acquired at sea (kJ per km²) based on feeding Kittiwakes observed at sea, ship-based surveys June-July 1991-2004 within and just beyond the principal study area.

Peak densities of foraging seabirds in the shallow sea front area were encountered at distances between 20 and 80 km from the coast, and were considerably more distant, indicating a wider foraging range in some years than in others (Chapter 8). Measured along transects perpendicular to the coast between 55°30'N and 57°30'N (Fig. 1.5.4) within 150km from the coast, the median distance of Kittiwakes in 1997 and 2002 was roughly twice that in 1993, 1999, 2001, and 2003 (Figure 7.1.3). The feeding opportunities for Kittiwakes in type 3 MSFAs were relatively short-lived in areas with numerous large *Larus*-gulls as a result of differences in competitive strength (cf. Camphuysen & Webb 1999). Kittiwakes were constantly searching for 'interesting' flocks of large auks, and the larger gulls would join when feeding seemed profitable (resting flocks of Kittiwakes near auks were ignored, active flocks of Kittiwakes near auks were joined). Even a few of those larger gulls arriving on the scene would immediately reduce access for Kittiwakes in the flock, while a pack of gulls of 10-20 individuals would simply exclude them. Within 40km of the coast, about a quarter of MSFAs (26%, *n* = 1518) were targeted by large *Larus* gulls. In contrast, only 6% (*n* = 1759) of MSFAs more than 40 km from land were targeted by large gulls, and Kittiwake foraging activities tended to be concentrated in these aggregations. The apparent avoidance by Kittiwakes of the inshore areas used by the large gulls, may have contributed to the counter-intuitive, non-significant but positive correlation between Kittiwake annual breeding success (chicks fledged per year) and median foraging distance (km) such that success tended to be lower in years when most birds occurred closer inshore ($r^2_9 = 0.10$, n.s.).

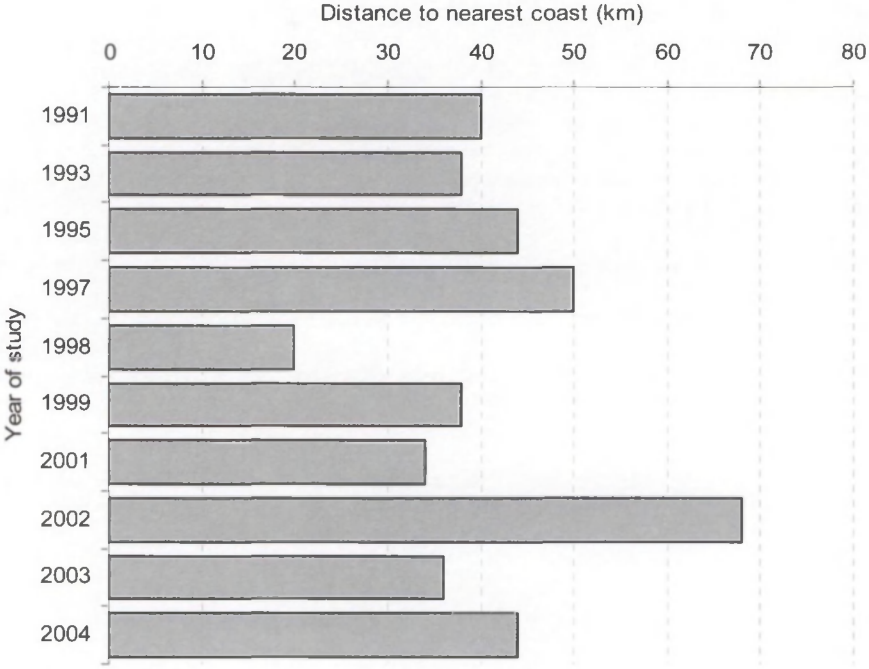


Figure 7.1.3. Median distance away from the coast of Kittiwakes within and around the principal study area (55°30'N-57°30'N, along perpendicular transects up to 150km to the east). The graph suggests that in 1997 and particularly in 2002, the main concentrations occurred at relatively great distances from the shore, whereas foraging was relatively inshore in 1998.

Guillemot

In the North Sea, the shallow sea front is important for mid-water divers (Chapter 5; Camphuysen & Webb 1999). In addition, these species can exploit the water column, and would be expected to target depths where prey are concentrated. The **at-sea surveys** suggested Common Guillemots were essentially highly widespread in a broad zone along the UK coast (Fig. 5.4.2), with relatively lower concentrations of feeding individuals in mixed coastal waters and beyond the shallow sea front in offshore stratified waters (Figs. 5.4.13C, Fig. 7.1.4). Foraging locations from Isle of May breeding birds equipped with compass loggers in 2002 and 2003 suggested that Guillemots from this colony foraged considerably nearer the colony than these overall densities would suggest (Fig. 5.5.4). Either many of the Guillemots encountered during ship-based surveys were non-breeders, or they originated from different colonies, or the signal derived from

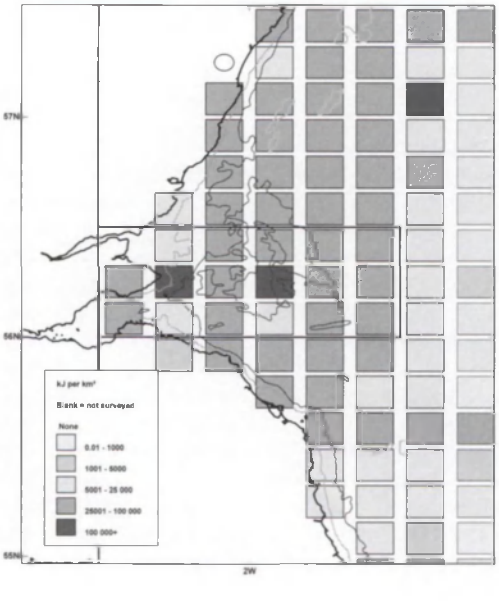


Figure 7.1.4. Daily energy acquired at sea (kJ per km²) based on densities of swimming Guillemots observed at sea, ship-based surveys June-July 1991-2004 within and just beyond the principal study area.

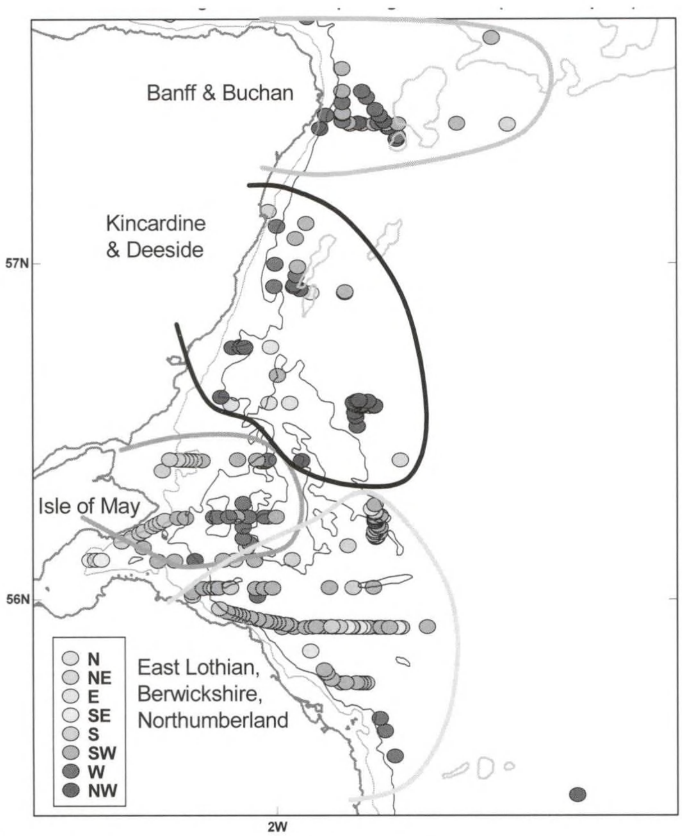


Figure 7.1.5 Individual plots of flight directions of prey-transporting Guillemots off the Scottish East coast and polygons drawn around birds heading for particular important breeding sites.

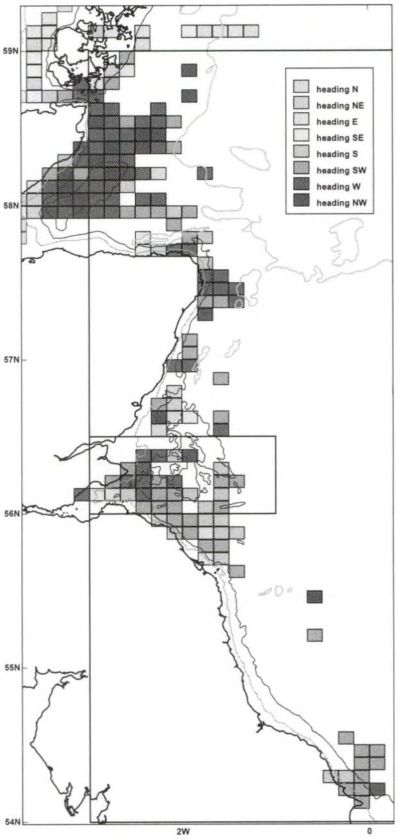


Figure 7.1.6. Predominant directions of flight of prey-transporting Guillemots in the breeding season per 5'x10' rectangle, from unpublished long-term data stored in the European Seabirds at Sea database (version 4.1).

instrumented individuals was misleading. In 2003, during dedicated surveys in hot-spot feeding area onboard RV *Pelagia*, it appeared that nearby locations produced highly different bearings of fish-transporting Common Guillemots, but that prey-loaded individuals flying towards land were seen all the way out to the shallow sea front. A subsequent analysis of survey data, plotting directions of flight of birds carrying fish in and beyond the principal study area, suggested a high degree of overlap between logger data and at-sea data with regard to feeding range, such that birds flying towards the Isle of May were exclusively seen in and immediately around the area where instrumented birds were found foraging in 2002 and 2003 (Third polygon from above in Fig. 7.1.5). These data seemingly hold as a general pattern, as the same was found in the long-term dataset of the European At Sea Database (version 4.1, released September 2004; Fig. 7.1.6), incidentally suggesting that mature birds catching prey for their chick rarely did so on the Marr Bank (Outer Bank area and adjacent offshore stratified water). a prolonged stay in that area in 2003, however, produced numerous sightings of birds transporting prey towards colonies in the northwest (Fig. 7.1.5).

This implies that Isle of May breeding birds utilise only a small part of the principal study area and mainly the west side of the Wee Bankie/Marr Bank complex. This implies that the bulk of the (adult) Guillemots in the eastern part of the principal study area breeds in Kincardine and Deeside and in East Lothian, Berwickshire and or Northumberland (Fig. 7.1.5). Assuming straight flights towards the colony, estimated maximum foraging ranges for Guillemots from the Isle of May from sightings during ship-based surveys are in the range of 50, whereas those from St Abb's Head can be estimated at *c.* 55 km, for Guillemots nesting on the Farne Islands at 70 km, and for birds nesting at Fowlsheugh at at least 110 km.

Concurrent data collected using compass loggers during **colony based studies** confirmed that Guillemots from the Isle of May were foraging principally between the colony and the Wee Bankie (Figure 5.5.4). In this region, the water is stratified in summer (Chapter 3). We equipped breeding birds with PreciTD loggers (Daunt *et al.* 2003; Chapter 5). The data confirmed that breeding Guillemots were foraging in stratified water in all three study years (Fig 7.1.7). The first two years were very similar in water structure, with the water slightly more mixed in 2003 (2002: sea surface temperature 11.8 ± 0.9 S.D. °C; bottom temperature 8.6 ± 0.3 °C; thermocline depth: top: 8.7 ± 6.8m; bottom 21.7 ± 6.4m; 2003: sea surface temperature 11.7 ± 0.8 S.D. °C; bottom temperature 9.1 ± 0.1 °C; thermocline depth: top: 9.1 ± 3.0m; bottom 20.8 ± 4.2m).

In stratified waters, primary production is typically concentrated at the thermocline (Mann & Lazier 1996). However, the extent to which the thermocline is an important zone for foraging seabirds is dependent on its use by their prey. We found that Guillemot foraging effort was strongly targeted at the zone below the thermocline in both 2001 and

2002 (Generalized Linear Mixed Model (GLMM) with individual as random effect, W = 28.0, $p < 0.001$; Figure 7.1.8). Despite this, data collected concurrently by fixed moorings allowed primary production concentration to be modelled throughout the water column, and demonstrated that primary production was highest at the thermocline, lowest below the thermocline and intermediate above the thermocline. Unfortunately, data were not available on fish distribution covering the whole daily cycle in 2002 for direct comparison.

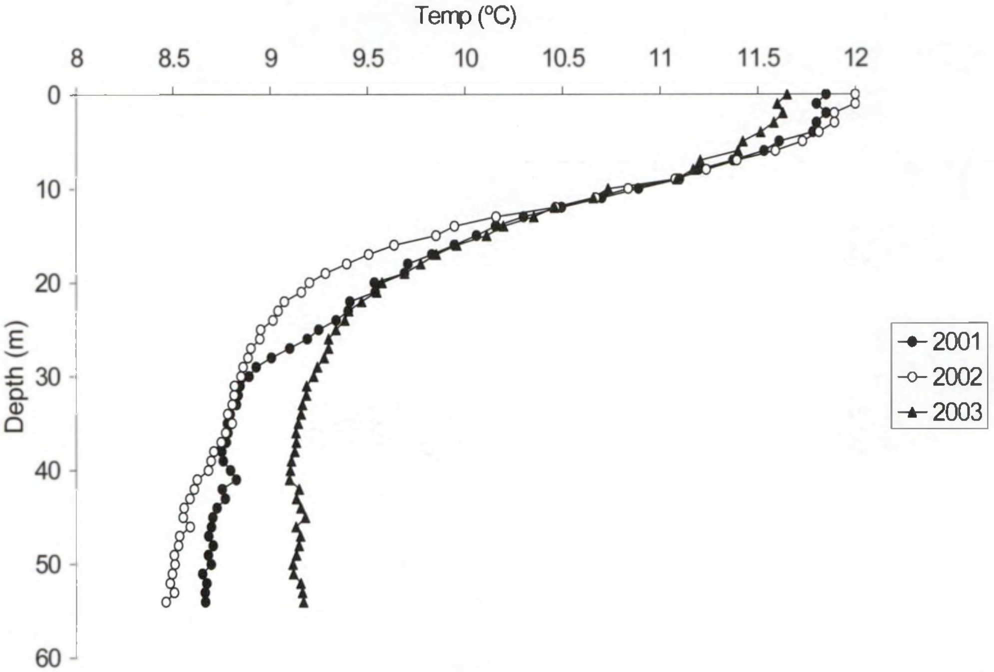
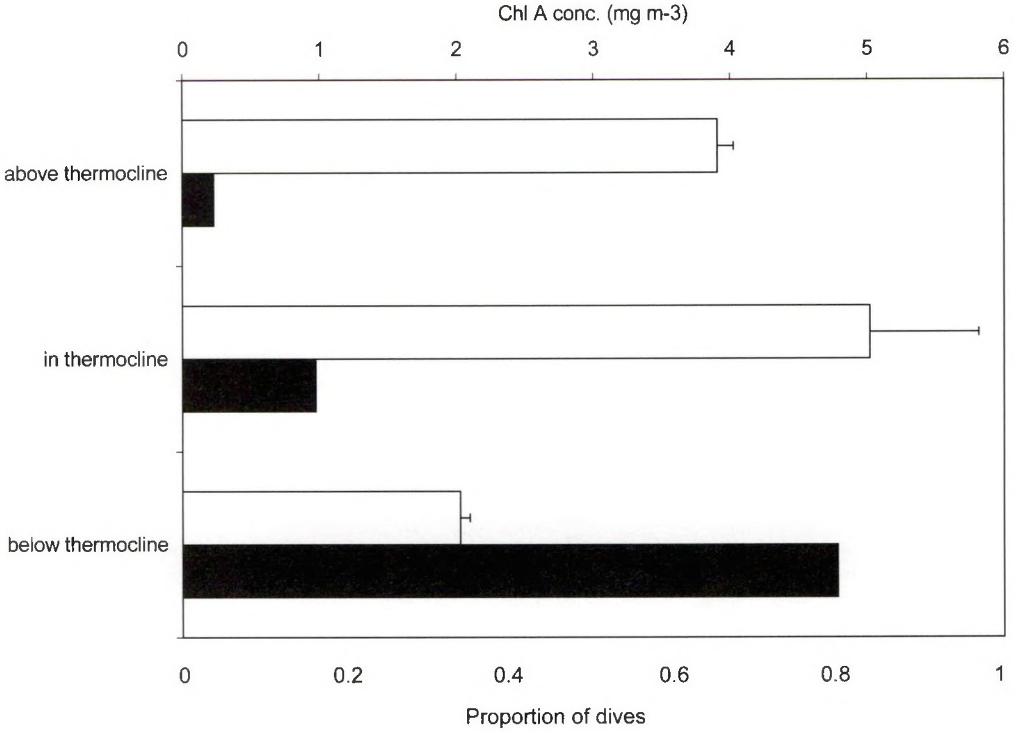


Figure 7.1.7. Mean temperature-depth profiles of Guillemots deployed with PreciTD loggers in 2001 (n = 9), 2002 (n = 8) and 2003 (n = 5).

In 2003, Guillemot foraging distribution was very different with the area above the thermocline as well as below the thermocline extensively foraged in. As in previous years, the thermocline was not targeted (Fig 7.1.8). In the same year, data on depth distribution of primary production and Lesser Sandeels were collected over the whole daily cycle on the *Pelagia* cruise. These data confirmed the findings of the 1D model that the concentration of primary production was highest at the thermocline. Acoustic surveys are unable to measure fish densities in the top 10m of the water column (Chapter 4), so no estimates above the thermocline were available. However, mean distribution throughout the day shows a higher density of sandeels below the thermocline than in the thermocline. Thus, the data appear to show that the mismatch between Guillemot and plankton distribution is partly explained by the distribution of their prey. However, data on the density of sandeels above the thermocline, and density of clupeids (the other main prey of Guillemots, Chapter 5) throughout the water column, are required to strengthen this assertion.

Associated with the different depth utilisation in 2001 and 2002 compared with 2003, there were strong differences in diurnal patterns of foraging depth. In the first two years, there was a marked decline in foraging depth as dusk approached in all cases, a cessation of diving in the darkest period of the night (min. two hours), and a gradual increase in foraging depth from dawn. Shallow foraging was rarely observed during the main part of the day (Fig 7.1.9). In 2003, shallow foraging was observed throughout the day. In all three years, Sprats predominated in the diet of chicks. The typical diurnal depth distribution of clupeids (Blaxter & Hunter 1982) matches very closely the foraging depths of Guillemots in 2001 and 2002. However, as described in Chapter 5, 0 group Lesser Sandeels predominated in the diet of adults in 2003. This prey item may also have been important in the first two years, when adult diet was not recorded. Thus, the high numbers of shallow dives throughout the day in 2003 may have been due to shoals of 0 group sandeels or clupeids being commoner near the surface during the 2003 deployment period than in the other two years.

Diurnal patterns of distribution of sandeels and Sprats were available for part of the daily cycle in 2002 (from the *Clupea* cruise). The region where Isle of May Guillemots were foraging was surveyed from 04:00 – 08:00 and 11:00 – 15:00. During these periods, Sprats were associated closely to the sea floor (Fig 7.1.10). Sandeels were also generally associated with the sea floor, although maximum densities were recorded in midwater during some hours. The distribution of sandeels throughout the daily cycle was measured in 2003 on the *Pelagia* cruise (Fig 7.1.10 lower graph). Sandeels divided their time between the sea floor and the sea surface, with no clear diurnal pattern. Sandeels may have been more abundant at the sea surface in 2003 than 2002, which would accord well with our data on Guillemot foraging depth. Unfortunately, no data on Sprat distribution in the water column were available in 2003.



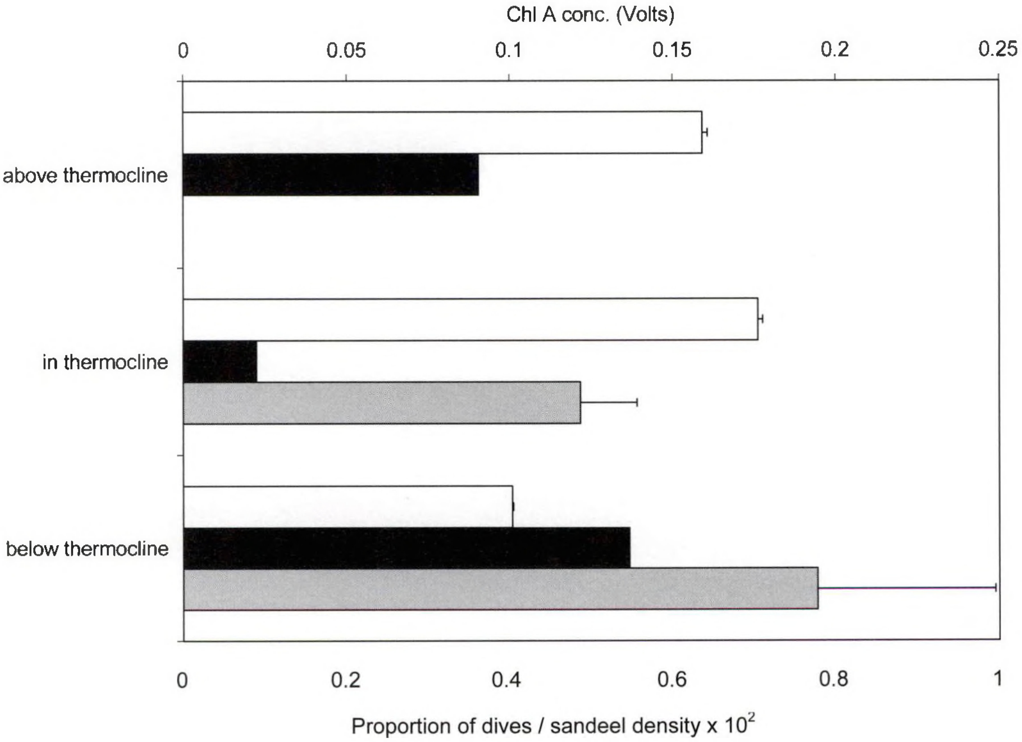


Fig 7.1.8. Mean depth distribution throughout the daily cycle in relation to the thermocline of primary production, Lesser Sandeels and Guillemots. The figures show Chlorophyll A concentration (white bars) and proportion of dives of Guillemots (black bars) above, in and below the thermocline in 2002 (upper graph). These data for 2003 are shown in the lower graph, with density of sandeels also shown (grey bars). The primary production values for 2002 are modelled data from the 1D model described in chapter 3, whereas the 2003 values are real data collected on the Pelagia *cruise.*

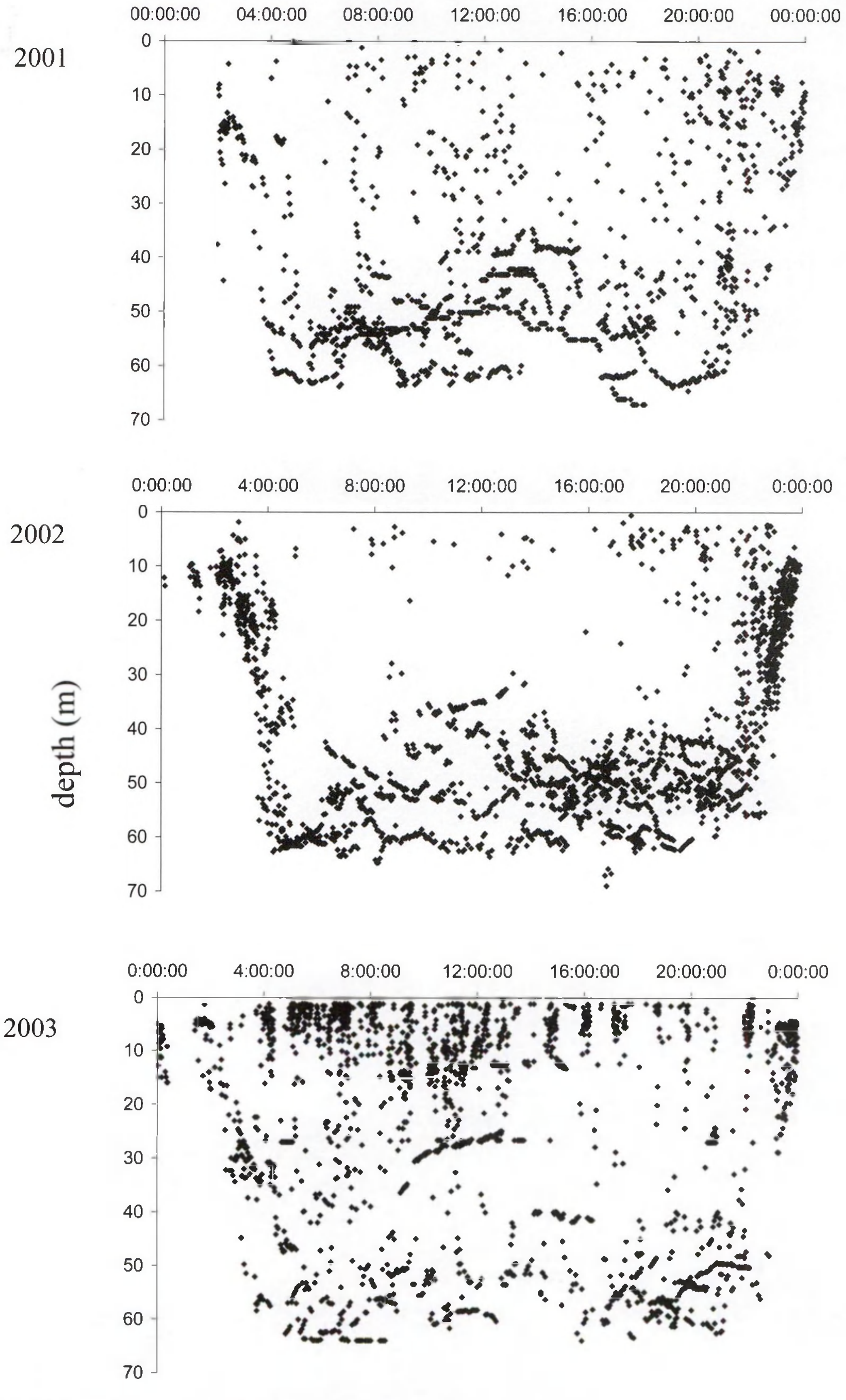
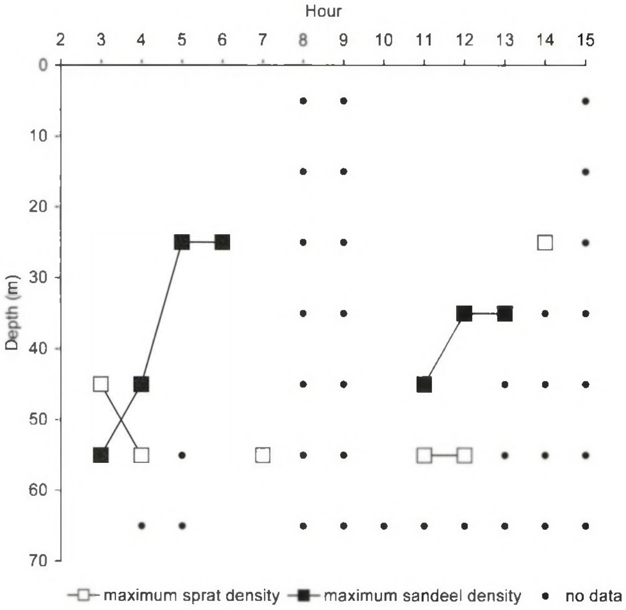


Fig 7.1.9. Diurnal patterns of foraging depth in Guillemots in the three study years.



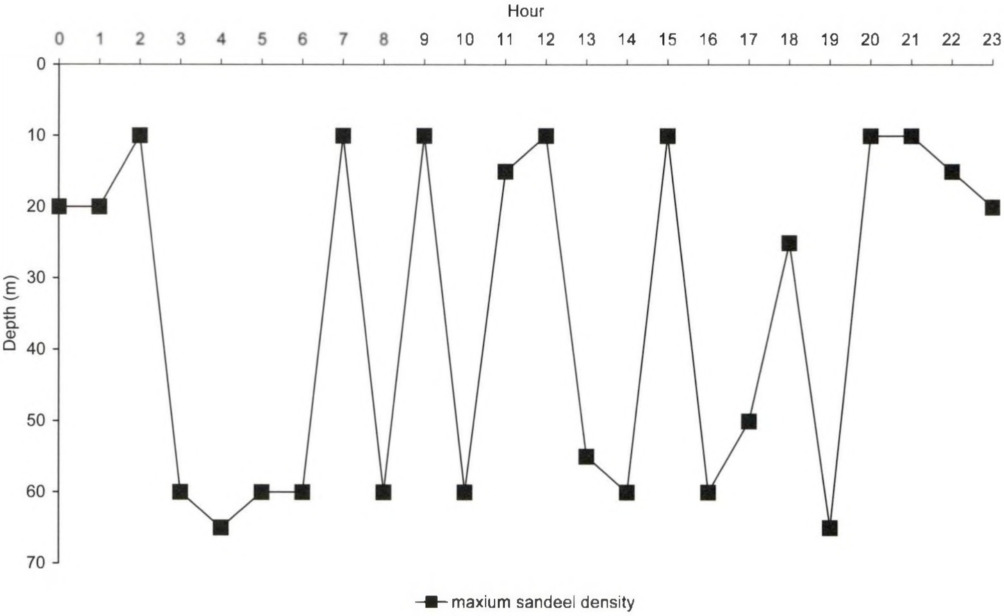


Figure 7.1.10. Depth of maximum density each hour surveyed. Upper graph shows data from Clupea *cruise, 16-19 June 2002, in the zone targeted by Isle of May Guillemots (see Fig 5.5.4). Hours in which surveying took place but no density symbols are shown represent periods when no fish were detected. Lower graph shows dats from* Pelagia *cruise mini-survey 12:00 12th June to 13:00 June 13th 2003. Only sandeel densities were recorded.*

Shag

In contrast to other species groups, the feeding distribution of benthic feeding species is not expected to be associated with fronts or thermoclines (Daunt *et al.* 2003). In all three years, Shags were foraging inshore of the Isle of May (Fig 5.5.2) and, in contrast to Guillemots, the water they foraged in was very mixed (Fig 7.1.11). Ship-based surveys have generally contributed little to the data collected from the Isle of May itself, except that the close inshore distribution was a general finding for the study area at large (Fig. 5.4.2), that all birds in the principal study area were encountered in freshwater influenced areas (Chapter 5), and that few Shags participated in feeding flocks (in fact none were seen to do so within the principal study area; Table 5.4.2).

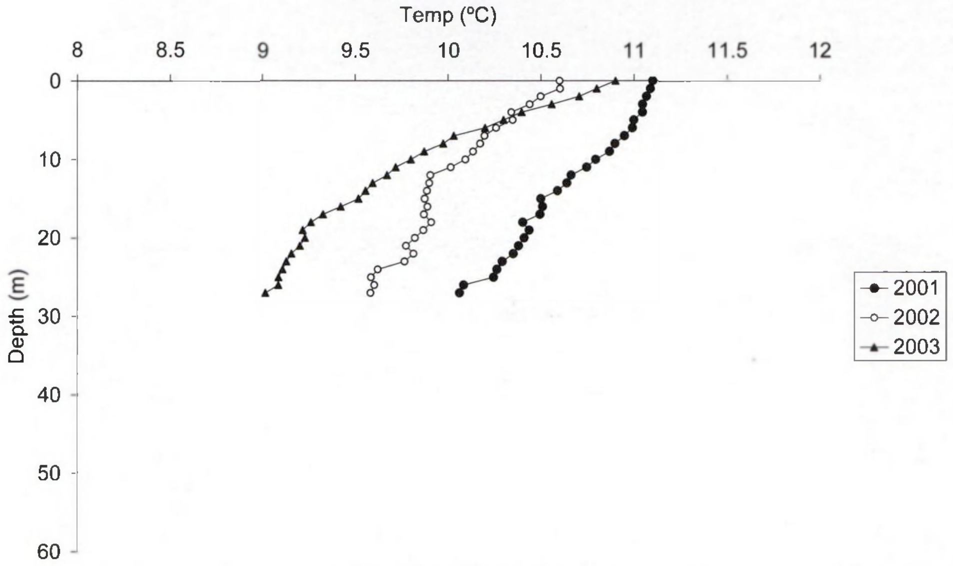


Figure 7.1.11. Mean temperature-depth profiles of Shags deployed with PreciTD loggers on similar dates to Guillemots in 2001 (n = 4), 2002 (n = 10) and 2003 (n = 6).

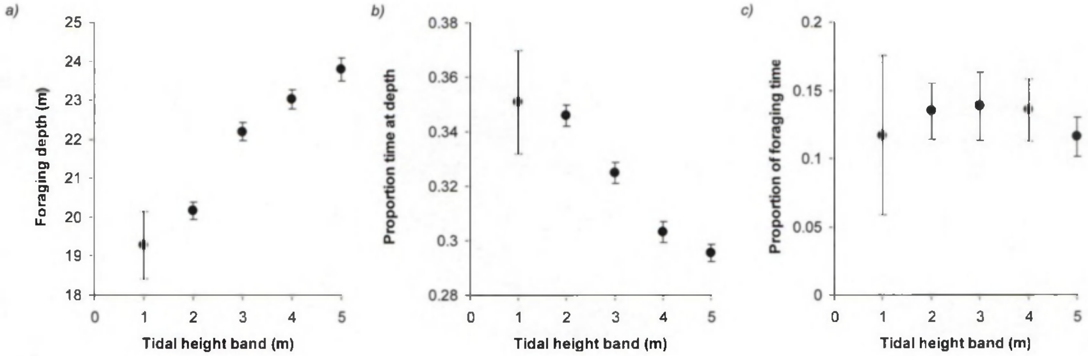


Fig 7.1.12. (a) Foraging depth; (b) proportion of time on water spent at foraging depth; and (c) proportion of time spent foraging in each tidal height band (1 = 0.5-1.5m, 2 = 1.5-2.5m,....) corrected for availability.

Within this inshore mixed water structure, benthic feeders are expected to be affected by the daily tidal cycle, because it impacts directly on the distance between the sea surface and foraging habitat. Specifically, benthic divers are predicted to forage preferentially at low tide. We examined diving behaviour during different phases of the tide in the Shag. We found that dive depth closely matched tidal height, with a 1m change in tidal height corresponding on average to a 1.2m increase in dive depth (Figure 7.1.12a; regression: depth = 18.6 + 1.2 height; Restricted Maximum Likelihood (REML) with individual as random effect: tidal height: $F_{1,46} = 234.7$, $p < 0.001$). The increased time spent travelling through the water column, together with a disproportionately longer recovery period between dives (see Wanless *et al.* 1993), resulted in the proportion of time at foraging depth being 20% lower at high tide than low tide (ratio of time at foraging depth to dive + surface duration, REML, tidal height: F1,46 = 76.1, $p < 0.001$, Figure 7.1.12.b). Despite this, there was no evidence that birds preferred to forage during low tide (Figure 7.1.12c, GLMM: W = 0.2, p = 0.94).

The lack of a preference for different phases of the tide by Shags suggests that there are patterns in the behaviour of adult Lesser Sandeels that are more important in determining the timing of foraging than reduced distance between sea surface and foraging habitat apparent during low tide. The only data on distributions of Lesser Sandeels within the foraging range of the Shags were obtained on 8th June 2001. This survey was not able to examine patterns of distribution in the water column at different times of the day, but was able to map sandeel x-y distributions (Fig 7.1.13). There was no correspondence between the distributions of sandeels and foraging Shags. This may have because the data were collected on different dates. Alternatively, the acoustic survey records sandeels present in the water column, whereas Shags appear to forage benthically, and may thus be targeting sandeels buried in the sand. Therefore, Shag foraging distributions appear to be tied more closely to the distribution of sandy habitats, as can be seen in Fig 5.5.1.

Fig 7.1.13. Density of Lesser Sandeels (gm-2) on 8th June 2001 in relation to foraging locations of Shags on 27th May (white triangles), 10th June (white circles) and 15th June (white squares).

Northern Gannet

Compared with the other three species, Northern Gannets were by far the furthest ranging species, foraging abundantly within and beyond the principal study area (Figs. 5.4.2, 5.5.8-11). Behavioural observations during ship-based surveys indicated that the foraging techniques, the tendency to participate in multi-species feeding frenzies, the tendency to join hunting cetaceans as well as the opportunities to scavenge at fishing vessels varied considerably in different parts of their range(Chapter 5).

From **at-sea surveys**, numbers of northern Gannets around the Bass Rock declined with distance from 11.1 km^{-2} immediately around the colony to less than 0.01km^{-1} at over 400km from the colony (Fig. 7.1.14). From extrapolated numbers of adult Gannets based on densities with increasing distance within 400km around the Bass Rock (Table 7.1.1), under the assumption that each of these should originate from that colony, it may be suggested that one third (31%) occurred within 80 km from the colony, another third (34%) between 80 and 200 km, and 35% at greater distances away from the colony. Hence, two-thirds of the birds were recorded in areas where mean densities were very low (mean 0.47 km^{-2}). Thus, most northern Gannets were seen to forage and feed in areas with relatively low densities of conspecifics (Table 7.1.1). Within 400km around the colony, 66.1% were feeding in low-density areas (<1 Gannets km^{-2}; >100km away from Bass Rock), 25.8% in areas with moderate densities (1-5 Gannets km^{-2}; 40-100km from Bass Rock), and only 8.1% in high-density areas (>5.0 Gannets km^{-2}; <40km from Bass Rock).

Behaviour types categorised as foraging Gannets include actively searching as well as feeding birds (deep and shallow plunge diving, scooping, pursuit diving and scavenging at trawlers; the latter usually being a mixture of plunge diving and surface seizing). The initial attack is usually a plunge dive, even although this may just be a way of entering the feeding frenzy and prey may subsequently be taken from the surface (surface seizing, scooping, pursuit diving). Feeding behaviour was typical for the situation the Gannets were in, with scooping being exclusively observed in MSFAs where auks had driven small prey to the surface. Gannets joining cetaceans were typically deep plunging, most birds at trawlers would enter the water with a deep plunge and use a variety of techniques to obtain discards after that (deep plunging, surface seizing and pursuit diving). Foraging Gannets that were not associated with other predators or vessels were normally (deep) plunge diving.

Foraging associations changed with distance away from the Bass Rock (Table 7.1.1). MSFA participation typically occurred within 100 km from the Bass Rock (particularly so within 80km from the coast). Associations with marine mammals largely occurred at greater distances (>60 km from the colony), and typically over >50m deep, stratified offshore waters (Chapter 5). The frequency at which 'natural'MSFAs were joined mirrors the possibilities at sea (such MSFAs were developing mainly within 80km from the coast; Fig. 5.4.4), the latter seemed a preference for cetaceans hunting in deeper waters, since these animals were widespread and occurred in similar numbers closer to both colony and coast (Figs. 5.4.5 and 5.4.7). Offshore feeding assemblages with marine mammals involved (>80 km from the coast) normally attracted Gannets as a single species (90.7%, *n* = 237), whereas nearshore assemblages were normally MSFAs (57.9% multi-species; *n* = 95). Trawlers were joined where they occurred.

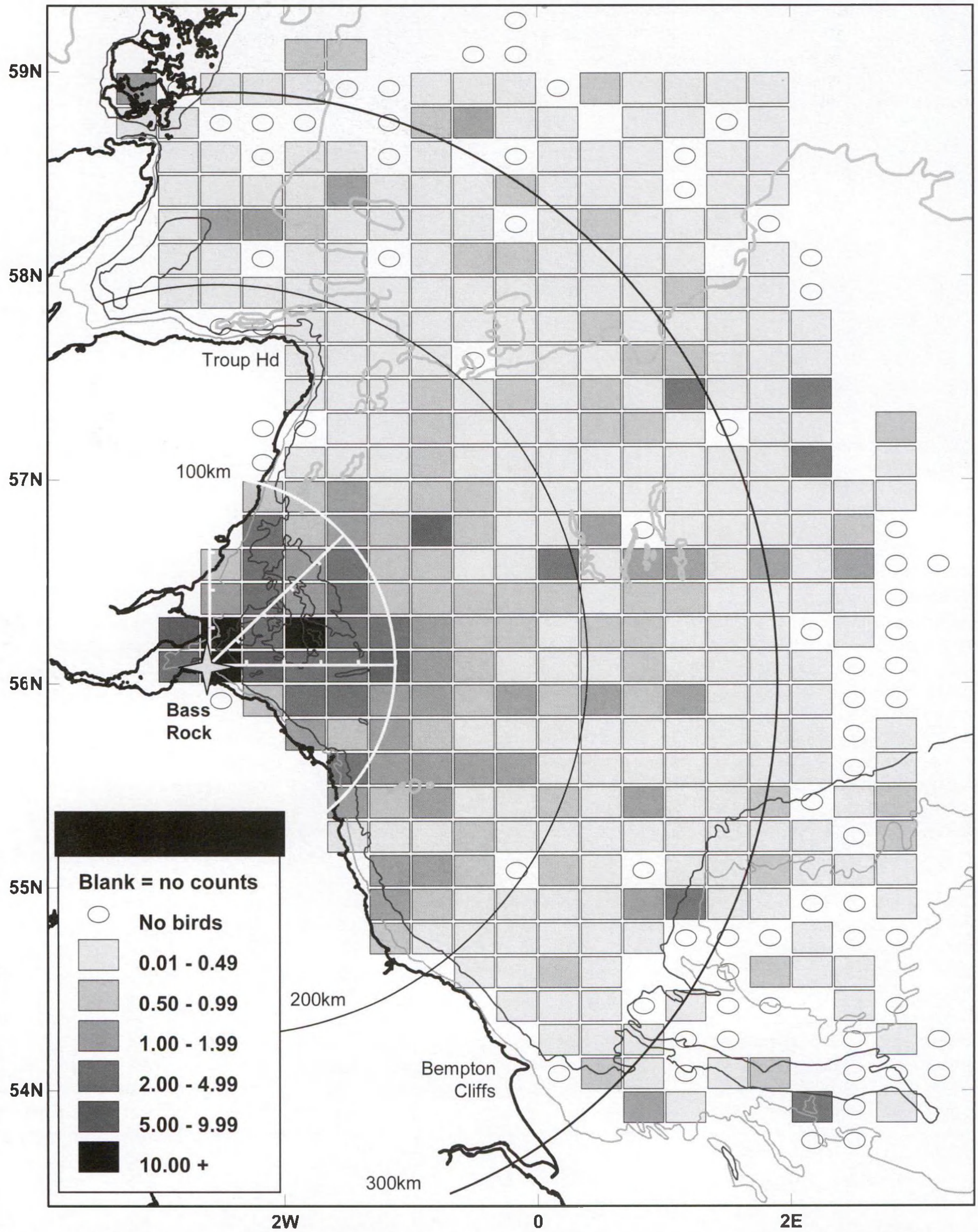


Fig. 7.1.14. Mean densities ($n\ km^{-2}$) of Northern Gannets around Bass Rock based on June-July surveys 1991-2043. The circles indicate 100km distance contours around the colony (indicated with a star), with 20km intervals along axes pointing N, NE, and E within 100km.

Combining at-sea distribution data with locations obtained from Gannets carrying instruments (from PTTS and GPS loggers; Figs. 7.1.15-16) confirms the enormous range of these birds around the colony, as well as their tendency to travel NE and E rather than N, with a second 'stream' of birds heading SE and into the deeper gullies to the SW of the Dogger Bank. The three sets of data are in perfect agreement with eachother.

From activity recorders attached to the Gannets, diving locations and 'shallow-feeding' locations could be pin-pointed. The former activity has always been recognised as feeding behaviour in Gannets, under the textbook assumption that these birds dive to feed and disappear at least several metres deep under water. The surface behaviour recorded, including very shallow depths reached (0.5m), were often ignored. From ship-based observations, however, it became obvious that Northern Gannets do join MSFAs in a rather peculiar manner and that a more pelican-like scooping behaviour is typical when these birds attack surface-driven sandeel shoals (see image). Behaviour labelled as 'diving' from instrumented Gannets matched rather poorly with the areas where Gannets have been seen to participate in 'natural' MSFAs (Fig. 7.1.17), whereas behaviour labelled as 'surface feeding' was observed in quite exactly the areas where MSFAs were joined (Fig. 7.1.18).

*Table 7.1.1. Densities (n km^{-2}) and estimated total numbers of adult northern Gannets (densities * surface area; rounded to nearest 10) broken down for behaviour and feeding associations with distance within 400km around the Bass Rock colony (see Fig. 1).*

Distance aroung colony (km)	0-20	- 40	- 60	- 80	- 100	- 150	- 200	- 250	- 300	- 350	- 400	Totals	%
Density (*n* km^{-2})	11.06	5.35	3.73	2.43	2.03	0.94	0.46	0.32	0.25	0.20	0.19		
Scavenging at trawler	0	0	930	0	540	220	190	70	780	80	90	2900	3.5
Assoc. with dolphins	0	10	0	20	330	670	570	690	1430	960	1400	6080	7.3
'Natural'MSFAs	300	800	850	1190	940	620	150	210	30	60	1280	6430	7.7
Mono specific feeding	530	90	40	340	320	1250	770	490	790	870	440	5930	7.1
On water (resting)	940	120	230	460	500	1200	830	1140	1280	1440	690	8830	10.7
In flight (travelling)	2820	5630	5690	5030	4960	8250	5730	4950	2790	3480	3610	52940	63.7
Totals	4590	6650	7740	7040	7590	12210	8240	7550	7100	6890	7510	83110	

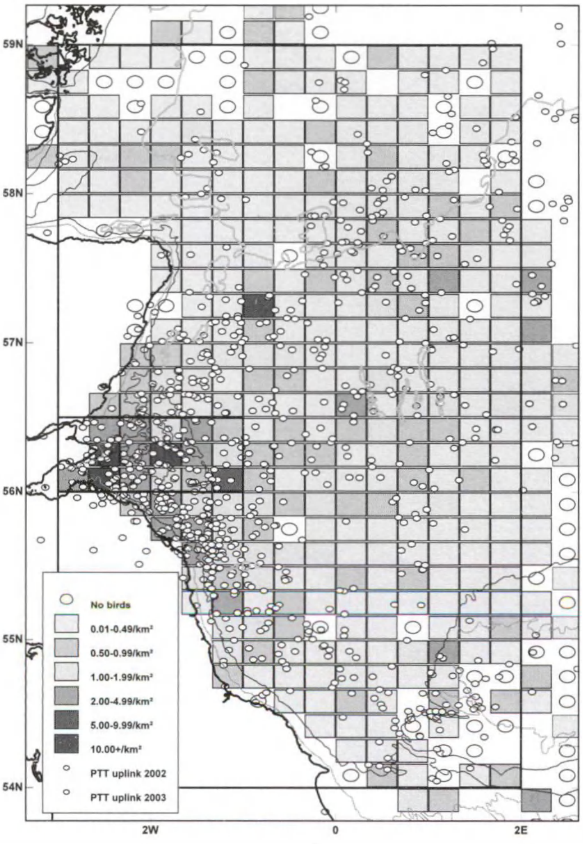


Figure 7.1.15. Generalised distribution pattern of Gannets from ship-based surveys 1991-2004 and PTT uplinks (satellite transmittor data) in 2002-2003.

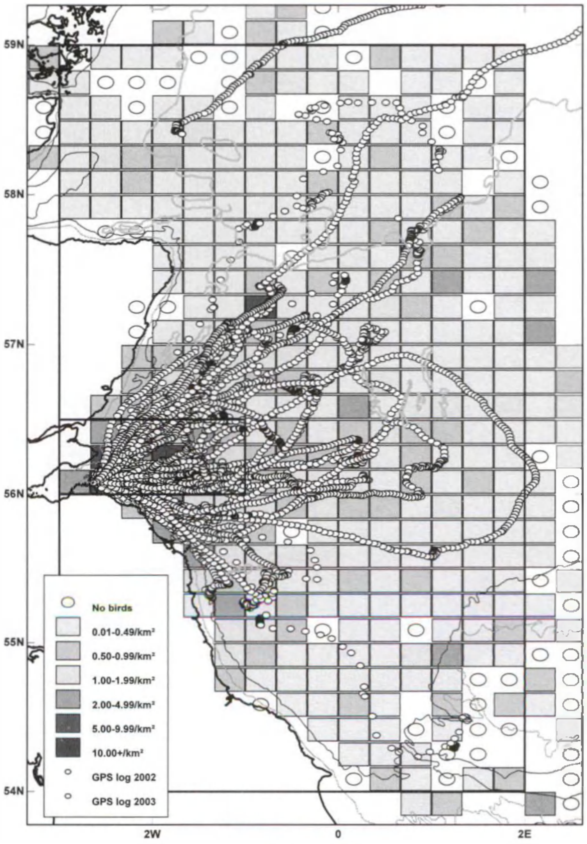


Figure 7.1.16. Generalised distribution pattern of Gannets from ship-based surveys 1991-2004 and GPS uplinks (logger data at regular intervals) in 2002-2003.

Scooping Northern Gannets targeting sandeels (Wee Bankie, summer 2002, C.J. Camphuysen). Kittiwakes try to obtain further access to the prey after having been displaced by three adult Gannets. The left bird is swallowing a mouthful of prey, the right bird is just taking another bite.

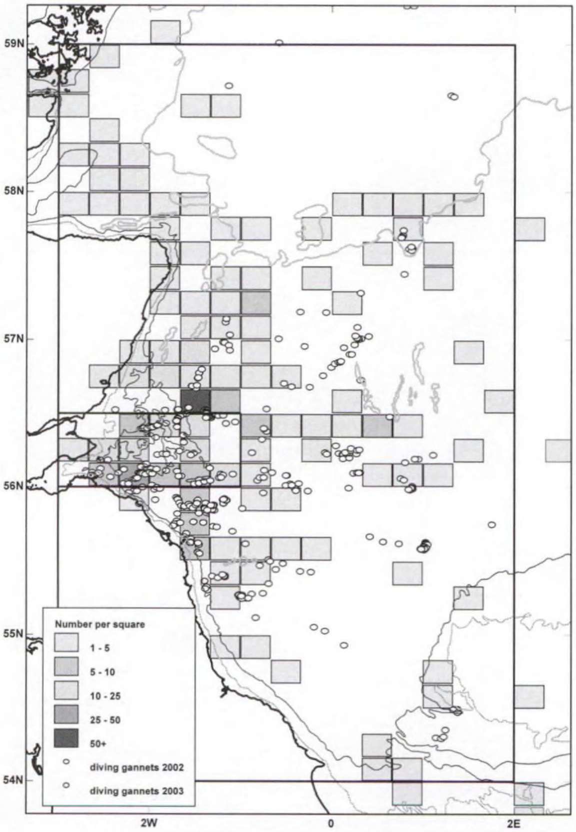


Figure 7.1.17. Gannets joining MSFAs from ship-based surveys (rectangles) and dive locations from instrumented birds in 2002-2003 (plots)

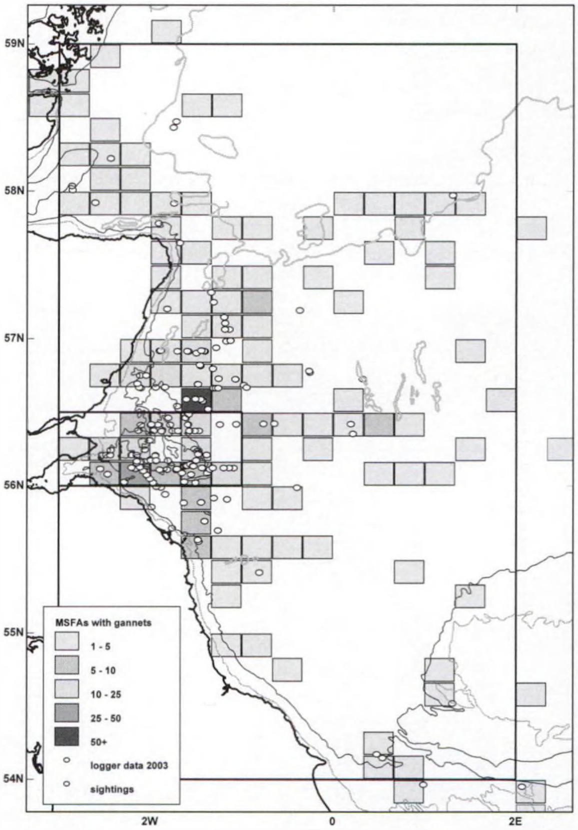


Figure 7.1.18. Gannets joining MSFAs from ship-based surveys (rectangles) and locations from instrumented birds where Gannets were presumably scooping (plots)

Scooping, recognised and recorded as a distinct behaviour only since 1997 from ship-based sightings, was relatively frequent in Freshwater influenced waters (0.29 birds per km travelled), and over the inner, outer and offshore banks (0.20 km^{-1}; see Chapter 3 for area partitioning). Scooping was hardly ever recorded in mixed waters (0.06 km^{-1}) and not very frequent in stratified offshore waters (0.10 km^{-1}), a result that was supported by data obtained from birds carrying instruments (Fig. 7.1.18).

Deep diving Gannets (Fig. 7.1.17) were recorded within as well as beyond the areas where most Gannets were seen to participate in multi-species feeding frenzies. Deep diving is not necessarily an attack at depth. Northern Gannets joining fishing vessels can be seen to enter the feeding frenzy with a deep plunge dive, to swim up to the sinking discards and grab preferred prey considerably closer to the surface (Camphuysen *et al.* 1995). Gannets joining MSFAs were often entering a frenzy with a deep plunge, to commence feeding (by scooping) only after surfacing. Therefore, some of the dive-locations in Fig. 7.1.17 may actually have referred to MSFA participants that obtained prey at the surface.

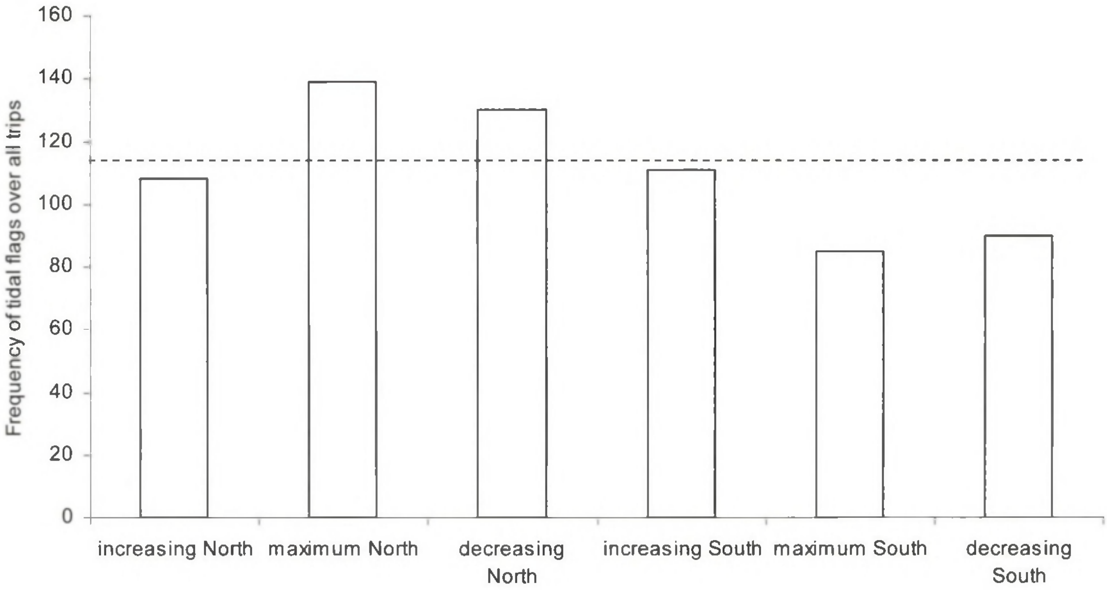


Figure7.1.19. Frequency of tidal stages (see Chapter 3.2 for details) encountered by Gannets whilst at sea on foraging trips (dashed line is expected frequency based on uniform distribution).

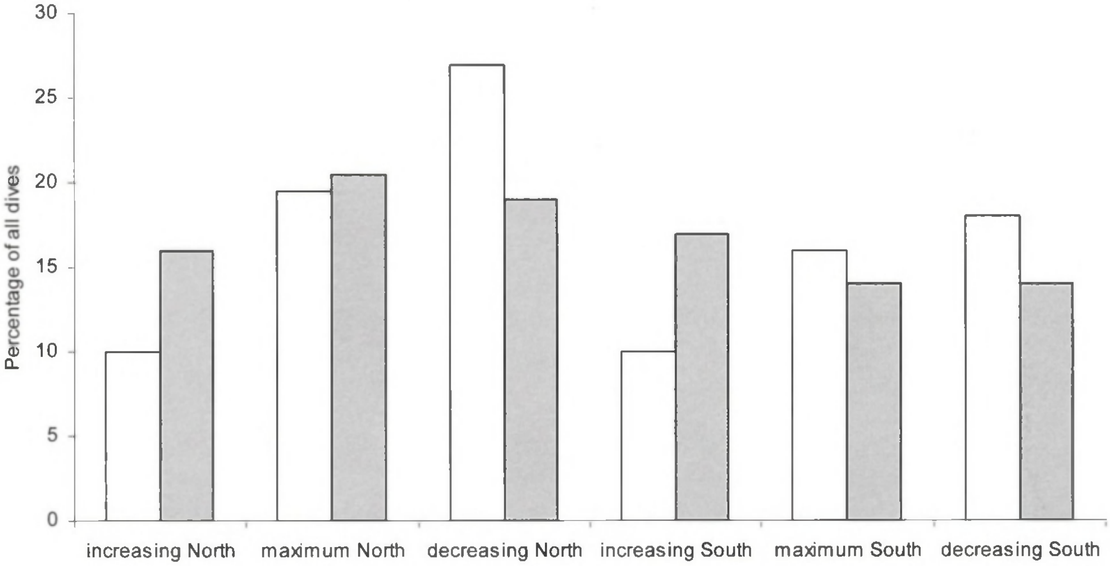


Figure 7.1.20. Frequencies of diving events (n = 375) over the tidal cycle (white bars, observed frequencies; grey bars, predicted frequencies based on tidal stages encountered at sea).

Colony based studies of birds equipped with GPS loggers and PreciTD loggers (Chapter 5) indicated that breeding adults were at sea more during maximum North/decreasing North and less during maximum South/decreasing South tides than would be expected by chance (Fig. 7.1.19, $\chi^2_5 = 13.8$, $n = 683$, $p = 0.01$). As the start of each foraging trip is determined primarily by the return of the partner to the nest, then birds probably exercised choice over the foraging conditions that they encountered at sea by adjusting the time when they returned to the nest or the direction in which they foraged. Data also indicated that diving events occurred at higher frequencies during decreasing North tides than would be predicted given the frequencies of the different tidal stages that birds encountered at sea (Fig. 7.1.20, $\chi^2_5 = 35.3$, $n = 375$, $p < 0.001$). Analysis of diving behaviour in relation to the position of the North Sea's characteristic summer longitudinal tidal front (interpreted from a composite of satellite images of sea surface temperatures in July 2003), indicated that the frequency of dives during different tidal stages differed significantly between locations inshore and offshore of the front (Fig. 7.1.21, $\chi^2_5 = 16.3$, $n = 375$, $p < 0.001$).

Analysis of dive depths indicated that birds made shallower dives inshore of the tidal front (mean depth = 2.07 ± 0.19 m) than offshore (mean = 4.31 ± 0.16 m, REML: W = 69.37, $p < 0.001$). The phase of the tide was also important, with the deepest dives occurring during decreasing South and increasing North tides (Fig. 7.1.22, REML: W = 41.96, $p < 0.001$). Birds dived primarily in stratified water (Fig. 7.1.23) and only very occasionally penetrated the thermocline (most dives were < 5 m).

There was some evidence that dives were more numerous at locations exhibiting higher horizontal variation in sea surface temperature (SST; Fig. 7.1.24). This may in part reflect variation in distance to land. However, at equal distances from the colony, locations with higher horizontal SST variation were also more often used for diving. When comparing the interpolated SST map with the location of dives and of assured feeding events (data from birds equipped with gastric temperature loggers; Chapter 5), areas with stronger gradients seem to have been exploited more often. This was partly so for dives (Fig. 7.1.25) and quite clear for feeding events (Fig. 7.1.26). Altogether, these data suggest that Gannets from the Bass Rock used areas with higher than average SST variation for feeding. This is corroborated by the modelling of habitat suitability of diving gannets using distance to Bass Rock, topographic variables like water depth, slope and aspects of the seafloor and SST data overlapping the dives (Ecological Niche Factor Analysis, Fig. 7.1.27). The factor analysis showed that the feeding events in 2003 had a preference zone covering the extent of the shallow sea front.

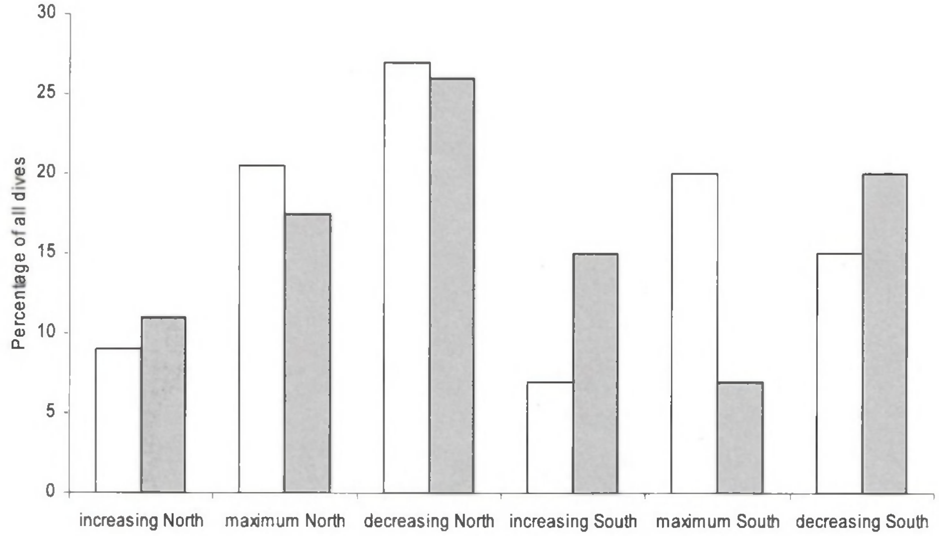


Figure 7.1.21. Frequency of diving events (n = 375) over the tidal cycle (white bars, inshore; grey bars, offshore).

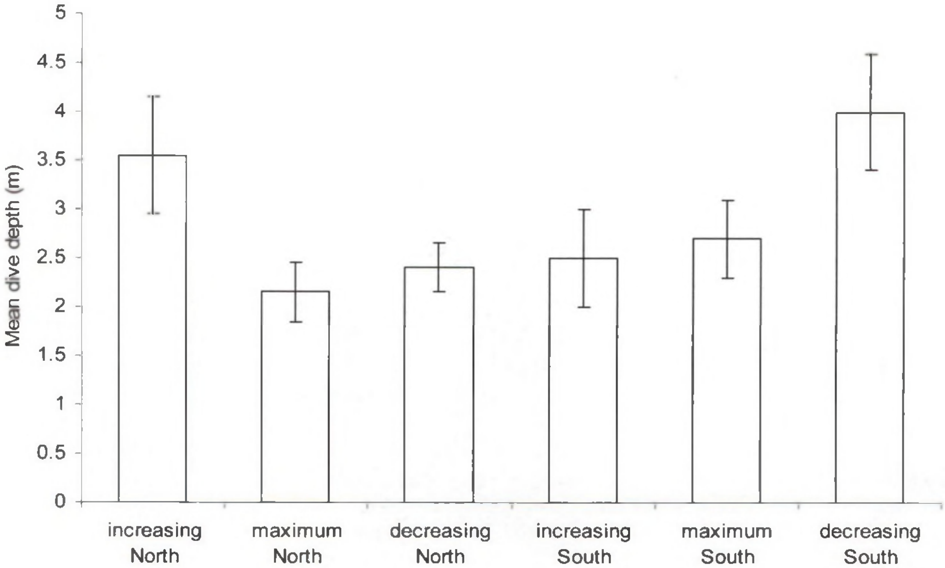


Figure 7.1.22. Mean dive depths of northern Gannets over the tidal cycle.

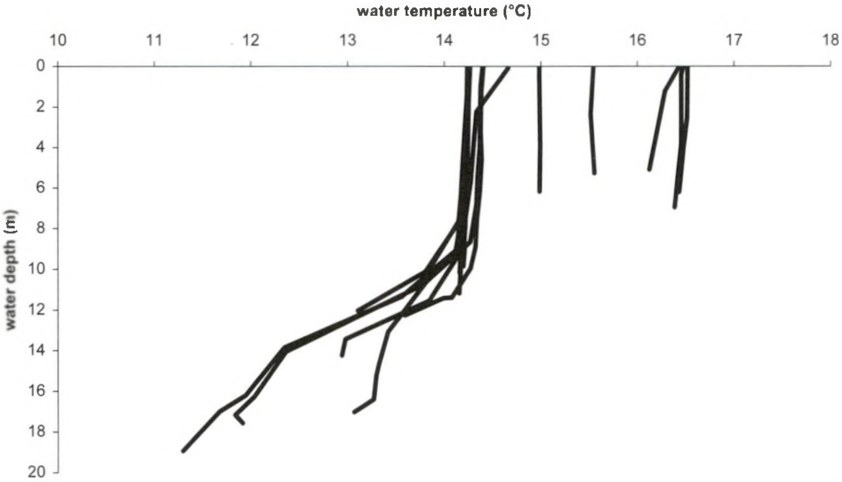


Figure 7.1.23. Vertical temperature profiles measured by diving Gannets during 13 dives reaching at least 5 m water depth in July 2003. Each dive is shown by a solid line. The geographic area considered here ranges from –1.5 to 0° Longitude and 55.67° to 56.33° Latitude.

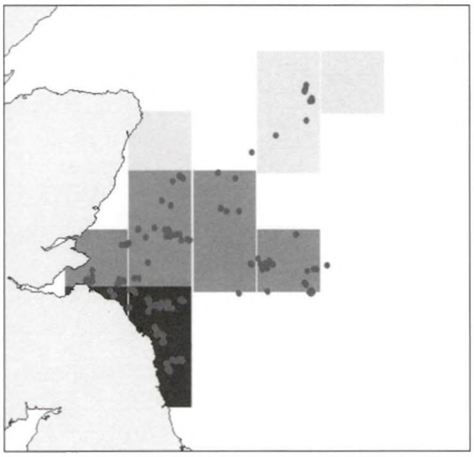


Figure 7.1.24. Location of Gannet dives (dots) in relation to SST variation (in squares) from 9-12 July 2003. SST variation ranges from very light blue with a SD of SST measurements of <0.1°C to dark blue with a SD of >0.63°C.

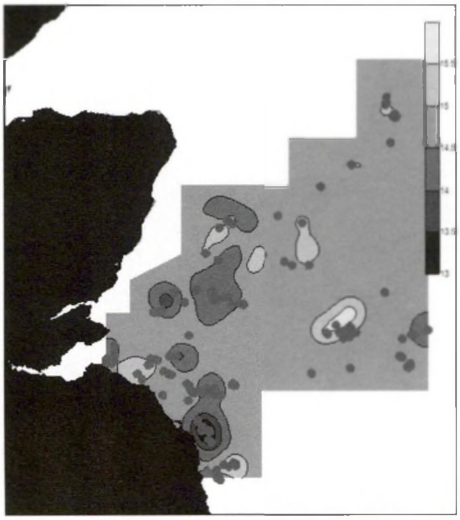


Figure 7.1.25. Location of Gannet dives (red dots) on an interpolated map of SST measured by Gannets (for SST values see legend). All data originate from 9-12 July.

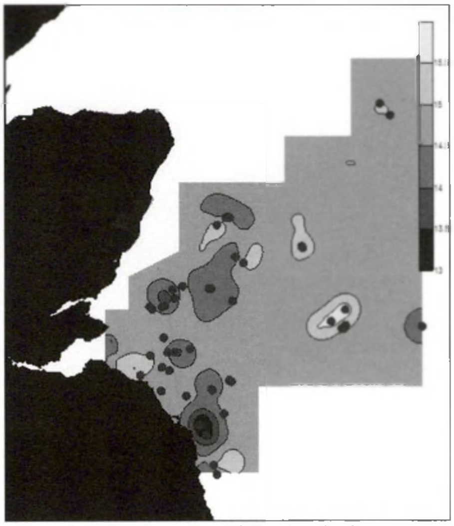


Figure 7.1.26. Location of Gannet feeding events (blue dots) on an interpolated map of SST measured by Gannets. All data originate from 9-12 July.

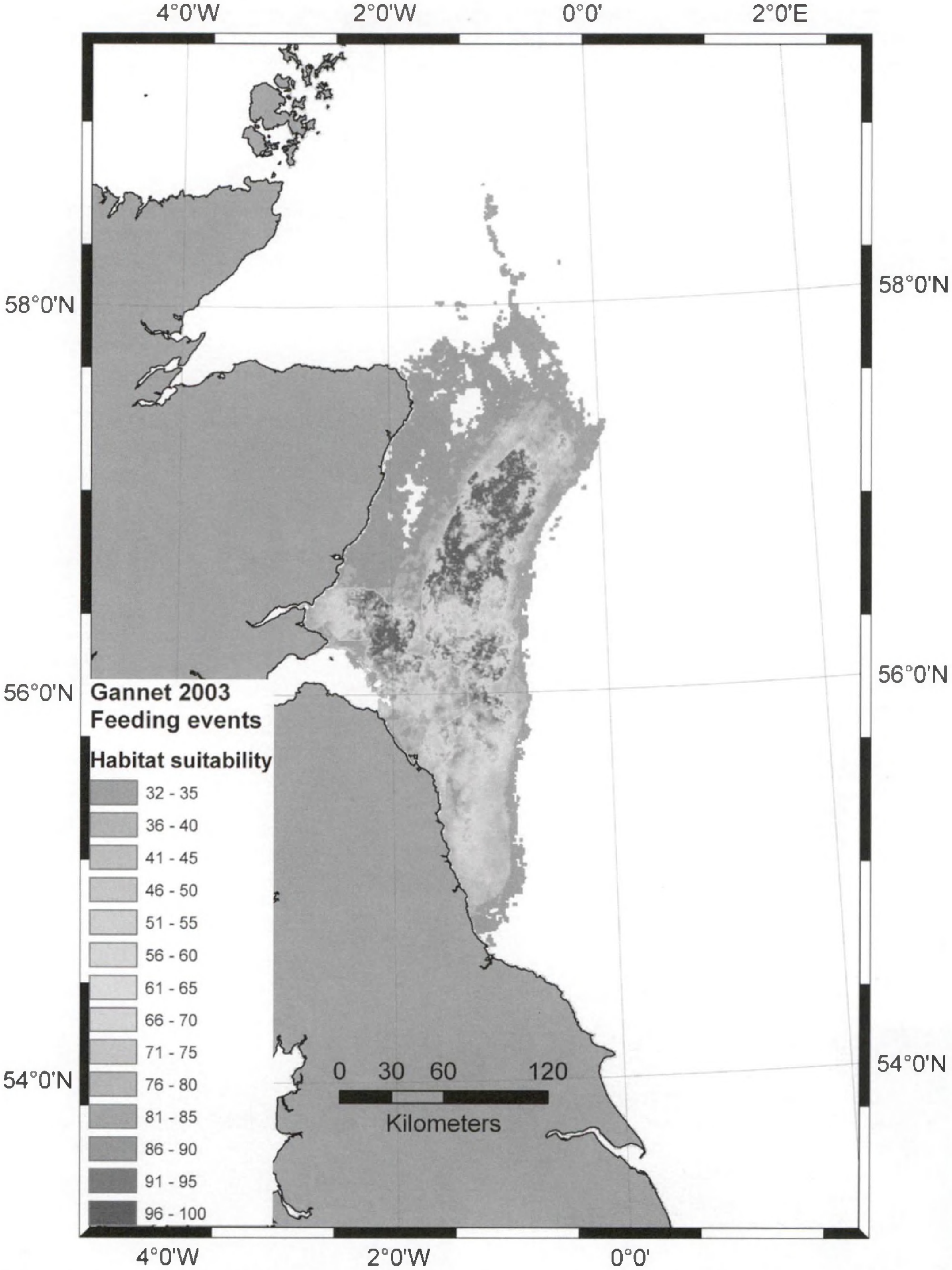


Figure 7.1.27. Model (GIS-based Ecological Niche Factor Analysis) of suitable habitat of feeding Gannets calculated from feeding events and SST data, topographical variables and distance to Bass Rock. Values range from 0-100, - values below 33 reflecting areas avoided by feeding gannets and values above 66 reflecting areas preferred by feeding gannets.

7.2 Seabird foraging habitats

Beth Scott

The description of different regions in the study area in Chapter 3 was based on physical attributes, mainly the mixing properties of the water column determined by the strength of tidal currents and the water depth. This is a static description of the regions, one that will remain constant between years as tidal strengths and depths do not vary annually. Due to the different mixing properties of these regions, different levels of primary production would be expected, and possibly different trophic chains with different species of phyto- and zooplankton. These differences in mixing properties will also affect the aggregation level of primary and secondary production and therefore may influence the aggregation level of foraging fish species. The difference in aggregation of the seabird's prey may play an important role in determining the availability of fish to bird species with a range of foraging techniques.

The continuous oceanographic data (from the *Pelagia* 2003 cruise) produced a very detailed 'snapshot' of the water column characteristics underneath foraging birds. Therefore we investigated the differences in water column characteristics that the three species of seabirds (Guillemots, Kittiwakes and Gannets) selected to forage in. The mean and standard error of a range of physical and biological characteristics are calculated from the locations of all foraging birds of each species observed during the transect surveys on the Pelagia 2003 cruise (Table 7.2.1). The results of this analysis show that indeed the mixing properties (as indicated by stratification, i.e. the differences between the top and bottom of the water column, using either temperature or density differences) of the water column in which different species feed were significantly different. Gannets were found foraging in the most stratified water, while Kittiwakes used water that was less stratified than that of the Gannets, but more so than the water columns over which Guillemots mainly foraged.

Table 7.2.1. The means (± SE) for water column attributes of locations where seabirds were found foraging across the study area during the June 2003 RV Pelagia survey. The physical and biological data is derived from scanfish data in 5-min bins, corresponding with the 5-min binned bird observations. Means which are significantly different between all three species (one-way ANOVA, S-Plus) are marked with an asterisk (*).

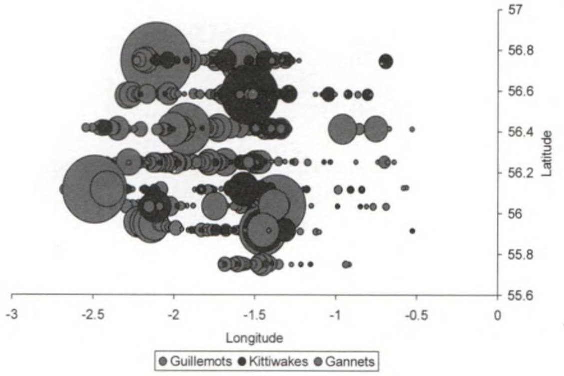
Physical parameter	Guillemot (n=351)	Kittiwake (n=142)	Gannet (n=49)
SST	11.7 ± 0.03*	11.9 ± 0.05*	12.4 ± 0.09*
BT	8.7 ± 0.01*	8.6 ± 0.02*	8.4 ± 0.03*
Difference in temperature	3.0 ± 0.04*	3.3 ± 0.06*	3.9 ± 0.11*
SSS	34.47 ± 0.011	34.55 ± 0.015	34.62 ± 0.025
BS	34.71 ± 0.006	34.77 ± 0.010	34.85 ± 0.018
Stratification ± difference in density	0.71 ± 0.011*	0.75 ± 0.015*	0.88 ± 0.024*
CHL max	0.282 ± 0.015	0.255 ± 0.007	0.243 ± 0.013
Depth of food max	14.2 ± 0.22*	14.8 ± 0.32*	17.6 ± 0.76*
Top of pycnocline	5.7 ± 0.15	6.0 ± 0.23	7.8 ± 0.51
Bottom of pycnocline	22.8 ± 0.40	22.9 ± 0.54	25.9 ± 0.77
Gradient of pycnocline	0.056 ± 0.004	0.055 ± 0.002	0.056 ± 0.003
Maximum Depth	47.9 ± 0.44*	50.8 ± 0.63*	54.7 ± 1.15*

Using this information on what numerical value of stratification (note that this will be particular to the 2003 data as the level of stratification at any given time is weather dependant) is important to the individual bird species. We can now proceed to define the regions of study area in terms of the water column characteristics that the study species appear to use. The following definitions of the regions are used in the following analysis.

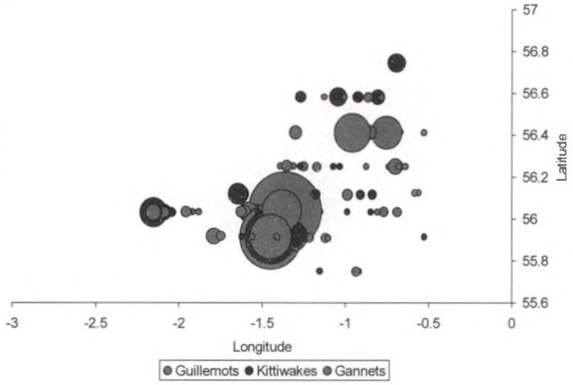
- **Offshore Stratified**: Difference in top – bottom temperatures is ≥ 3.8°C
- **Well mixed** (shallow and deep): Difference in top – bottom temperatures is ≤ 2.0°C (note that is called well mixed in a relative sense as compared to the remainder of the study area)
- **Inner Bank**: Difference in top – bottom temperatures is ≥ 2 & < 3.1°C, with SSS (sea surface salinity) > 34.40 PSS -78
- **Outer Bank**: Difference in top – bottom temperatures is ≥ 3.1 < 3.8°C, with SSS (sea surface salinity) > 34.40 PSS -78
- **Freshwater influenced**: SSS (sea surface salinity) < 34.40 PSS –78

Figures (7.2.1-6) show the spatial results in terms of numbers of birds found foraging within regions defined by these physical characteristics. The regions defined with the 2003 'snapshot' data correspond very well to the static regions defined in Chapter 3 (Fig. 3.2.8). The numbers and percentage of birds of each species found foraging in each region is presented in Table 7.2.2. Guillemots were relatively evenly distributed across the regions, but were most abundant in the Inner Bank region. Nearly half of all Kittiwakes seen foraging were observed within the Outer Bank region and two thirds of all Gannets were found in the Offshore stratified region. This separation of bird species determined mainly by the difference in stratification (using top and bottom temperature differences) indicates that their foraging habitat can be defined using rather straightforward and predictable physical characteristic of the water column. Within the Freshwater

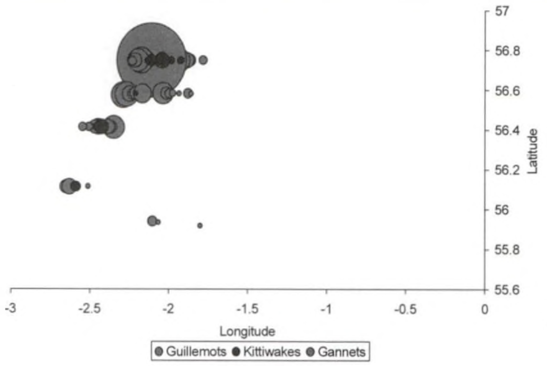
All foraging birds



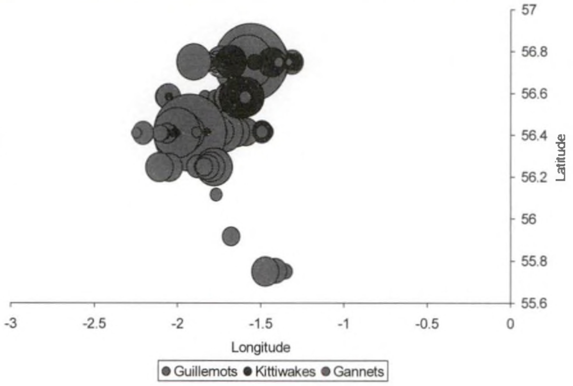
Foraging birds in water with top-bottom temperature difference of ? 3.8°C
Corresponds to offshore stratified region



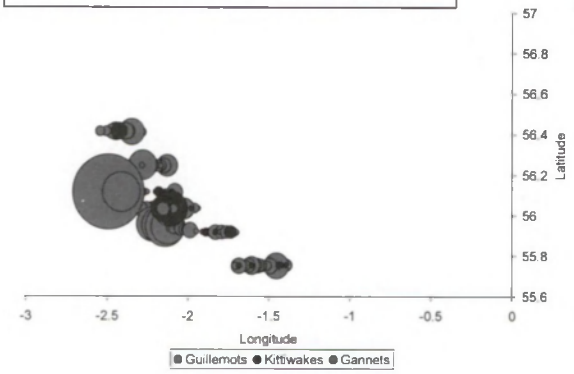
Foraging birds in water with top– bottom temperature difference of ?2.0°C
Corresponds to Well mixed region



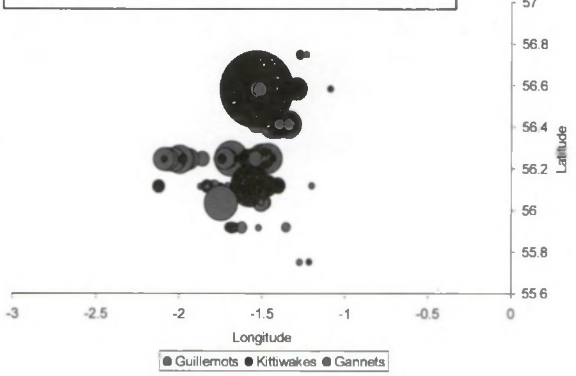
Foraging birds in water with top– bottom temperature difference of > 2.0 & < 3.1°C
Corresponds to Inner Bank region



Foraging birds in surface water with sea surface salinity values < 34.40 (PSS-78)
Corresponds to Freshwater influenced region



Foraging birds in water with top– bottom temperature difference of ? 3.1 & < 3.8°C
Corresponds to Outer Bank region



Figures 7.2.1-6 Spatial results in terms of numbers of birds found foraging within regions defined by physical characteristics. The regions defined with the 2003 'snapshot' data correspond very well to the static regions defined in Chapter 3 (Fig. 3.2.8).

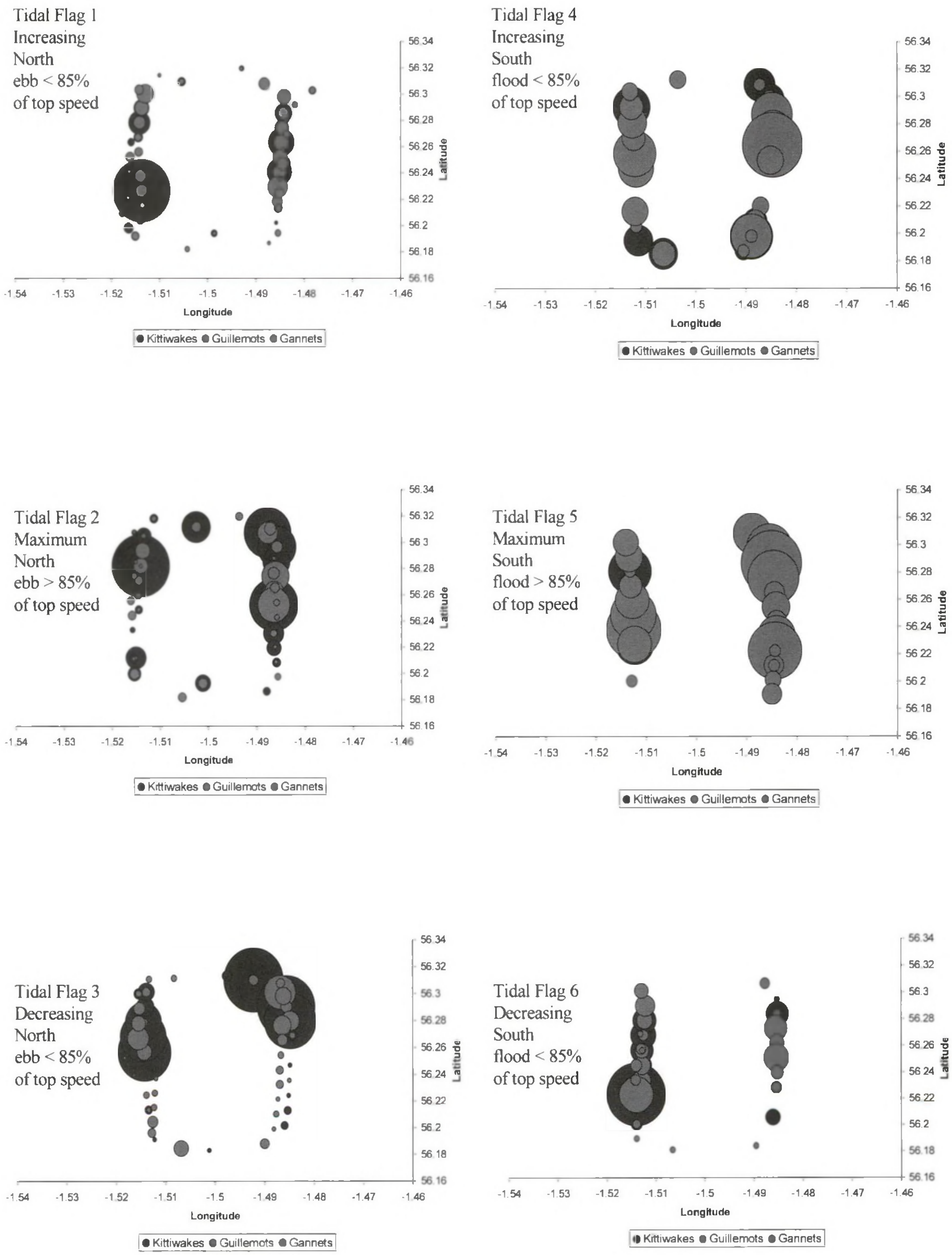


Fig. 7.3.1-6. The number and location of foraging Kittiwakes, swimming Guillemots and diving Gannets found per 5 minute observation during each of six tidal phases of mini-survey #1, June 2003, RV Pelagia survey.

influenced region, even with the additional stratification differences driven by the presence of fresh water, the same difference in top and bottom temperatures still separates species with 77% and 95% of Kittiwakes and Gannets (respectively) being found in locations with a temperature difference of greater than 3.1°C. In those same locations only 32% of the total number of Guillemots within the Freshwater influenced region are present.

Table 7.2.2. The total abundance and percentage of foraging birds found within the different regions of the study area.

	Guillemot (n=3423)	Kittiwake (n=921)	Gannet (n=344)
Well mixed	627 (18.3%)	31 (3.4 %)	0 (0.0%)
Inner Bank	1241 (36.3%)	172 (18.7%)	14 (4.1%)
Outer Bank	553 (16.2%)	402 (43.6%)	57 (16.6%)
Offshore stratified	357 (10.4%)	202 (21.9%)	231 (67.2%)
Freshwater influenced	645 (18.8%)	114 (12.4%)	42 (12.2%)

It is clear that on both large (10s of km) and small (<10km) spatial scales, Kittiwakes were foraging in more stratified water than Guillemots. The mechanism behind this need for more stratified water is probably that Kittiwakes depend upon the presence of internal wave movement to bring their prey closer to the surface (more on that in section 7.3 on foraging and tides). The need for more stratified water implies that Kittiwakes are more limited in the locations in which they can forage than Guillemots and at times of greater mixing (i.e. very windy weather, spring tides) they may have to fly greater distances to deeper water where stratification is more likely to be present. Guillemots were found to be able to exploit a greater range of water mass characteristics but do not select to forage in water that is strongly stratified. In this study area their preferred water column characteristics are found closer to the Isle of May colony than the strongly stratified water masses which occur seaward of the Shallow sea front. Gannets preferentially foraged in the strongly stratified waters seaward of the Shallow sea front.

7.3 Tidal influences on seabird foraging performance

Beth Scott

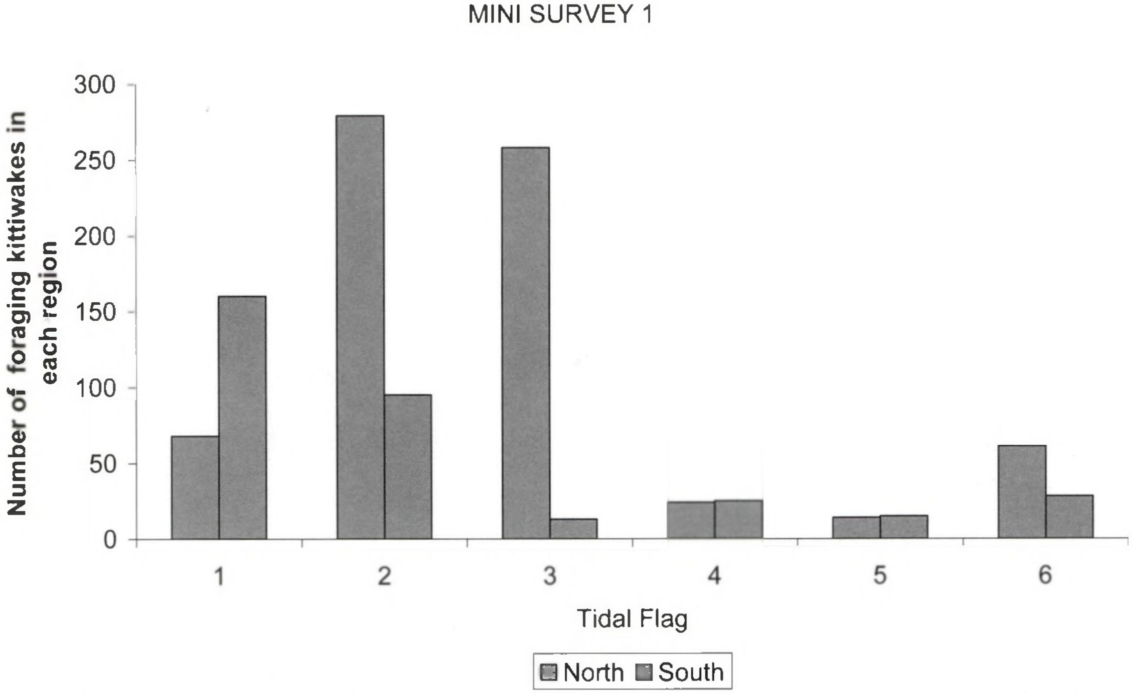
Data from both the mini-surveys and the transects steamed during the 2003 RV *Pelagia* survey (see Chapters 1.3-1.5 for details) were used are used to answer the question if the phase of the tide might have any clear influence on the feeding behaviour and location of feeding of different bird species. The sampling units used in this analysis were the bird observational data recorded in five-minute intervals and the physical oceanographic data used were therefore based on means of the important characteristics from the same time intervals. Within an area in which birds are found foraging, the speed and direction of the tide can alter the physical characteristics of the water column in which the birds are feeding. A case example of the temporal-spatial changes in foraging habitat was done using the mean and variance of the depth of the top of the pycnocline within mini survey #1 at six different phases of the tide (see Chapter 3 for description of the 6 tidal phases used).

To determine whether the speed of the tidal current influenced the number of foraging birds, we formulated GLM of the number of foraging birds recorded per 5-min observation period in relation to tidal stages. We used Poisson error and a log link and used *F*-test to test the influence of tidal phase in order to correct for the overdispersion in the data (Crawley 2003). Fitted values are presented. In a second analysis taking into account overdispersion, we fitted Generalized Linear Models with a log-link but used quasi-likelihood and assumed that variance scaled to the square of the mean).

The information from three mini-surveys were tested separately as the three areas chosen for these 25 hour repeated mini-survey transects represented different types of foraging areas. Mini survey #1, performed in the N→S direction, was sampling from an area with a relatively sharp rise in the topography from North to South. Mini survey #2, performed in the E→W direction, was sampling from an area with a relatively sharp rise in the topography from East-West. Mini survey #3, performed in the N→S direction, was sampling from an area that had relatively little change in depth of topography but was considered to be the along the North-South axis of the Shallow sea front. Only the 5-min observations with one or more foraging birds were included in the analysis to judge the effect of tide across transects. This was done because of the confounding effect of location. In other words: what does what does a count of zero mean when crossing through different habitats? To avoid attributing a lack of birds observed with a lack of bird foraging due to the tidal phase we only retained those observations where foraging by the species was occurring. This means we can be confident that for a given tidal phase the model will be testing whether the mean number of birds seen is related to tidal phase rather than a lack of foraging habitat.

Temporal and spatial movement of foraging location of Kittiwakes

There is an obvious temporal effect on the location of Kittiwakes foraging during mini-survey #1; see Fig. 7.3.1-6 for the locations and abundance of the 3 different species foraging during the 6 different phases of the tide. The majority of Kittiwakes (68%) are seen foraging in the Northern half of the survey area (defined as north of 56°25'N). The greatest change in topography occurs in this region with depths increasing and decreasing from 65 to 45m over a hill. In the southern half of the survey the topography is relatively flat at approximately 60 meters (Chapter 3). Within the survey area, over the six hour duration of the tidal currents in either the northerly or southerly direction, at a given point (marked by a distinct value of bottom density), the water column can be advected up to 5 km. The birds prey may be associated with either the bottom topography or the water column. If prey is only associated with the topography one would assume that the birds should maintain a foraging location over the prey that is constant in space. If however the prey is associated with the water column characteristics the forging birds should move with the water column as the tidal currents move it (approximately in this area) north or south. However the results of the changes in the distribution of the Kittiwakes suggest that it there is both an association with topography and with water column characteristics.



F

Fig. *7.3.7. The total number of foraging Kittiwakes per tidal phase in either the northern half (north of 56°25N) or southern half of the survey region, June 2003, RV Pelagia survey.*

Kittiwakes favoured the northern end of the survey area and when the tidal current was flowing northward (ebbing; Fig. 7.3.7). However, Kittiwakes also seemed to range into the southern area when the top of the pycnocline was shallower in the southern region than the northern region (Fig. 7.3.8 for mean depth of top of pycnocline). Looking at the depth of the top of the pycnocline, Kittiwakes may have been benefiting from the presence of internal waves. When the mean depth of the pycnocline either being shallower, or with the variance increased with the formation of internal waves, prey may be brought closer to the surface. One would expect that the largest internal waves (those with the highest amplitude) are produced as the tidal current starts to decrease from maximum values (Tidal flag 3 and 6), and note that the tidal flow needs to be flowing off a topographic bank to generate the waves. Some internal wave action could also begin to be present during the end of the 2-h period of maximum tidal speed (Tidal flags 2 and 5). We did find the expected shallower pycnocline depth in the expected tidal phases in the northern end of the study and during the ebb tides, but not in the southern end, nor in the flood tides. This suggests that the phenomenon may not only be driven by tidal speed, but by direction of the tidal current over the change in slope of bottom topography and that the foraging of Kittiwakes may be affected by a combination of tidal speed and local topography.

The observed phasing of the foraging is a potentially important result as it indicates that the favoured use of a particular phase of the tide by a species that is constrained to foraging in the surface waters can be at different phases of the tide in regions with very different topography, (i.e. regions with change in slope at different angles to the tidal current). Further studies are required to provide more evidence that internal wave action drives the foraging opportunities.

Tidal phase effect on the foraging of Kittiwakes, Guillemots and Gannets

The fitted mean values of the observed number of birds foraging are compared to the different tidal phases in each of the three different Mini Surveys in Fig. 7.3.9. There are differences in foraging abundances between the surveys with Mini Survey 3 (the location of the Shallow Sea front) being the an area rich in feeding Kittiwakes and Gannets, while Guillemots predominated in the area covered by mini survey #2. Kittiwakes and Gannets responded significantly different at various tidal phases (Table 7.3.1). Decreasing tidal speed during the ebb were the phases mostly used by Kittiwakes and

Gannets targeting the maximal current speeds on both the ebb and flood tides in their preferred foraging region of the Shallow sea front. Guillemots showed almost no difference in foraging abundance with tidal phase, except in mini survey #3 where they were significantly more abundant at the decreasing ebb flow.

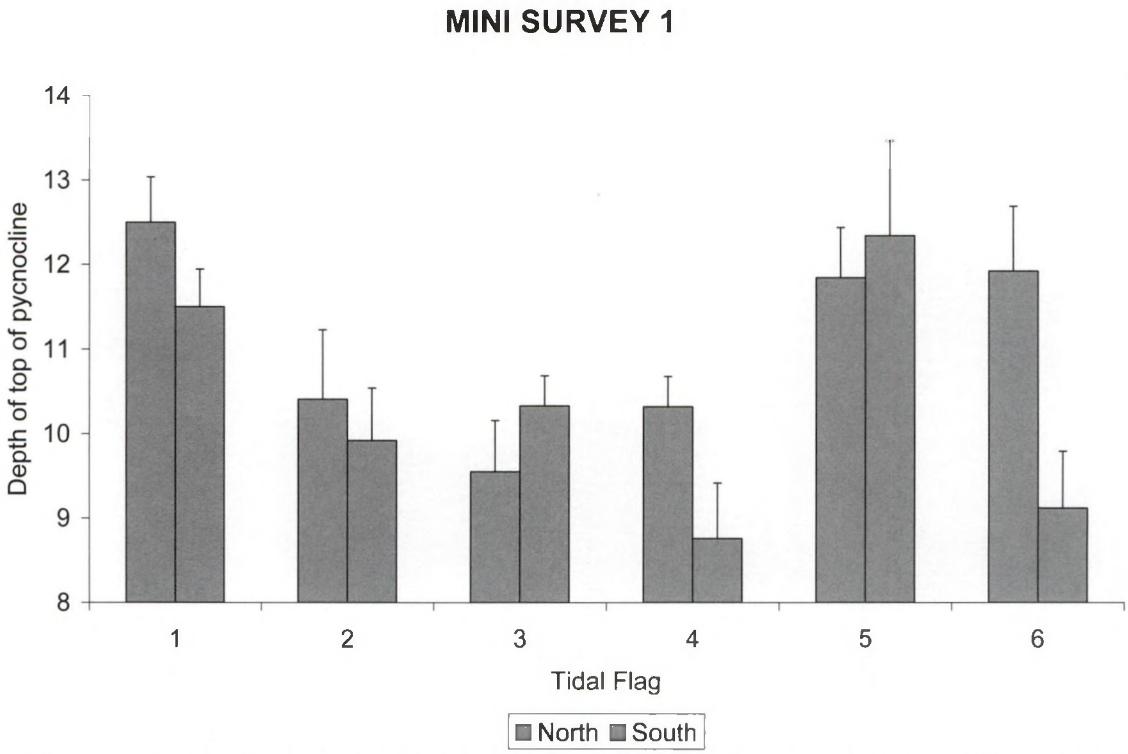


Fig. 7.3.8. The mean height (and standard error) of the depth of the top of the pycnocline in either the northern half (north of 56°25'N) or southern half of the survey region, June 2003, RV Pelagia survey.

Table 7.3.1 The results of the analysis (GLM Poisson and GLM with a log-link and a quasi-likelihood) to determined whether the inclusion of tidal phase helped explain the variance in the fitted mean number of birds foraging. Those models with significant differences in predicting the number of birds foraging due to tidal phase can be due to a significant difference between any two different tidal phases. For comparisons across tidal phases within the regions see Figs *7.3.9-10.*

Species	Kittiwake (foraging)		Guillemot (swimming)		Gannet (Diving)	
Region	GLM Poisson	GLM Quasi	GLM Poisson	GLM Quasi	GLM Poisson	GLM Quasi
Mini 1	*P* =0.02	*P* =0.001	*ns*	*ns*	*P* <0.001	*P* <0.001
Mini 2	*ns*	*P* <0.001	*P* <0.001	*P* <0.001	*P* <0.001	*P* <0.001
Mini 3	*P* =0.007	*P* <0.001	*ns*	*ns*	*ns*	*P* <0.001
Transects	*P* =0.02	*P* <0.001	*P* =0.02	*P* =0.002	*ns*	*ns*

The same analytical approach for the mini surveys was applied to the observations of foraging birds throughout the primary study area on all transects. The results show that for fitted mean number of Kittiwakes and Guillemots is significantly influenced by the phase of the tide but that the mean number of Gannets is not (Table 7.3.1). The Guillemots show a preference for the flood (current flowing from the North) tide. However, as the transects cut across all the different habitat types (see Chapter 7.2) and given the interaction between location and tidal phase that we found, it is not surprising that a clear signal is not emerging.

The speed and direction of the tidal currents appeared to influence the number of birds foraging. This may be because tidal currents are important forcing factors in the aggregation and movement of prey, especially in the case of very constrained predators. However, it may be the combination of local topography and tidal current which determines the exact conditions in which prey are aggregated or influenced in such a way as to be more easily predated upon. As these conditions are dependant on local attributes it is very difficult to generalise these findings over larger feeding areas. Suggestions that individual seabirds tend to specialise on certain conditions and study results demonstrating foraging area fidelity (i.e. Irons 1998) become quite understandable. Seabirds are likely to enhance their foraging efficiency by learning and remembering where and when they were successful and to use that knowledge to find prey on future trips.

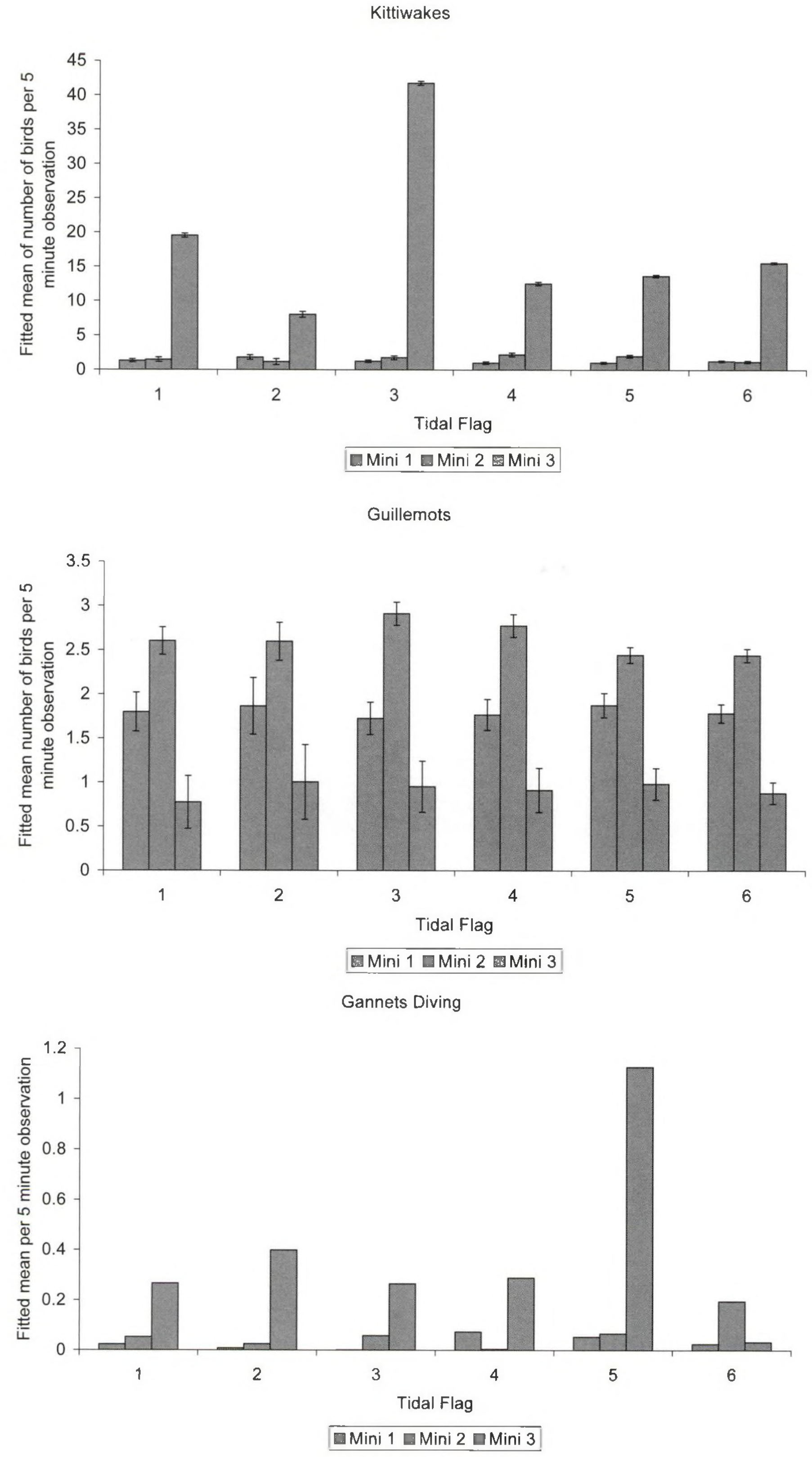


Fig. 7.3.9. *Fitted means ± 2SE of the observed number of birds per tidal flag in each of three mini surveys. (a) Kittiwake, (b) Guillemot, (c) Gannet, June 2003, RV Pelagia survey.*

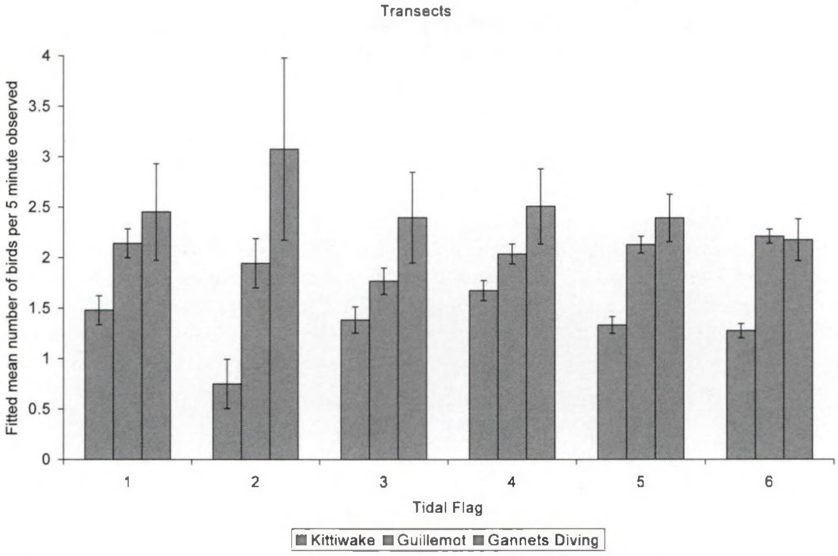


Fig. *7.3.10. Fitted means ± 2SE of the observed number of birds per tidal flag across all transects sailed, June 2003, RV Pelagia.*

7.4. Impact of ocean physics on North Sea seabird prey

Simon Greenstreet, Eric Armstrong, Helen Fraser, Gayle Holland & Iain Gibb

Individual maps showing distributions of the total sandeel, herring and sprat populations in each year, as well as distributions of the individual age groups of each species, are given in Appendix 4. Acoustic data are presented as contour maps interpolating the mean density values calculated for each 5' latitude by 10' longitude rectangle in the study area, as well as bubble plots indicating variation in density calculated for each individual 5min survey period. Demersal trawl data are presented as bubble plots indicating the density of eaqch species/age group at each trawl station in each year. Grab survey data are presented as bubble plots indication grab sample density at each station in each year. Here we focus on the acoustic survey data summarising variation in the density of each species/age group in broad habitat zones defined by variation in bathymetry and hydrography in the area (Fig. 3.2.8).

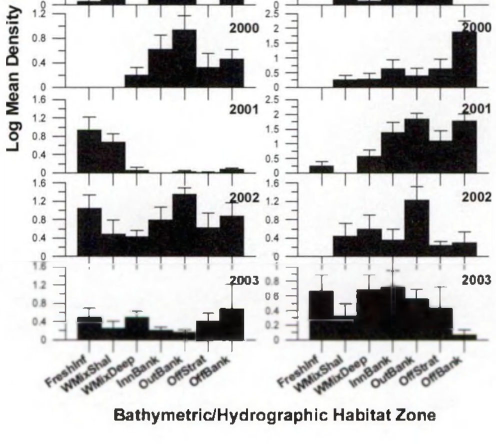


Fig. 7.4.1. Variation in the Log (x+1) mean density of 0 and 1+ sandeels in seven bathymetric/hydrographic habitat zones in each year. Error bars show plus one SE. Habitat zoning is indicated in Fig. 3.2.8. FreshInf is the Freshwater Influenced zone, WmixShal is the Well Mixed Shallow zone, WMixDeep is the Well Mixed Deep zone, InnBank is the Inner Bank zone, OutBank is the Outer Bank zone, OffStrat is the Offshore Stratified Zone and OffBank is the Offshore Bank zone.

Sandeels *Ammodytes marinus*

The variation in the mean density of 0 and 1+ sandeels across the seven habitat zones in each year is shown in Fig. 7.4.1. 0 group sandeels were relatively abundant across all seven habitat zones in 1997, 2002 and 2003. Significant differences in habitat use by 0 group sandeels were only observed in 1999 (ANOVA, $P = 0.032$), 2000 (ANOVA, $P = 0.002$) and 2001 (ANOVA, $P = 0.000$), but preferred choice of habitat differed markedly in these years. Significant habitat selection by 1+ group sandeels was apparent only in four years: 1998 (ANOVA, $P = 0.000$), 2000 (ANOVA, $P = 0.003$), 2001 (ANOVA, $P = 0.000$), and 2002 (ANOVA, $P = 0.026$). In 1998 and 2000 1+ group sandeel densities were much higher in the Offshore Bank zone than in any other. In these two years, variation in the density of sandeels across the different habitat zones was significantly related to variation in the degree of temperature stratification in the water column in each zone (Fig. 7.4.2). In 2001 both the Outer Bank and Inner Bank zones held high 1+ group sandeel densities as well as the Offshore Bank zone. In 2002 habitat use by 1 group sandeels was heavily biased towards the Outer Bank zone. In the remaining three years habitat use by 1+ sandeels was more ubiquitous. Only in 1998 and 2000 was variation in the density of either 0 group or 1+ group related to variation in the temperature stratification across the different habitat zones (Fig. 7.4.1). Between year variation in water column temperature stratification in each of the habitat zones had no significant influence on the density of either 0 or 1+ group sandeels present in each year.

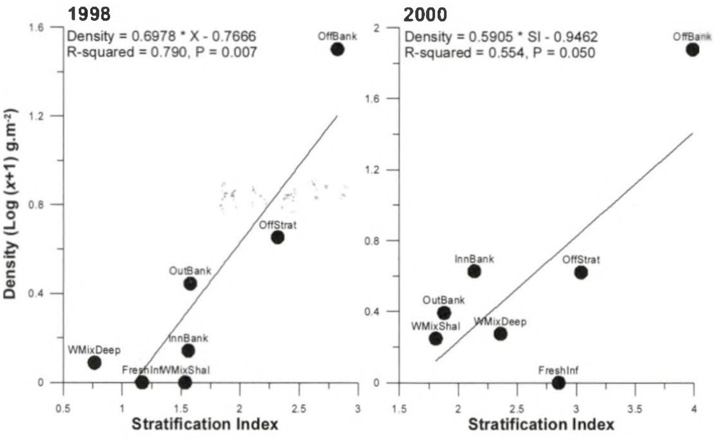


Figure 7.4.2. Effect of variation in the degree of water column stratification (index is surface temperature – bottom temperature) on the density of 1+ group sandeels in the different habitat zones in 1998 and 2000.

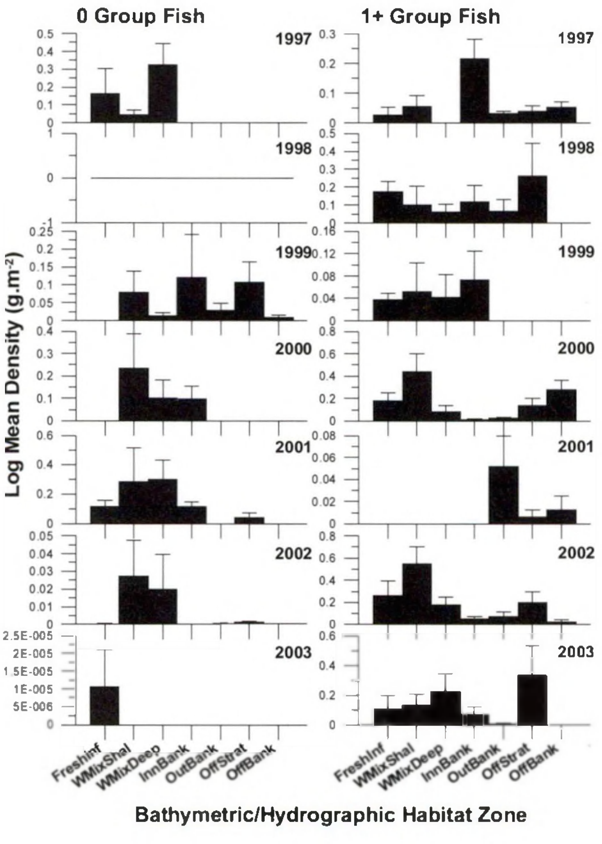


Fig. 7.4.3. Variation in the Log (x+1) mean density of 0 and 1+ herring in seven bathymetric/hydrographic habitat zones in each year. Error bars show plus one SE. Habitat zoning is indicated in Fig. 4.3.3.1. FreshInf is the Freshwater Influenced zone, WmixShal is the Well Mixed Shallow zone, WMixDeep is the Well Mixed Deep zone, InnBank is the Inner Bank zone, OutBank is the Outer Bank zone, OffStrat is the Offshore Stratified Zone and OffBank is the Offshore Bank zone.

Herring *Clupea harengus*

The variation in the mean density of 0 and 1+ herring across the seven habitat zones in each year is shown in Fig. 7.4.3. Significant habitat zone selection by 0 group herring was only evident in 1997 (ANOVA, $P = 0.047$), when they were restricted, in relatively high densities, to the three inshore habitat zones: Well Mixed Shallow, Well Mixed Deep, and Freshwater Influenced. Habitat use by 1+ group herring differed significantly in 1997 (ANOVA, $P = 0.001$), 2000 (ANOVA, $P = 0.004$), and 2002 (ANOVA, $P = 0.005$). In 1997 1+ group herring appeared to favour the Inner Bank zone. Habitat use by 1+ herring was similar in both 2000 and 2002, with the Well Mixed Shallow and Offshore Stratified or Offshore Bank (also stratified in most years) zones being preferred. In 2002, the distribution of both 0 group and 1+ group herring appeared to be influenced by variation in water column stratification in the different habitat zones (Fig. 7.4.4). Between year variation in water column temperature stratification in each of the habitat zones had no significant influence on the density of either 0 or 1+ group herring present in each year.

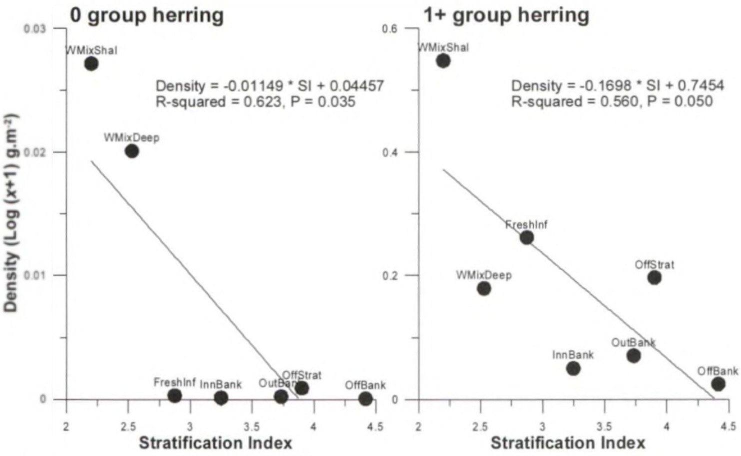


Figure 7.4.6. Effect of variation in the degree of water column stratification (index is surface temperature – bottom temperature) on the density of 0 and 1+ group herring in the different habitat zones in 2002.

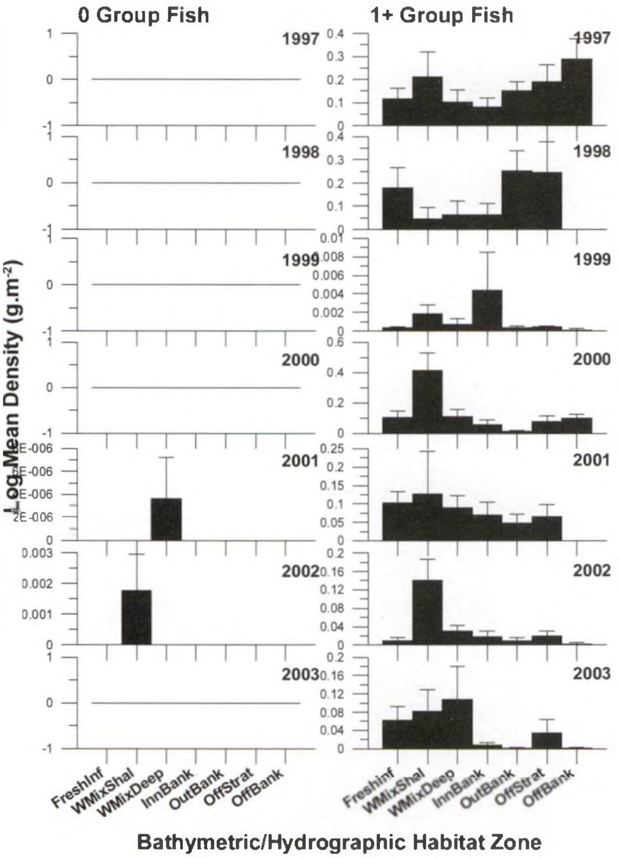


Fig. 7.4.5. Variation in the Log (x+1) mean density of 0 and 1+ sprats in seven bathymetric/hydrographic habitat zones in each year. Error bars show plus one SE. Habitat zoning is indicated in Fig. 4.3.3.1. FreshInf is the Freshwater Influenced zone, WmixShal is the Well Mixed Shallow zone, WMixDeep is the Well Mixed Deep zone, InnBank is the Inner Bank zone, OutBank is the Outer Bank zone, OffStrat is the Offshore Stratified Zone and OffBank is the Offshore Bank zone.

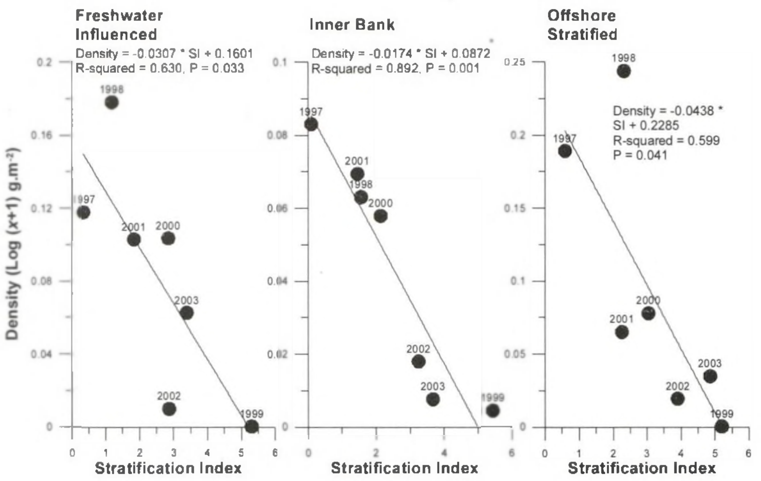


Figure 7.4.6. The effect of between year variation in the degree of stratification in the water column (surface temperature – bottom temperature) in three habitat zones on the density of 1+ group sprats occupying each zone in each year.

Sprat *Sprattus sprattus*

The variation in the mean density of 0 and 1+ sprats across the seven habitat zones in each year is shown in Fig. 7.4.5. 0 group sprats were absent in most years. In 2001 and 2002 when they were present, densities were so low in the zones they occupied to register any significant difference in habitat zone use. 1+ group sprats displayed significant preference for the Well Mixed Shallow zone in 2000 (ANOVA, $P = 0.000$) and 2002 (ANOVA, $P = 0.000$). In any particular year, variation in the degree of water column stratification across the different habitat zones had no significant influence on the density of sprats in each of the habitat zones. However, in three of the habitats, the Freshwater Influenced, Inner Bank, and Offshore Stratified zones, between year variation in 1+ group sprats was significantly affected by between year variation in the level of stratification (Fig. 7.4.6).

7.5. Seabird distribution versus fish

Simon Greenstreet, Helen Fraser and Gayle Holland

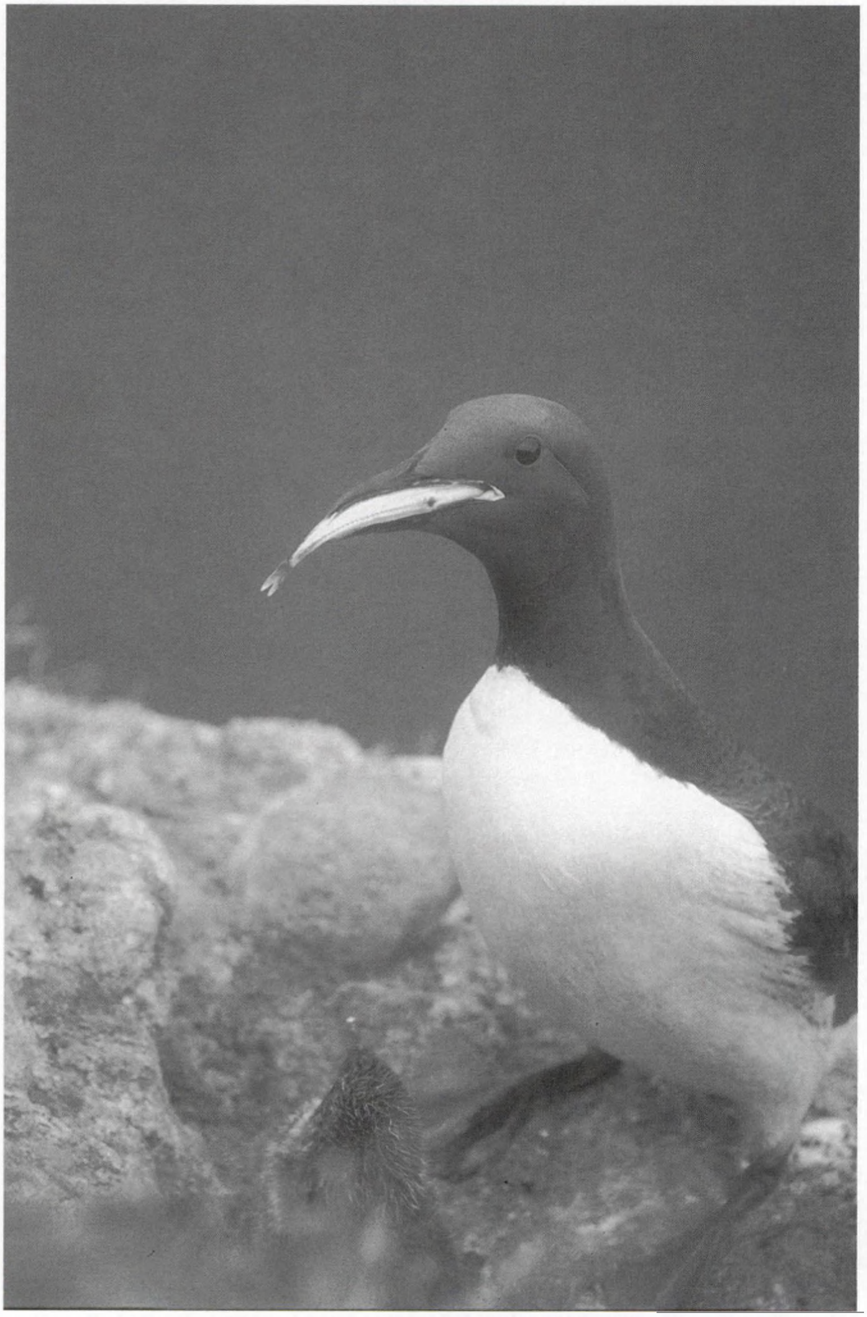
Seabirds were surveyed at sea from the FRV Clupea during the seabird breeding seasons of 1997 to 2003. This section focuses on annual variation off the Firth of Forth, on data collected late May to early July and on the relation between seabird distribution and their (potential) prey studied simultaneously. A long series of maps is available for consultation, comparing densities of each of six sandeel specialist seabirds as bubble plots (density in each 5 min survey period) plotted over contour plots of the density of sandeels, Herring and Sprat in each 5' latitude by 10' longitude rectangle as determined by acoustic survey (Figure 4.6.1.1a-f to 4.6.1.6a-f in the Appendix 5).

Large numbers of Guillemots on the water were associated with concentrations of **sandeels** on the Wee Bankie in 1997, Berwick's Bank in 2000, and Marr Bank in 2002. In 2001, when sandeel densities on the eastern edge of the Wee Bankie were extremely high, Guillemots appeared to concentrated around the periphery of a "patch", on the western edge of the bank, closest to the colony. In 1999, sandeel densities were very low, and Guillemots appeared uninterested in the highest density patch of sandeels on the Wee Bankie. In 1998, when sandeel biomass in the area was relatively low and patch densities at intermediate levels, the highest concentrations of sandeels were located on the Berwick's Bank, far from the Isle of May, and few Guillemots were observed there. All in all, there was no obvious close link between the generalised distributions of Guillemots (and any of the other auks) and the distribution of sandeels. Large numbers of Kittiwakes were observed on the water around the Isle of May in 1997, a year when sandeel densities in the study area were generally low, but when a comparatively high proportion of the sandeel population in the water column was located close to the island. Kittiwakes on the water were associated with high densities of sandeels on the Berwick's Bank in 1998, 2000 and 2003, and on the Marr Bank in 2002. The situation for Gannets observed on the water was similar to the Kittiwakes; high numbers were associated with sandeels near the Isle of May in 1997, on the Berwick's Bank in 1998 and 2000, and on the Marr Bank in 2002. Shags on the water were only seen near the Isle of May. Sandeels were detected here in most years, but at relatively low densities. Only in 1997 did the densities of sandeels here compare favourably with densities elsewhere in the study area.

Herring generally had a coastal distribution, being found in the Firth of Forth, around Fifeness, and in St Andrews Bay. Guillemots were always present in these areas, but not in particularly high numbers. In 1998, when large shoals of Herring were located in the south of the study area, relatively large numbers of Guillemots were also present Distributions of Kittiwakes on the water showed little correspondence with the distribution of Herring. Gannets, however, did tend to concentrate in areas where Herring were present, particularly in the Firth of Forth in 1997, off Berwick's Bank in 1998, and off Fifeness in 2000 and 2001. Shags on the water showed little affinity to areas where Herring were present.

In 1999, 2000, and 2002 the distributions of **Sprats** and Herring were very similar. In 1997, however, Sprats were concentrated in St Andrew's Bay, where few Herring were detected, whilst few Sprats were observed in the Firth of Forth, where a major Herring hot-spot was located. Relatively large numbers of Guillemots, Razorbills and Kittiwakes were recorded in St Andrew's Bay associated with these Sprats. In 1998 high densities of Sprats were found in the south of the study area immediately west of Berwick' Bank, coinciding with a major Herring concentration. But a second Sprat hot-spot was also located closer inshore to the southwest of the Wee Bankie and relatively high numbers of Guillemots, Razorbills, Puffins and Kittiwakes were associated with this.

In conclusion, no clear absolute relationship between the density of any seabird species and the density of either sandeels, Herring or Sprats could be determined. High densities of each of the major sandeel, or small pelagic fish, predators could be linked to patches of one or other, or all three, of the prey species.



Common Guillemot Uria aalge with Sprat Sprattus sprattus (C.J. Camphuysen)

Chapter 8 Interannual scale hydrography, fish and seabird interactions

One of the main aims of the IMPRESS project was the integration of measures of seabird performance with area and year-specific hydrographic data and prey availability in order to elucidate some of the mechanisms underlying trophic interactions in the ecosystem. Information on oceanography is given in Chapter 3, and on fish abundance in Chapter 4, and on seabird performance at sea and in the colonies in Chapter 5. Here we bring the three sets of material together, with emphasis on interannual variability.

8.1 Recent seabird population trends and reproductive success

To summarise the breeding population trends of the study species (Chapter 5.2), for Northern Gannets, a population increase was assumed (regular counts at 10 year intervals only) and the reproductive success was measured only in 2002 and 2003 (0.6-0.7 chicks pair^{-1}). Shag breeding numbers (*n* nests) were generally increasing, but with a dip in 1999 when many adults did not breed, and breeding success was consistently higher during 2000-2003 than in the three earlier years. The Kittiwake population gradually declined, while the breeding success was highly variable (lower in 1997-1999 than in any of the more recent years). Guillemot numbers increased while the fledging success was variable but declined overall (1999 and 2001-2003 were the lowest values). For the birds nesting on the Isle of May, in terms of reproductive success, 1999 was the worst breeding season recorded between 1997 and 2003. Shags were very late or skipped breeding in that year, Kittiwakes bred late and experienced the worst year after 1998, Guillemots bred late and had the second worst year after 2001. Guillemots produced unusually few chicks in 2001 (lowest recorded), and had a particularly bad year compared with the other two species. Both 1998 and 1999 were seasons when most species bred late and in 1998 only Guillemots reproduced as normal.

Table 8.1.1. Summary of breeding population trends, reproductive success and timing of seabirds nesting on the Isle of May, 1997-2003 (from Chapter 5.2).

		Shag	Kittiwake	Guillemot
Breeding population (nests or pairs)		increase	decline	increase
Breeding success (chicks pair^{-1})	1997-1999	0.3-1.0	0.0-0.4	0.65-0.78
	2000-2003	1.5-1.8	0.4-1.0	0.62-0.73
	low	1999	1998, 1999	1999, 2001
	high	2003	2000	1997
First eggs layed	earliest	1998	2000	2003
	latest	1999	2001	1998
Median eggs layed	earliest	1997		1997
	latest	1999		1998
First fledged chicks	earliest	1998	2000	2003
	latest	1999	2001	1998
Median fledged chicks	earliest	1997		1997
	latest	1999		1998

The year 2004 was a season when no fieldwork under *IMPRESS* was scheduled. However, in response to the concerns raised in the NW North Sea, notably in Shetland (Heubeck & Shaw 2004), that breeding was delayed and that breeding success would be low again, a ship-based survey was scheduled to be able to evaluate any differences with previous seasons. It is of interest that in 2004 observations were done on breeding success of the study species and other seabirds on several study plots including the Isle of May. A very poor breeding season was reported for Shags (as bad as 1999), all three auks on the Isle of May had a very low success (Guillemot lowest on record, Razorbill second lowest), Kittiwakes reproduced less than the long-term average, and Fulmar production was the lowest ever recorded. These results should be put into the context of a much larger area with the productivity for most species on the nearby Farne Islands for example being the lowest in recent history and sandeel shortages were evident from dietary studies on these islands. Considerable mortality among tern chicks occurred and Shag and Kittiwake breeding success was lower than ever recorded before (Wilson 2004).

Seabird numbers and breeding success in the UK have been monitored at a large number of sites since the late 1980s as part of the Seabird Monitoring Programme of the Nature Conservancy Council (nowadays Joints Nature Conservation Committee; Walsh *et al.* 1990). For the **Shag** in SE Scotland and NE England, a wreck in 1994 resulted in a crash of the breeding population, but between 1994-2002, the percentage annual change amounted to +6.2% and +5.8% respectively. In both areas, breeding numbers in 2003 were again (substantially) higher indicating that these populations were returning to levels recorded prior to the wreck (Mavor *et al.* 2004). Mean breeding success (± SE) at selected colonies within and around the principal study area amounted to 0.92 ± 0.10 chicks fledged per occupied nest between 1986 and 2002 on the Isle of May (17 years of data), 1.32 ± 0.12 on nearby St Abbs Head (13 years of data), and 1.04 ± 0.10 on the Farne Islands (14 years). The comparison shows that the reproductive success on the Isle of May in 1997 and 2000-2003 was well above average and that in 1998 and 1999 was low and very low respectively.

The population of **Kittiwakes** in SE Scotland increased between 1986 and 1989, but has decreased significantly since, at -6.1% per annum. Together with persistent declines since at least the early 1990s in Shetland (1985-2002, -9.9% p.a.), Orkney (1991-2003, -5.8% p.a.), NE England (1992-2003, -3.5% p.a.), and SE England (1995-2003, -14.9% p.a.) it is clear that this species is having difficulties in all regions in the north and east of the British Isles. The mean breeding success (± SE) at selected colonies within and around the principal study area amounted to 0.68 ± 0.09 chicks fledged per apparently occupied nest between 1986 and 2002 on Fowlsheugh (15 years of data), 0.55 ± 0.09 on the Isle of May (17 years of data), 0.94 ± 0.09 at Dunbar (16 years), 0.68 ± 0.08 at St Abbs Head (16 years of data), and 0.92 ± 0.07 on the Farne Islands (16 years). The comparison shows that the reproductive success on the Isle of May was on average a bit lower than in most other areas, which is probably an artefact of the high monitoring intensity at the Isle of May, (catching early failers).

Guillemot numbers in SE Scotland were slightly variable in recent years, but increased significantly by +3.4% between 1986 and 2002. An even more marked increase was found at Farne Islands (+5.2% p.a., 1986-2002). The mean breeding success (± SE) amounted to 0.77 ± 0.02 chicks fledged per site between 1986 and 2002 on the Isle of May (17 years of data), showing that six out of seven recent years (1998-2003, plus 2004) were just or well below the long term mean for the colony. With the 2004 breeding success being the lowest on record, a decline is continued that may lead to a population decline eventually.

8.2 Annual indices for sandeels and other preyfish

Estimates of total biomass **sandeels** (tonnes) within the principal study (Table 8.2.1) area were obtained by calculating the absolute abundance in the sediment from the demersal trawl index and by adding this figure to the absolute abundance in the water column from the acoustic survey (Chapter 4.2 for details). A breakdown of these data per cohort (1+ group and 0 group sandeels) has been presented in Figs. 4.2.6 and 4.2.9. These data were used to estimate the fraction (%) of sandeels available in the water column and in the sediment in each of the years that surveys took place. The results indicate that total sandeel biomass was substantially higher in 2000-2003 (250 000-335 000 tonnes) than in the three earlier years (25 000-89 000 tonnes), and also that a highly variable fraction was available in the water column (ranging from 3% in 1999 to 96% in 1998).

Table 8.2.1 Sandeel abundance estimates from acoustic surveys (biomass, 1000 tonnes), demersal trawls (biomass, tonnes) and grab sampling (densities, n m^{-2}), 1997-2003, plus estimates of total sandeel biomass (tonnes), the fraction (%) available in the water column (see for details Chapter 4.2) and the commercial/(monitoring) catch (tonnes of 1+ group sandeels) in each of the seasons within rectangles 41E7 and 41E8 (Fig. 2.4.2-3)..

	0 group sandeel			1+ group sandeel			Total sandeel		
	Acoustic 1000t	Demersal 1000t		Acoustic 1000t	Demersal 1000t		stock 1000t	estim. % in water column	catch 1000t
1997	15.1	2.8	17.9	3.5	3.8	7.3	25.2	73.8%	13
1998	10.4	0	10.4	47.9	2.4	50.3	60.7	96.1%	38
1999	1.6	34.1	35.7	1.2	52.3	53.5	89.2	3.1%	2
2000	29.0	61.1	90.1	105.4	131.9	237.3	327.4	41.1%	(3)
2001	27.7	12.3	40.0	234.8	61.2	296.0	336.0	78.1%	(5)
2002	91.0	1.5	92.5	111.4	49.2	160.6	253.1	80.0%	(n.d.)
2003	28.0	83.1	111.1	33.8	105.2	139	250.1	24.4%	(n.d.)

Table 8.2.2 Herring and Sprat abundance estimates from acoustic surveys (biomass), 1997-2003 (see for details Chapter 4.2).

	Herring *Clupea harengus*			Sprat *Sprattus sprattus*		
	Total herring tonnes	1+ group tonnes	0 group tonnes	Total sprat tonnes	1+ group tonnes	0 group tonnes
1997	3825	958	2867	2606	2606	0
1998	3173	3173	0	2999	2999	0
1999	1703	474	1229	14	14	0
2000	5843	3763	2081	2468	2468	0
2001	6371	148	6223	1347	1347	0
2002	4910	4820	90	451	448	3
2003	3950	3950	0	647	647	0

Estimates of total biomass **Herring** (tonnes) within the principal study from acoustic surveys (Table 8.2.2) significantly correlated with abundance estimates from demersal trawl surveys in the area (Fig. 4.2.12). Substantially higher biomass estimates were found in the last four seasons (3950-6370 tonnes) than in the earlier years (1700-3800 tonnes), but with

0 group Herring being virtually absent in 1998 and 2003, whereas 1+ group Herring were relatively rare in 1999 (28%) and 2001 (2%). Estimates of total biomass **Sprat** (tonnes) within the principal study from acoustic surveys (not significantly correlated with abundance estimates from demersal trawl surveys in the area, but both techniques indicated that Sprat biomass was relatively low in all years; Chapter 4.2) produced a more variable pattern, always dominated by 1+ group fish. Relatively high biomass was found in 1997, 1998, and 2000 (>2000 tonnes from the acoustic survey), a particularly low stock was found in 1999.

A combination of the prey-fish biomass estimates suggests that 1997 was an exceptionally poor year with a combined estimate of only *c.* 32 000 tonnes of prey fish (Tables 8.2.1-2). Total biomass in 2000-2003 was 8-11 times more than in that poor year. Sandeels dominated the biomass estimates in all years with at least 80% of total prey fish biomass. With regard to the available fraction of sandeels in the water column, 1999 stood out as particularly poor (<3000 tonnes), 2000-2002 as very rich (water column sandeel biomass 48-93x the value for 1999) and the other seasons as moderate years (7-22x the value for 1999). However, the proportion of sandeels present in the water column varied through the season and the outcomes of these surveys depended on their timing relative to the development of spring bloom. The 1999 surveys were relatively late in the season, so that by that time many sandeels had probably finished feeding (particularly 1+, but also 0 group) and were down in the sediment (Chapter 1.5.1, 4; Appendix 4).

8.3 Relationships between annual indices of bird performance and annual oceanographic indices

First we evaluate how the output from the finalised 1- D physical-biological model from 1974-2003 (Chapter 3) could be used in conjunction with the long-term data from seabirds nesting on the Isle of May and to propose mechanisms that might link multiple meteorological conditions and the effect on primary production to higher trophic levels. In particular, we have used the timing of stratification and the spring bloom as possible indicators of sandeel availability. While previous studies have demonstrated statistical relationships between larger-scale oceanographic or climatic variables and seabird performance (e.g. Thompson & Ollason 2001; Frederiksen *et al.* 2004) our approach intends to identify proximate factors that could directly affect seabird prey availability. In a system where experimental manipulation is impossible, this type of model is a promising tool in the search for causal relationships among ecosystem components.

The breeding season is the most energetically demanding part of the seabird life cycle, and a successful outcome is critically dependent on the availability of sufficient amounts of high-quality food. If the initiation of the annual increase in primary production is the driving factor for the emergence of adult sandeels to feed, than the timing and progress of the spring bloom may be important for seabirds targeting sandeels. From the dietary work, the availability of adult sandeels is important in the early stages of the breeding season, during egg laying and incubation (Chapter 5). During chick rearing in June and early July, adult sandeels disappeared out of the diets of both Kittiwakes (abruptly) and Guillemots (gradually), but continued to be utilised by Shags (Chapter 5; Harris & Wanless 1985; Lewis *et al.* 2001). Possible explanations are that adult sandeels spend more time in the sands as the availability of their own food is declining (by this time of the year, primary production is falling rapidly due to the lack of free nutrients for phytoplankton growth; Miller 2004), or that adult seabirds choose to feed their offspring with different prey for other reasons. Note that the results presented in Chapter 5.3 are prey fish delivered to chicks and that the diet of adult breeding individuals may be quite different (Camphuysen 2001; Wilson *et al.* in press). In later phases of chick-rearing, Kittiwakes depended more on 0 group sandeels and occasional other prey species such as Clupeids to feed their chicks. Guillemots had an increasing tendency over time to deliver Clupeids to their offspring. Spring conditions and their effect on the timing of primary production will have influenced the growth and survival and therefore the availability or profitability of 0 group sandeels. Seabird fledging success may thus have been influenced in turn by the timing and location of spring blooms. As such, spring bloom timing could influence several components of breeding success.

Timing of the bloom and seabird breeding success

The breeding success of Kittiwakes and Guillemots nesting on the Isle of May was compared with the timing of the spring bloom and stratification in the Bank and the Shallow Sea Front regions. During 1997-2003, the onset of stratification occurred between 7 April and 30 April (23 d difference between seasons at most) and was very early in 2002 (7 April) and very late in 2001 (30 April) (Table 3.1). Spring bloom (when modelled chlorophyll exceeded 5 mg m^{-3}) lasted between 5.8 (2001) and 7.5 weeks (2000) and commenced between 14 April (2002) and 1 May (2001), or a two-week difference between seasons.

Breeding success of Kittiwakes increased by 0.13 chicks $pair^{-1}$ for every five days delay in timing of the spring bloom (Note that data were available for more years for both the onset of the spring bloom and the breeding success of the birds on the Isle of May; Fig. 8.3.1). Kittiwakes bred thus more successfully in the years when the spring bloom and stratification in either region occurred later, but the variability was considerable. There was no evidence that the effect of date of the spring bloom on breeding success was different in fishing and non fishing years (interaction: $F_{1,16} = 2.40$, $P = 0.14$), but breeding success was 0.66 ± 0.098 (SE) chicks higher in years without fishing than in years with fishing ($F_{1,16} = 44.92$, $P < 0.001$). The final model containing both the effects of spring bloom date and the sandeel fishery explained 74% ($P< 0.001$) of the variance in breeding success. Separating years with or without a fishery, the effect of climate alone explained 56% of the variance in breeding success in years without a fishery and 10% of the variance in years with a fishery. This suggests that important climatic variables are more easily identified in the absence of the confounding effects of a fishery.

Because Kittiwakes are surface feeders and are more dependent on prey being present in the upper water column, this finding leads us to speculate that a later spring bloom increases the availability of prey in the upper water column during the breeding season. We suggest that the mechanism by which this is achieved is through a slowing down in the growth of juvenile sandeels, possibly coupled with a delay in the emergence of adult sandeels. With elevated levels of food occurring relatively late in the season, the trade off between predation and feeding may force fish to take longer to acquire adequate levels of food needed to survive the next winter. Either the slowing of fish growth or the extension of the time window during which sandeels are feeding actively in the water column, could potentially provide an increase in prey availability, especially to surface feeders.

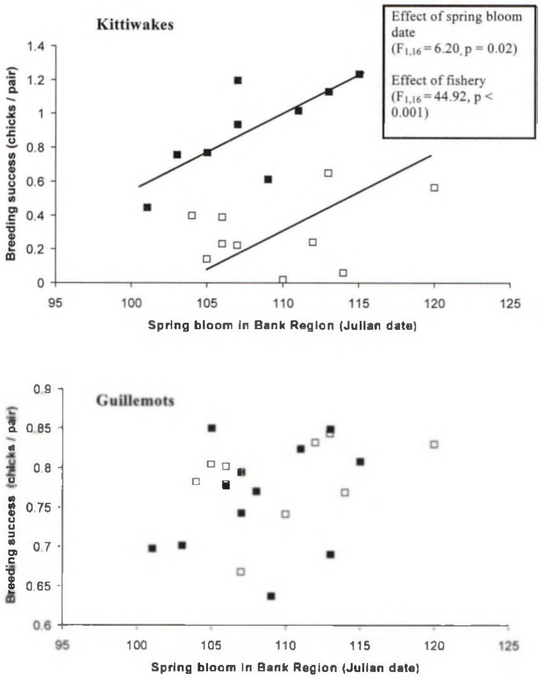


Figure 8.3.1. Breeding success of Kittiwakes (1985-2003; top panel) and Guillemots (1982-2003; bottom panel) on the Isle of May in relation to the start date of the spring bloom in the Bank region as estimated by the 1-D physical-biological model. Years with no commercial fishery for sandeels are represented by filled squares and years with a fishery with open squares.

These results accord well with those of Rindorf *et al.* (2000) who found that breeding success of Isle of May seabirds was higher when sandeel abundance peaked later in the season. Although spring bloom timing here is modelled rather than measured, it is a more proximate and thus a much more interpretable correlate of breeding success than a single weather variable such as sea temperature. Using this biologically meaningful and locally specific index we conclude that, under similar climatic conditions, Kittiwakes suffered an additional reduction in breeding success in years when a commercial sandeel fishery is operating. This approach allows us to separately quantify fishing and climate effects and indicates that the presence of a local sandeel fishery decreases breeding success of Isle of May Kittiwakes by 0.66 chicks pair^{-1} whereas every five day delay in the date of the spring bloom increased breeding success by 0.13 chicks pair^{-1}.

For Guillemots, annual variation in breeding success was not explained by the timing of spring blooms, nor stratification in either oceanographic region or the sandeel fishery (Fig. 8.3.1). One explanation is related to an unexpected outcome of the IMPRESS project: the fairly limited foraging range of Guillemots nesting on the Isle of May, that were found to only just reach the Inner Bank area to forage (Chapter 7.1; Fig. 7.1.5). Another explanation is that Guillemots are pursuit divers and are therefore less constrained in their foraging depths than Kittiwakes (*cf.* Furness & Tasker 2000). Guillemots have access to sandeels in the whole water column (Chapter 5.5) and are probably less likely to encounter food limitation. This would explain why annual variations in breeding success of different species at the same colony utilising similar prey may not be in phase and that Guillemot and Kittiwake breeding success on the Isle of May are not correlated ($r_p = 0.26, P > 0.2$).

Relative timing of the bloom and seabird breeding success

In further investigations into the timing of the bloom and other biologically meaningful indices we found that a high proportion of the variation in the breeding success of all three study species of seabirds can be explained when the date of egg laying (Table 5.2.1) relative to the timing of the bloom (Table 3.1) is taken into account (Table 8.3.2, Fig. 8.3.2a-c). The best model (using AIC) explaining breeding success for Guillemots used the difference in days between the timing of the bloom and the median date of egg laying as the explanatory variable. These results indicate that for both Kittiwakes and Shags there is an interaction between the timing of events and the effect of the fishery.

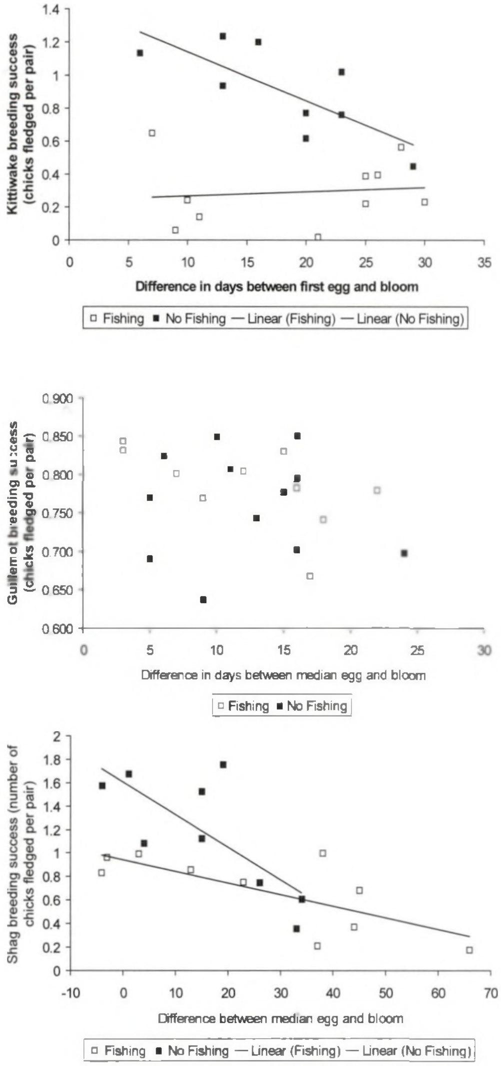


Figure 8.3.2. Breeding success of black-legged Kittiwakes (1985-2003, top panel), common Guillemots (1982-2003, middle panel) and European Shags (1986-2003, bottom panel) on the Isle of May in relation differences in timing between the start date of the bloom and timing of breeding (first egg date, for Kittiwake, median egg date for other two species) in the Bank region as estimated by the 1-D physical-biological model. Years with no commercial fishery for sandeels are represented by filled squares and years with a fishery with open squares.

Table 8.3.2. Best models (AIC) for explaining variance in breeding success due to timing differences between date of egg laying (Table 5.2.1) and date of spring bloom and fishing presence or absence. NA = not available.

Guillemot		Kittiwake		Shag	
1^{st} egg date	Median egg date	1^{st} egg date	Median egg date	1^{st} egg date	Median egg date
ns	med egg – bloom	Fishing 1^{st} egg – bloom Fish*1^{st}egg	NA	Fishing 1^{st} egg – bloom	Fishing med egg – bloom Fish*med
	$r^2 = 0.24$	$r^2 = 0.77$		$r^2 = 0.39$	$r^2 = 0.67$
	$P = 0.02$	$P < 0.001$		$P < 0.02$	$P < 0.001$

Table 8.3.3. Explanation of timing of egg laying using single weather variables (means from Julian day 60 to 110) and indices from 1-D model. Best model selected by AIC.

Bird Species	Guillemot		Kittiwake		Shag	
	1^{st} egg date	median egg	1^{st} egg date	median egg	1^{st} egg date	median egg
Combination of weather and indices	Heat flux Bloom DewT	Heat flux DewT	NS Windvel DewT	NA	Rain Radiation	Rain Radiation Bloom DewT
Whole model values	$r^2 = 0.48$ $P = 0.007$	$r^2 = 0.31$ $P = 0.03$	$r^2 = 0.22$ $P = 0.08$*		$r^2 = 0.20$ $P = 0.04$	SST $r^2 = 0.65$, $P = 0.01$

*note without 2 extreme years $r^2 = 0.37$, $P = 0.02$

We hypothesise that the state of individual birds drives the timing of egg laying and that their states are influenced by the local environmental conditions which affect food availability earlier in the year during the pre-breeding season. To test this hypothesis we compared the annual date of egg laying of the 3 species with individual measures of weather from the spring time period and biologically meaningful indices from the 1-D model. The date of egg laying for either the 1st and /or median egg can be predicted for Guillemots using a combination of the annual timing of the date at which the heat flux remains positive (an indication of when primary production becomes physically possible), the timing of the spring bloom and the mean dew point temperature over the period from Julian date 60 to 110 (see Table 8.3.3). The date of first Kittiwake egg is influenced by wind speeds and dew point temperature, whereas for Shags it is rain and radiation which play an important role (see Table 8.3.3).

Primary production and seabird breeding success

In an attempt to identify the actual mechanisms that are affecting the breeding success of the three study species of seabirds we have assumed that fish growth and availability are the key drivers in the relationship. We hypothesise that it is the effect of meteorological conditions on the timing and amount of production (ultimately leading to the sandeel food availability) that is the most direct mechanistic link. Therefore we extracted out of the model the amount of primary production defined as the 'pre-bloom' production, which represents the sum of primary production from when production is first possible (the timing of the positive heat flux) to the start of the bloom. We also calculated annual estimates for the amount of production during the bloom period and the duration of the bloom. We compared these variables to the breeding success of each of the three species and found that for both Guillemots and Kittiwakes, the addition of the pre-bloom and bloom production or length of bloom provided better models for breeding success than models simply using variables linked to timing (Table 8.3.4). In contrast, for Shags the timing variables remained the better explanatory variables. However, the best models for all three species now include fishing as a variable or an interaction term which helps to explain the variance in annual breeding success. These results provide further evidence that the presence of a fishery in the area has an additional adverse effect on seabird reproductive output.

Table 8.3.4. The best models (AIC) for explaining the variance in breeding success of the different species, now considering the more direct influence of primary production on the food chain leading to differences in sandeel availability and quality.

species	Guillemot	Kittiwake	Shag
Whole model results	Fishing Pre-bloom production Length of bloom r^2=0.46 *P*= 0.02	Fishing Pre-bloom production Length of bloom Fishing * Difference between egg laying and bloom r^2=0.85 *P*< 0.0001	Fishing Difference between egg laying and bloom Fishing * Difference between egg laying and bloom r^2=0.67 *P*< 0.0001

Table 8.4.1. Densities of seabirds (n km^{-2}), and their participation in natural MSFAs (% of all foraging seabirds observed within the principal study area.

	Gannet		Kittiwake		Guillemot	
	density	% in MSFAs	density	% in MSFAs	density	% in MSFAS
1997	9.4	98.6	16.7	95.9	109.7	95.5
1998	1.0	8.5	6.2	45.1	30.3	75.0
1999	2.4	68.4	7.4	25.1	3.0	81.8
2000	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
2001	2.7	97.1	11.9	95.9	105.4	100.0
2002	5.6	30.8	7.7	46.2	24.8	83.2
2003	4.2	48.2	8.3	19.5	13.8	62.0
2004	1.5	25.0	14.3	96.9	48.2	99.4

8.4 Annual indices of at-sea distributions and behaviour of seabirds

Between years, in the study area at large, the density of Guillemots was fairly consistently four times the density of Kittiwakes which was in turn about twice the density of Gannets at sea (Fig. 8.4.1, 8.4.3). Within the principal study area, however, from the annual *Tridens* surveys, a rather erratic pattern in the relative abundance of Guillemots was found (Fig. 8.4.2, 8.4.4). This pattern did not match the results of the more stable densities of Guillemots found a month earlier in the year during the *Clupea* surveys, and it is likely that the variability has been caused by non-breeders that were more abundant within the principal study area in some years than in others. The proportion of Guillemots showing active post-nuptial moult of the head was indeed very high in 1997 (34%), but low in 2001, so that this suggestion cannot be confirmed from visual observations. Another explanation is the incomplete coverage of the principal study area in some years, so that the variability may in part have been an artefact.

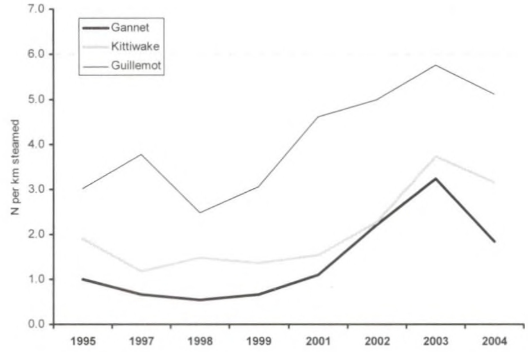


Fig. 8.4.1. Relative abundance (n per km steamed) of Gannets, Kittiwakes and Guillemots in the study area at large

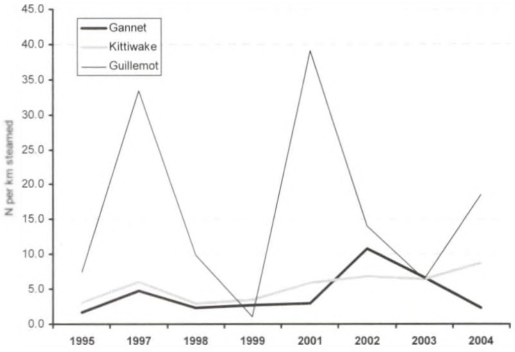


Fig. 8.4.2. Relative abundance (n per km steamed) of Gannets, Kittiwakes and Guillemots in the principal study area

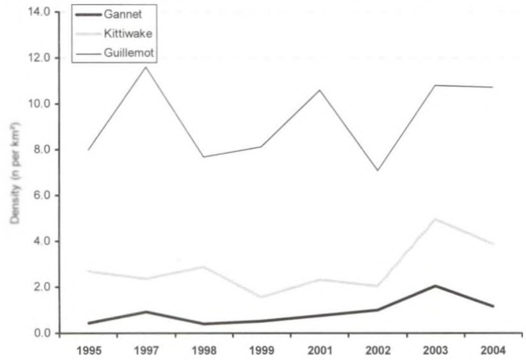


Fig. 8.4.3. Relative abundance (density, n per km²) of Gannets, Kittiwakes and Guillemots in the study area at large

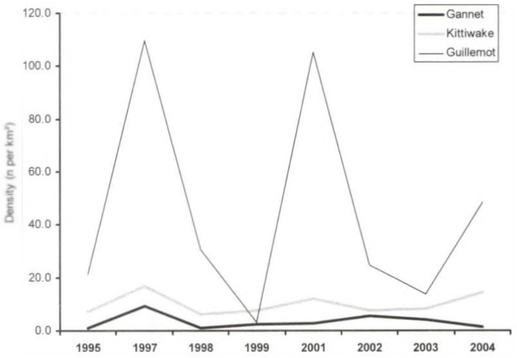


Fig. 8.4.4. Relative abundance (density, n per km²) of Gannets, Kittiwakes and Guillemots in the principal study area

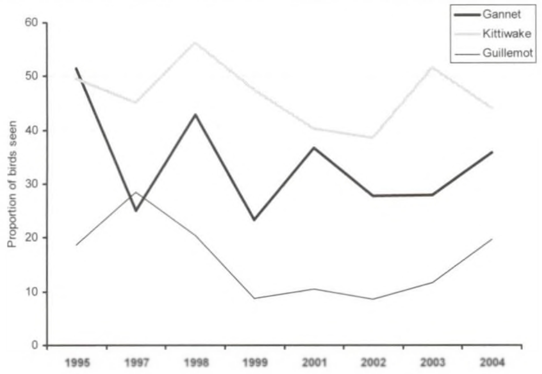


Fig. 8.4.5. Proportion recorded as foraging of Gannets, Kittiwakes and Guillemots in the study area at large

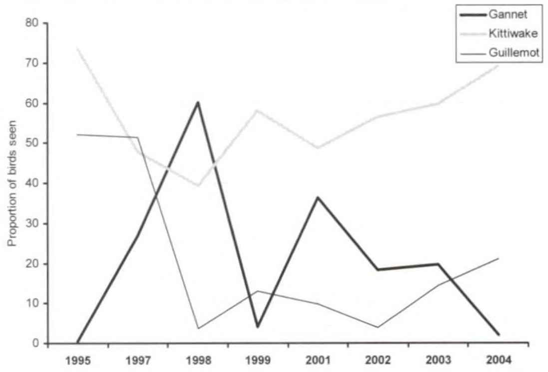


Fig. 8.4.6. Proportion recorded as foraging of Gannets, Kittiwakes and Guillemots in the principal study area

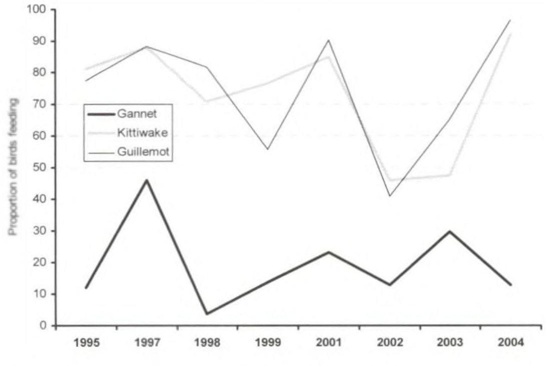


Fig. 8.4.7. Proportion recorded as flock-feeding (i.e. participation in natural MSFAs) of Gannets, Kittiwakes and Guillemots feeding in the study area at large.

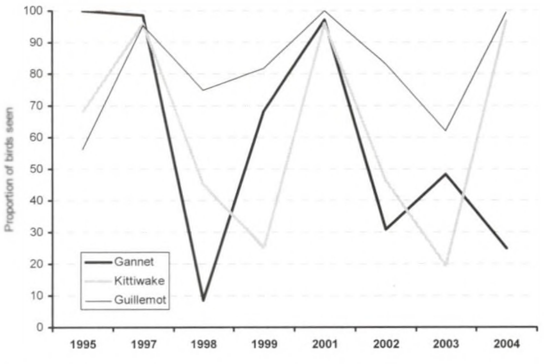


Fig. 8.4.8. Proportion recorded as flock-feeding (i.e. participation in natural MSFAs) of Gannets, Kittiwakes and Guillemots feeding in the principal study area.

Table 8.5.1. Seasonal qualifications of patterns observed in hydrography, sandeel fisheries, prey fish stocks, prey size and seabirds prior to and during the IMPRESS project. Blank cell: no data.

Hydrography	range		1997	1998	1999	2000	2001	2002	2003	2004	trend
Onset stratification	07-Apr	30-Apr	early	mod	late	late	late	early	mod		variable
Start spring bloom	14-Apr	01-May	early	mod	mod	late	late	early	early		variable
End spring bloom	28-May	20-Jun	mod	mod	late	late	late	early	early		variable

Prey fish	range		1997	1998	1999	2000	2001	2002	2003	2004	trend
Sandeel 0 group	10,400t	111,100t	low	low	low	high	low	high	high		increase
Sandeel 1+group	7,300t	296,000t	low	low	low	high	high	high	high		increase
Sandeel % water column	0%	100%	high	high	low	mod	high	high	low		variable
Herring 0 group	0t	6223t	mod	low	low	mod	high	low	low		variable
Herring 1+ group	148t	4820t	low	mod	low	high	low	high	high		variable
Sprat 0 group	0t	3t	low	low	low	low	low	some	low		stable
Sprat 1+ group	14t	2999t	high	high	low	high	mod	low	low		decline
Sandeel landings											
- closed area	10,000t	55,000t	mod	high	mod	low	mod				decline
- 41E7-41E8	2,000t	38,000t	high	high	low	low	mod				decline
Sandeel 0-group size											
-acoustic survey	4.55mm	7.02mm	large	small	mod	large	large	mod	large		variable
-demersal trawl	5.58mm	8.19mm	mod		mod	large	mod	small	small		variable
Sandeel 0-group mass											
-acoustic survey	0.28g	0.97g	large	small	mod	large	large	mod	mod		variable
-demersal trawl	0.48g	1.63g	mod		mod	large	large	small	small		variable

Seabirds	range		1997	1998	1999	2000	2001	2002	2003	2004	trend
Breeding population											
- Shag	210n	1000n	low	mod	low	mod	high	mod	high		increase
- Kittiwake	3500n	6500n	high	mod	mod	mod	low	low	low		decline
- Guillemot	16,800p	20,400p	low	low	low	mod	mod	high	high		increase
Breeding success											
- Gannet	0.63c/p	0.69c/p									
- Shag	0.3c/p	1.8c/p	mod	low	low	high	high	high	high	[low]	increase
- Kittiwake	0.01c/p	0.95c/p	mod	low	low	high	mod	mod	high		variable
- Guillemot	0.62c/p	0.78c/p	high	mod	low	mod	low	mod	mod	[low]	decline
% Sandeel in chick diet											
- Gannet	0%	100%		low			mod	mod	mod		variable
- Shag	0%	100%	high	high	mod	high	high	high	high		variable
- Kittiwake	0%	100%	high	high	high	high	high	high	high		stable
- Guillemot	0%	100%	high	low	low	mod	low	low	low		decline
Seabirds at sea June *Clupea* surveys (full area surveys)											
- Gannet	3 km^{-2}	9 km^{-2}	low	high	low	high	low	high	high		variable
- Kittiwake	1 km^{-2}	4 km^{-2}	mod	high	low	high	mod	high	high		variable
- Guillemot	8 km^{-2}	18 km^{-2}	mod	mod	mod	low	low	high	high		increase
Seabirds at sea July *Tridens* surveys (partial area surveys)											
- Gannet	1 km^{-2}	10 km^{-2}	high	low	low		low	mod	mod	low	variable
- Kittiwake	6 km^{-2}	17 km^{-2}	high	low	low		mod	low	low	high	variable
- Guillemot	3 km^{-2}	110 km^{-2}	high	low	low		high	low	low	mod	variable
Natural' MSFA participation July											
- Gannet	0%	100%	high	low	high		high	low	mod	low	variable
- Kittiwake	0%	100%	high	mod	low		high	mod	low	high	variable
- Guillemot	0%	100%	high	high	high		high	high	mod	high	stable

The proportion recorded as foraging or feeding of all birds observed is probably too low in Guillemots (escape responses obscured the picture; see chapter 5.4), but is a reliable figure in the surface feeders (Fig. 8.4.5-6). The proportion was rather stable in Kittiwakes in either area, but variable in the Gannet within the principal study area, suggesting that more Gannets were feeding at greater distances away from the Bass Rock in 1995, 1999, and 2004 (<10% recorded as foraging or feeding) than in other years in July (20-60% recorded as feeding).

The proportion of Guillemots and Kittiwakes foraging in natural MSFAs in the study area at large was generally very high, but notably lower in 2002 and 2003 (Fig. 8.4.7). In Gannets, the interest to join these frenzies in the area at large was substantially lower. All species showed a remarkable variability in their tendency to forage within natural MSFAs in the principal study area, with very high values for all three species in 1997 and 2001 and a high figure for Guillemots and Kittiwakes in 2004 (Fig. 8.4.8). Very low values were found for Gannets in 1998, 2002, and 2004, and very low values for Kittiwakes in 1999 and 2003. Most these natural MSFAs were driven by hunting

Guillemots (driving prey fish towards the surface in a concerted action), and peak attendances in MSFAs occurred in years when these birds were particularly abundant (Table 8.4.1).

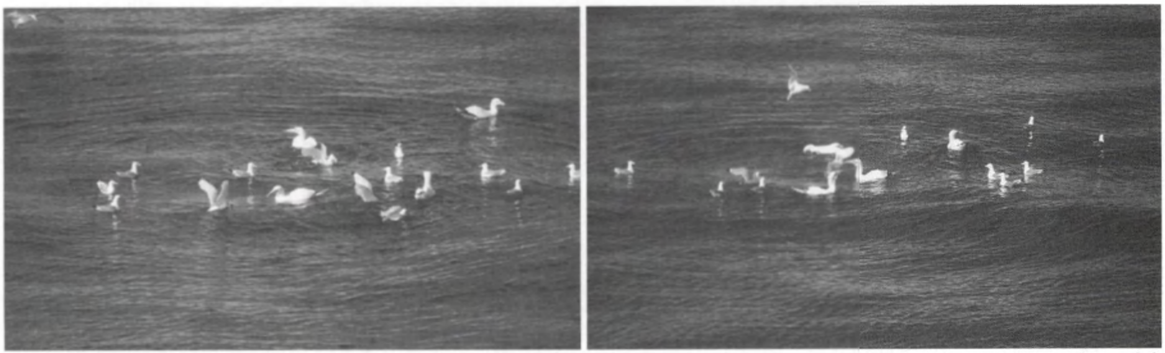
8.5 Discussion

The results from the multi-year comparison in this chapter show that there was considerable inter-annual variability in most parameters measured and that few fluctuated entirely in concert. The year 1999 came out as an extreme season, with very low prey fish stocks (sandeels, Herring and Sprat), a low presence of sandeels in the water column, and a very low breeding success in Shags, Guillemots and Kittiwakes, and low numbers of seabirds at sea in the principal study area (Table 8.5.1). It was a year when stratification developed rather late, but spring bloom started more or less as normal (compared with other years), and there was no commercial fishery for sandeels of significance. Rather few Kittiwakes were observed to participate in natural MSFAs, probably in the absence of (suitable) Guillemots in the area. By contrast, 2001 was a season in which rather high prey-fish stocks were found, with abundant sandeels in the water column, substantial amounts of Herring and Sprat, with a late development of stratification and spring bloom, high densities of Guillemots and a very strong tendency by Gannets and Kittiwakes to join these birds in natural MSFAs. It is interesting to note that 0 group sandeel stocks were rather low in this year, but that these fish were relatively large and heavy.

Sandeel biomass was significantly higher in 2000-2003 than it was in the three years prior to the project and the reproductive success of Shags and Kittiwakes was relatively high in these years, albeit variable in Kittiwakes. For the Guillemot, however, the reproductive success declined and relatively few sandeels were brought into the colony in recent years. The at-sea surveys revealed that Guillemots did prey en masse on 0-group sandeels in July in all years of study and this was confirmed by diet studies of adult Guillemots in the colony and found drowned at sea. We have no information, however, suggesting that the sandeel consumption of adult Guillemots has varied from year to year.

Few data exist for 2004, a year in which for most birds the breeding success was extremely low, as it was low in large parts of the NW North Sea. We have evidence that nesting was seriously delayed in some species (notably Guillemots), but with timing of nesting and fledging near normal in others (for example in Razorbills). On the Farne Islands, alternative prey fish were fed to terns, suggesting a scarcity of sandeels (Wilson 2004). In the North Sea as a whole, sandeel stocks were exceptionally low and substantial non-breeding (or breeding failures) of seabirds occurred at the Northern Isles of Britain. During the ship-based surveys in July 2004, a highly different feeding method was observed, described as ‘drive hunts’. Natural MSFAs in 2004 were different from any of the (9) preceding years in that not an avian or mammalian predator seemed to be the driving force, but that large schools of fish occurred near the surface, but travelling fast, with seabirds and marine mammals following an trying to keep up. On the Wee Bankie, the Bank waters, normally packed with foraging seabirds were nearly empty, and chicks of Guillemots (later than normal) appearing at sea were smaller than in any previous year. The situation in 2004 within the study area at large was similar to worsening environmental conditions around the Northern Isles (notably Shetland) since the late 1980s, and particularly in the early 21st century.

Despite several significant correlations, the variability of the material collected from year to year is substantial and the predictive value of the parameters measured is relatively low. Mechanisms influencing prey availability are clearly species-specific, but other factors must have influenced breeding populations and reproductive success, given the contrasting trends in the seabird population monitored on the Isle of May.



Multi-species feeding frenzy, just prior to collapse. Scooping Northern Gannets have displaced shallow-plunging Kittiwakes, while prey-driving auks have already abandoned the scene (C.J. Camphuysen)

Chapter 9 Synthesis

9.1 Introduction

Sandeels are major prey for a variety of top-predators including seabirds and severe ecosystem effects of sandeel stock collapses may occur. The industrial sandeel fishery is the largest single fishery in the North Sea, but the fishing industry contests the view that its activities negatively affect top-predators. Fishing for sandeels for industrial purposes in the North Sea started in the early 1950s, but annual landings never exceeded 200 000t until the early 1970s. The highest annual catch of 1 149 000t was recorded in 1997. Part of the explanation for the continued upward trend in annual sandeel landings over the last 25 years has been the opening up of new sandeel grounds. One such fishing ground was on the Wee Bankie/Marr Bank sandbank complex of the Firth of Forth in southeast Scotland, where a significant fishery took off in the early 1990s. Coincident with the increase in the removal of sandeels from areas close to the Scottish east coast, seabird breeding success at colonies along the coast started to decline.

There is very little evidence, generally, of the fishery directly reducing availability of sandeels to breeding seabirds, but fishery managers should take account of the needs of other predators in the ecosystem. The consumption of sandeels by seabirds can be high in the vicinity of major seabird colonies, such as off the Scottish east coast, but is low in central regions of the North Sea. The potential for a fishery to negatively affect seabirds is much greater when coastal areas are fished than for example when the fishery is restricted to offshore areas. However, the extent to which seabirds may suffer reductions in food supply as a consequence of the sandeel fishery depends especially on whether recruitment varies in relation to prevailing levels of spawning stock biomass but also depends on the age classes and quality of fish selected by birds (Furness & Tasker 1997). It has been suggested to closely control industrial fishing in regions where high numbers of seabirds breed of high sensitivity to sandeel abundance, to avoid depleting the local sandeel stocks on which the seabirds depend (Furness & Tasker 2000). Concerned that the sandeel fishery, by reducing feeding potential in waters close to the colonies, might cause a decline in seabird breeding performance, fisheries managers adopted a precautionary stance and prohibited fishing for sandeels in nine ICES statistical rectangles close to the coast off the Firth of Forth (Chapter 2). All commercial fishing in the Firth of Forth area has been prohibited since 2000, except for a maximum of 10 boat days in each of May and June for stock monitoring purposes. The closure has been extended until 2006, with an increase in the effort of the monitoring fishery to 20 days, after which the effect of the closure will be evaluated.

The relationship between prey density and prey availability to predators is still poorly understood and the IMPRESS project set out to study predator-prey relationships in a marine ecosystem in unprecedented detail using advanced technology. Availability is related to the interaction between the spatial patterns in the abundance of specific size classes of sandeels and the feeding behaviour of mixed feeding flocks of seabirds. The project aimed at determining the relationship between hydrography, sandeel population characteristics and the foraging performance of four key species of seabirds and to find threshold values of prey density, under which feeding is not feasible for seabirds. This knowledge should enable to define or revise exploitation strategies of the industrial sandeel fisheries that mitigate the impact on the top-predators of the marine ecosystem.

9.2 Sandeels and sandeel fisheries

Sandeels

Sandeels mature between one and three years of age and have a live span of less than 10 years. During the summer period (Apr-Sep), sandeels form large schools that feed on zooplankton in the water column during part of the daytime period. During the remainder of the time, particularly at night, they bury in the sediment. Sandeels stay buried in the sediment through the late summer to early spring period, emerging briefly to spawn in winter (Dec-Jan). The eggs, deposited on the seabed, hatch after a few weeks (Feb-Mar). and the larvae passively drift in the currents (planktonic phase) for a period of several months, after which they settle on the sandy seabed in summer. Sandeels settle after their at around 5cm length, and may reach as much as 10cm length within three months of hatching. Sandeels off the Firth of Forth are relatively slow growing compared to those in the main fished areas, around the Dogger and Fisher Banks. Shetland sandeels also tend to be slower growing, although they generally grow faster than Firth of Forth sandeels (FRS, Aberdeen website).

Different components of a sandeel population, for example 0 group fish compared with older aged fish, may spend different fractions of the available time feeding in the water column and buried in the seabed. Their main prey is calanoid copepods, but other planktonic prey, including fish and bivalve larvae, are also taken. Sandeels tend to emerge during daylight hours to forage close to their burrows and because sandeels show a strong preference for particular habitat types to bury, with the ease of penetration into the sediment being an important factor in determining sediment habitat choice, predators and fisheries could focus on so-called ‘sandeel grounds’. Sandeels are known to prefer depths of 30-70m and a specific sand grain size and silt content (<10%) that makes the bottom both easy to penetrate and not too muddy (Chapter 2; Wright *et al.* 2000).

Sandeels constitute important prey for many marine top predators, including marine mammals (pinnipeds and cetaceans), (commercial) fish species, such as gadoids and Mackerel, and many seabird species. Sandeels in the North Sea may consist of several discrete populations rather than a single homogenous stock and while the population might appear "healthy" at a North Sea spatial scale, regional fluctuations in stock size may influence breeding success locally. Similarly, it is possible that at a more "local" scale, individual sandeel meta-populations may have been over-exploited because of the patchy distribution of sandeel fishing.

Sandeels and other prey fish stocks within the principal study area

Between 1997 and 2003, three different instruments were deployed to sample the abundance and age-/size structure of prey fish in the study area (Chapter 4). Total sandeel abundance from acoustic surveys and demersal trawls peaked in 2000 and 2001, was high in 2002 and 2003 and was substantially lower in 1997-1999. Each of the different sampling devices (acoustic survey, demersal trawl, grab survey) produced different estimates of overall abundance or densities between years (Fig. 4.2.1), suggesting that highly variable fractions occurred in the sediment (settled) and in the water column (pelagic). The fraction 0 group fish of the total stock varied also and not in concert with 1+ group stock estimates (Fig. 4.2.2). The year 1999 stands out as a season with a low stock and an exceptionally low fraction of sandeels in the water column and was a season when other prey fish stocks (Clupeids) were very low also. Note that the timing of a survey relative to the growth season of 0 group sandeels (spring bloom) is important, however, and that the 1999 acoustic survey was later than in any other year.

In terms of both abundance and biomass, sandeels dominated the forage fish resource available to marine top predators in every year. Even in the years when the fishery was in operation and large quantities of sandeels had been removed from the area by the fishery, particularly in 1997 and 1998, sandeel biomass in the area still exceeded the combined clupeid resource biomass by a factor of three and nine respectively. In 1999 when the acoustic survey was much later in the year, and substantially later relative to the timing of the spring bloom, the acoustic survey estimate of sandeel biomass in the water column was still almost twice the combined clupeid biomass estimate. For predators that are dependent on sandeels therefore, it seems implausible to consider that clupeids might constitute an adequate alternative prey resource in circumstances where the availability of sandeels to predators is significantly reduced.

Sandeel fisheries

The project worked in a small, rich area in the northwest North Sea targeted by industrial fisheries until 1999, but where a fishing moratorium was kept in place throughout our work (Chapter 2). Fishing pressure was low in 1999, probably as a result of the very low stock size in the area. In the analyses presented in Chapter 4, a sandeel fishery was used as a categorical variable to explore the effects of the fishery, and 1999 was treated as a "fishery in operation" year. Technically this is correct since the fishery was not closed until 2000. However, fishing effort in the area was much lower and the total sandeel catch taken was actually no higher than the catches made for scientific monitoring in all the ensuing years when the area was technically closed to fishing. When comparing the demersal trawl biomass estimates in fishery and non-fishery years, no significant effect of the fishery was detected, because the 1999 index exceeded the 2002 value. However, the two years during the course of this study when sandeel removals by the fishery were particularly high, 1997 and 1998, produced the two lowest demersal trawl index values in the time series. If we were able to measure (major) changes in sandeel availability for individual predator species within the principal study area, we could analyse the shape of functional responses of breeding seabirds to variations in their food supply. A next step would be to evaluate the influence of an industrial fishery on these shifts in availability.

North Sea sandeel stocks

There is circumstantial evidence that sandeel stocks within the principal study area were much reduced in 2004 and seabirds generally produced few chicks (Wilson 2004). This decline in prey abundance would have been in line with patterns found on a North Sea scale. In recent years, North Sea sandeel spawning stock biomass (SSB) declined substantially. Based on the most recent SSB estimates, ICES classifies the stock as having reduced reproductive capacity (ICES 2004) and the SSB in 2004 was estimated to be at a historic low value (325 000 t). Sandeel biomass in 2003 was above B_{lim}, but has in 2004 decreased to below B_{lim} due to a historic low recruitment in 2002.

9.3 Oceanography, influencing fish and seabird distribution

The study area at large is part of the Northeast Atlantic shelves province of the Atlantic coastal biome (Longhurst 1999) and contains two distinct hydrographic regions: North Atlantic waters, that occupy most of the central North Sea, and Scottish coastal waters (Otto *et al.* 1990; Scott *et al.* 2006). During the winter months, the water column throughout the North Sea is completely mixed but in spring the surface layer in deeper areas begins to warm due to increasing amounts of sunlight and decreasing winds. This warming creates a difference in density between the upper and lower layers of the water column and the onset of the resulting stratification allows plankton to stay above the critical depth needed for population growth and marks the beginning of seasonal primary production (Scott *et al.* 2006, Chapter 3). In shelf seas, Shallow Sea fronts, also known as tidal mixing fronts, separate inshore areas that are permanently vertically mixed due to their shallow depth and/or strong tidal currents, from areas that stratify due to deeper depths and/or weaker tidal currents (Simpson 1981). The exact locations of the fronts change over the spring and summer months in response to weather conditions and the monthly and daily rhythm of tidal speeds. A 'stratification index', defined as the difference in density between the sea surface and the bottom, can be used to identify the locations of fronts (Anon. 2001).

Spring blooms and stratification

Oceanographic data were obtained using a grid of moored instruments recording temperature, salinity, current direction and speed, while satellite images, a scanfish survey (2003) and oceanographic modelling provided spatial information on a variety of scales. The link between hydrography, prey and predators was established by spatial statistical approaches and by modelling the mechanisms of the foraging process. The competition between the mixing and buoyancy inputs is particularly important in determining the strength of vertical stratification, and the depth of the surface mixed layer. The extent to which a water column is mixed or stratified is pivotal in setting the environmental conditions for primary production. The data up to and including 2000 provided a basic understanding of the seasonal dynamics of the principal study area. Typical of a Shallow Sea, the water column for the principal study area was well mixed for most of the year (especially during the winter months of October to March). The onset of stratification was usually observed in April and reached a maximum in late July/ early August. Summer data showed a variable picture in terms of how strongly or weakly stratified the water column could be and also indicated that there was great spatial variability in the stratification of the water column. The western and/or eastern extremes of the primary study area generally being the more strongly stratified regions. The western region, close to the coast, is influenced by fresh water while the eastern region away from the coast is deep enough for surface thermal stratification not to be mixed by tidal friction.

Both the onset of stratification and the start of spring blooms were variable, with 2000 and 2001 being relatively late seasons and 2002 rather early. The scale of variability is shown in Chapter 3 (Fig. 3.3.1, Table 3.1) and in Chapter 8 (Table 8.5.1).

Ocean physics and prey fish

Pelagic fish distributions are likely to involve multivariate processes with numerous factors, such as water depth, topographic and hydrographic characteristics, seabed sediment types and prey availability all playing a part (Appendix 4). The distribution of sandeel was mostly influenced by the seabed topography, sandeels being most abundant in the shallower water over the sandbanks. The degree of temperature stratification appeared to have little impact on the distribution of sandeels. Little linkage was apparent between the level of mixing and the distribution of Herring. The densities of Sprats, however, appeared highest in areas of intermediate mixing, i.e. on the boundaries between stratified and non-stratified water.

The variation in the mean density of sandeels across habitat zones in each year is discussed in Chapter 7. Sandeels were relatively abundant across all habitat zones in some years, while significant differences in habitat use were observed in other seasons. The apparently preferred choice of habitat differed markedly in these years. Between year variation in water column temperature stratification in each of the habitat zones had no significant influence on the density of either 0 or 1+ group sandeels present in each year.

Significant habitat zone selection by 0 group herring was only evident in 1997, when they were restricted, in relatively high densities, to the inshore habitat zones: Well Mixed and Freshwater Influenced waters. In 1997 1+ group herring appeared to favour the Inner Bank zone. Habitat use by 1+ Herring was similar in both 2000 and 2002, with the Well Mixed Shallow and Offshore Stratified or Offshore Bank (also stratified in most years) zones being preferred. Between year variation in water column temperature stratification in each of the habitat zones had no significant influence on the density of either 0 or 1+ group herring present in each year.

1+ group Sprats displayed significant preference for the Well Mixed Shallow zone in 2000 and 2002. In any particular year, variation in the degree of water column stratification across the different habitat zones had no significant influence on the density of sprats in each of the habitat zones. However, in three of the habitats, the Freshwater Influenced, Inner Bank, and Offshore Stratified zones, between year variation in 1+ group sprats was significantly affected by between year variation in the level of stratification.

Our hydrographical observations and modelling results were used to define seabird feeding-habitats in the study area at large and particularly within the principal study area in unprecedented detail and to examine tidal influences on seabird foraging performance (Chapter 7, summarised in 9.4).

9.4 Seabirds

Seabird breeding populations

With a conservative estimate of c45 000 Apparently Occupied Sites (AOS) of **Gannets** on the Bass Rock, about 90% of the Gannets breeding in the North Sea (51°-60°N latitude) is nesting within the principal study area. Further colonies are found on the English (Bempton Cliffs, 2500 AOS) and Scottish mainland (1100 AOS), on Fair Isle in Shetland (1100 AOS; Mitchell *et al.* 2004), and on Helgoland in the German Bight (145 AOS; Hennig 2004). In line with the world population, all the colonies are consistently increasing.

Nearly 5000 pairs of **Shag** breed along the British east coast (Mitchell *et al.* 2004), only 15% of which nest on the Isle of May and a further 7% within the principal study area on the coast of Kirkcaldy and East Lothian. Numbers of Shags have declined in most parts of Britain since the late 1980s. In a wreck of seabirds along the east coast of Britain in February-March 1994, 3-5000 Shag were found dead. The wreck was caused by a long period of onshore winds and, possibly, a shortage of food. The Isle of May population crashed to its lowest level for 35 years and was calculated to take at least 10 years for it to recover (Harris & Wanless 1996). During our project, the Isle of May breeding population increased markedly, and reached nearly 1000 AOS in 2003, but overall numbers are still some distance from the all-time high in the late 1980s and early 1990s.

Kittiwakes on the Isle of May declined with 4.3% per annum since the late 1980s and the decline continued during our project. Just over 3600 nests on the Isle of May in 2003, represented only 2% of the breeding population of Kittiwakes along the east coast of Britain (Mitchell *et al.* 2004). Considerably larger populations are situated along the east coast of Caithness (44 000 AON), in Banff & Buchan (30 600 AON), Berwickshire (19 000 AON) and Humberside (42 000 AON). Kittiwake populations in most of Britain are declining since the late 1980s, and between 1988 and 2000, the Southeast Scottish population declined with 16.9% (1.2% per annum).

Of just over 500 000 breeding **Guillemots** nesting along the east coast of Britain, only 6% inhabit the Isle of May. As in Kittiwakes, the highest numbers of breeding birds are located the east coast of Caithness (195 000 ind), in Banff & Buchan (74 000 ind), Berwickshire (45 000 ind) and Humberside (47 000 ind). Most these populations increased since the late 1980s (by 53%, or 2.7% per annum on the Isle of May; Mitchell *et al.* 2004).

Seabird breeding success

Trends in breeding success of our study species have been evaluated in Chapter 8. Both Shags and Kittiwakes reproduced at much higher levels in 2000-2003 than in 1997-1999, whereas Guillemot breeding success declined more or less consistently over time. Prey availability is just one factor that may determine breeding success, and density dependent mechanisms may easily mask (or exaggerate) the effect of fluctuating prey stocks. In 2004, a year in which a 'seabird crisis' occurred in the northwest North Sea (Wilson 2004), the breeding success of Guillemots was particularly low, and prey availability (or prey quality) is most likely to have played a role in this.

Seabirds and other top-predators at sea

In terms of biomass, the endotherm component of the top predator community in the northwest North Sea is dominated by marine mammals, primarily cetaceans (Camphuysen *et al.* 2006). Together with predatory fish and, in some years, an industrial sandeel fishery, marine mammals are likely to be major consumers of sandeels in the region. The largest species, the Minke Whale *Balaenoptera acutorostrata*, increased from 0.001 km^{-1} surveyed in 1991-1995, to 0.002 km^{-1} in 1997-1999, and 0.005 km^{-1} in 2001-2003. The lack of dietary information and consumption rates for Minke Whales, prevents assessments of their impact on prey stocks.

Of the 50 charismatic top predator species studied during the ship-based surveys (that is, predatory fish excluded), many were strictly coastal, some were far-ranging, while others showed intermediate distribution patterns (Camphuysen 2005). Near the coast, where densities of birds and seals were greater and avian species richness was also higher, inter-specific interference competition was presumably most intense. Many of the top predators were associated with the Shallow Sea front marking the transition zone between mixed coastal waters and thermally stratified offshore waters. Kittiwakes, Razorbills, Guillemots, Harbour Porpoises *Phocoena phocoena* and Minke Whales were all most abundant in this frontal region. Travelling further offshore of the Shallow Sea front area, densities of seabirds remained high at first, although species richness declined immediately. However, with relatively high densities of marine mammals, notably Minke Whales, exploitation competition may have been more important in this part of the North Sea.

Ship-based surveys resulted in considerably higher numbers of seabirds at sea than could be expected solely on the basis of breeding numbers, suggesting a rather high component of non-breeders in the offshore population. July surveys produced roughly the numbers of Shags at sea, as might be expected form the breeding stock, assuming that one parent would be at the nest (even while censuses were generally too far offshore to obtain a full coverage of Shag feeding areas). Assuming one partner in the colony at any one time, numbers of Gannets, Kittiwakes and Guillemots at sea were 2-5x higher than could be expected from breeding numbers alone. These results suggest that a considerable non-breeding component exists in these seabird populations and that the area is important also for future generations summering here, or for non-breeders from breeding populations elsewhere.

In Guillemots, the semi-precocial young leave the colony ("fledge") as small downy young at c. 20 days of age at about one quarter of adult body mass (median 22 June-2 July; Table 5.2.1), accompanied by one of the adults (usually the male). Adult guillemots that guided their offspring away from the colony moved rapidly through the richest feeding areas (as deduced from overall numbers of seabirds foraging and species richness); probably zones with a high predation risk for the chick. These birds travelled into the open North Sea where there were very few avian predators, towards distant nurseries with low predator densities and predictable prey resources (Camphuysen 2002). Meanwhile, the accompanying breeding adults undergo a complete moult and become flightless for about 40-45 days. In the feeding concentrations of Guillemots more distant from land within the principal study area, head moult and primary moult were more advanced than in breeding adults (Camphuysen 2002). Advanced moult stages in these distant areas may be considered indicative for a high proportion of non-breeders.

Foraging behaviour and multi-species feeding associations (MSFAs)

Small, short-lived multi-species foraging assemblages (MSFAs), were frequently recorded in the coastal foraging zone, within and around the Shallow Sea front area (Chapter 5). For convenience, the commoner type was labelled as 'natural MSFA', as these were produced by prey-driving **Guillemots** and Razorbills operating in small flocks, *i.e.* not caused by

Kittiwakes foraging on 0-group sandeels in association with Guillemots and Razorbills and with some Manx Shearwaters taking advantage. The auks dive simultaneously in parties of 4-6 birds and drive prey fish balls towards the surface (H Verdaat, summer 2004).

The top images shows a situation where the auks frequently dive and only the rebreathing fraction is visible.The Kittiwakes are dipping actively and do not need to dive. The bottom image shows a situation where the auks have become largely inactive and where the prey fish ball is sinking down or dispersing. Some shallow plunge diving Kittiwakes just manage to reach some fish.

Kittiwakes and Gannets foraging on 0-group sandeels in association with Guillemots and Razorbills and with a Black-headed Gull taking advantage. The auks have driven prey fish balls towards the surface, but have given up, possibly as a result of the disturbance caused by surface feeding seabirds (H Verdaat, summer 2004).

The top images shows a situation where the Kittiwakes still have access to the prey fish ball, despite the presence of some (largely inactive) Gannets. Most of the feeding has ceased, however. The bottom image shows a situation where the auks have gone, where the Gannets are actively scooping and swallowing sandeels, but where the Kittiwakes have lost access.

the presence of a fishing vessel or any other anthropogenic factors, but also not driven by marine mammals! The tendency to participate in such 'natural' MSFAs differed among the various species (Table 5.4.2-3). **Kittiwakes** frequently acted as catalysts or initiators in MSFA formation, while large gulls, skuas and other seabirds quickly joined in. Large gulls and **Gannets** acted as scroungers or suppressors, while skuas were normally peripheral in the presence as aerial kleptoparasites. Auks were normally joined by other seabirds and rarely joined existing MSFAs. Within 40km of the coast, many MSFAs were targeted by large *Larus* gulls, thereby minimising further access to the prey by catalysts (mostly Kittiwakes). In contrast, only few MSFAs more than 40 km from land were targeted by large gulls, and Kittiwake foraging activities tended to be concentrated in these areas. Gannets joined 18% of MSFAs, and their arrival typically rapidly disrupted the foraging opportunities of all the other participants, including other gannets and auks. Unexpectedly, Gannets that joined these feeding frenzies obtained prey by scooping items from the surface rather than by plunge-diving and these observations proved vital for the successful classification of foraging behaviour from logger signals in instrumented birds (see below).

Large differences in feeding activity, as well as the frequency of occurrence of MSFAs, were recorded when comparing transects crossing the shallow sea front. On some occasions only large flocks of inactive (resting or preening) seabirds were encountered while on others high numbers of feeding birds and active MSFAs were recorded. Surveys in 2003 revealed that foraging activity in these areas varied during the day in relation to changes in tidal currents, suggesting that physical processes may help drive prey towards the surface (see below).

Gannets were encountered both inshore of the Shallow Sea front and further offshore in the deeper, stratified offshore regions of the central North Sea. They used contrasting foraging techniques in either area. In inshore areas, Gannets profited from 'natural' MSFAs, with birds alighting or making shallow, oblique plunge-dives into the frenzy and scooping up sandeels while they were swimming. In thermally stratified offshore waters, Gannets usually fed on fish shoals that were herded towards the surface by dolphins or Harbour Porpoises and made vertical, deep plunge-dives (Camphuysen 2004).

Piscivorous seabirds in most of the world's oceans exploit fish schools in multi-species flocks and the importance of these assemblages cannot be over-emphasised (Hoffman *et al.* 1981; Camphuysen and Webb 1999). In the principal study area, Kittiwakes and Gannets profited from the feeding activities of Guillemots and Razorbills that were driving (or herding) sandeels and other prey fish to the surface. Most MSFAs included species that used complementary tactics when feeding together (e.g. pursuit-diving, plunge-diving, dipping, scooping, surface-pecking and aerial-pursuit). Schooling by small fish does not apparently function as a deterrent to avian predators in the same way as it does for predatory fish (Brock & Riffenburg 1959). While some species such as Arctic Terns and European Storm-petrels rarely, if ever, joined MSFAs, for at least eight other surface-feeding species, MSFAs must have contributed significantly to their daily prey intake.

Seabird distribution and prey fish

The impact of ocean physics and prey distribution on top predator foraging behaviour is poorly understood, largely because of the complex trophic linkages involved. In particular, a detailed understanding of the interaction between seabirds and their prey is lacking. In optimal foraging theory, the patch choice model predicts that patches (e.g. habitats) will be selected according to their mean productivity (MacArthur-Pianka 1966; Charnov & Orians 1973). This and other models are to understand the daily and seasonal movement of (marine) foragers and the model should forecast a predator's habitat selection. The marginal value theorem predicts that if a bird is foraging optimally, a fishing ground should be abandoned when the marginal rate of return for fishing in that ground is equal to the mean return for the entire habitat or a set of visited feeding grounds. Several previous surveys have found a close link between quantities of prey found in an area (as a proxy of the quality or productivity of patches) and the densities of birds found, but correlations of seabirds with their prey was essentially scale-dependent (e.g. Schneider & Piatt 1986; Piatt 1990; Veit & Silverman 1993; Swartzman & Hunt 2000). Many more surveys failed to find a direct link, or at large scales only, but few of those have been published. From the *Clupea* surveys, no clear relationship between the density of any seabird species and the density of either sandeels, herring or sprats could be determined (Appendix 5). However, high densities of each of the major predators could be linked to patches of one or even all three fish prey species. From the large-scale surveys, highly consistent distribution patterns were observed on a 10s of kilometers scale (Camphuysen 2005), with a more patchy and less 'predictable' occurrence and distribution at smaller scales. Links with hydrographic patterns were much more obvious and frequently found (see above) than spatial correlations with fish densities measured simultaneously during these surveys (note that the upper *c.* 8m of the water column is not included in the acoustic census on FRV *Tridens*). Seabirds search for underwater prey from above water and prey are usually not possible to detect from a distance.

The weak link between distribution patterns and prey fish abundance at the smaller scale seems to support findings that individual seabirds tend to specialise on certain habitat characteristics and environmental conditions rather than to respond to the constantly changing distribution of the highest concentrations of prey. Hence, a response to "expected accessibility" of prey resources rather than to expected fish density. We therefore tried hard to further define and characterise preferred feeding habitats for each of the study species. To do so, we first combined findings from visual observations at sea with data collected by means of data loggers.

Seabirds at sea: logger data and visual observations combined (foraging range and diving depth)
The opportunity to study the foraging whereabouts of seabirds using a combination of techniques (i.e. following instrumented individuals of known breeding status at the same time of comprehensive seabirds at sea surveys where foraging behaviour was studied) was unique and has provided a large amount of useful data. Two main aspects were addressed: foraging whereabouts (range, habitat characteristics) and foraging behaviour (including dive depth).

From the at-sea surveys, it was demonstrated that **Kittiwakes** occupied a *c.* 100 km broad zone off the Scottish east coast and within that zone peak densities were often observed close to the Shallow Sea front. Between the colonies and the Shallow Sea front, flocks of Kittiwakes travelling to and from foraging areas, were a common sight, as well as more individually operating Kittiwakes with a meandering flight path (searching individuals). Chick-rearing Kittiwakes equipped with activity loggers carried out trips with a direct or narrow eliptical flight path and we estimated a maximum foraging range of 69 ± 6 km. This distance accords well with the distance from the breeding colony to the shallow sea front, which runs parallel to the coast in the principal study area, and the colony-based results from the activity loggers accord fairly well with at-sea surveys. The front appears to form an outer barrier for breeding Kittiwakes, and foraging occurred throughout the zone between the colony and the front. The stronger preference for the shallow sea front demonstrated from at-sea surveys (Fig 5.4.2) compared with colony-based work, or at least the rather high densities of Kittiwakes in that area, may be due to the former comprising a large proportion of non-breeding (adult) individuals.

The at-sea surveys suggested **Guillemots** were similarly widespread in a broad zone along the UK coast. Foraging locations from Isle of May breeding birds equipped with compass loggers, however, suggested that Guillemots from this colony foraged considerably nearer the colony than these overall at-sea densities would suggest. A subsequent analysis of directions of flight of birds carrying fish towards the colonies, suggested a high degree of overlap between logger data and at-sea observations with regard to the feeding range. It was concluded that Isle of May breeding birds utilised only a small part of the principal study area, mainly the west side of the Wee Bankie/Marr Bank complex, and that the bulk of the (breeding adult) Guillemots in the eastern part of the principal study area bred further to the north and to the south. Concurrent data collected using compass loggers during colony based studies confirmed that Guillemots from the Isle of May were foraging principally between the colony and the Wee Bankie. Maximum foraging ranges for Guillemots from the Isle of May were approximately 50 km, whereas those from other colonies were at 55 to as much as 110 km.

Instrumented **Shags** were foraging inshore of the Isle of May (max feeding trips <10km) and, in contrast to Guillemots, the water they foraged in was mixed. Ship-based surveys have generally contributed very little to the data collected from the Isle of May itself, except that the close inshore distribution was a general finding for the study area at large, that all birds in the principal study area were encountered in freshwater influenced areas, and that few Shags participated in feeding flocks (in fact none were seen to do so within the principal study area).

Compared with the other three species, **Gannets** were by far the furthest ranging species, foraging abundantly within and beyond the principal study area. Behavioural observations during ship-based surveys indicated that the foraging techniques, the tendency to participate in multi-species feeding frenzies, the tendency to join hunting cetaceans as well as the opportunities to scavenge at fishing vessels varied between areas. Densities of Gannets around the Bass Rock declined with distance and approximately one third occurred within 80 km from the colony, another third between 80 and 200 km, the remainder at greater distances away from the colony. Thus, most Gannets were seen to forage and feed in areas with relatively low densities of conspecifics. Locations obtained from Gannets carrying PTTS and GPS loggers confirmed the enormous range of these birds around the colony, as well as their tendency to travel NE and E rather than N, with a second 'stream' of birds heading SE and into the deeper gullies to the SW of the Dogger Bank. The three sets of data are in perfect agreement with eachother and the results underpin the fact that active breeders have such a long feeding range.

Water depth throughout most of the study area is less than 60 m and thus Shags, Razorbills, Guillemots, Puffins and all the marine mammals potentially have access to the entire water column within their respective foraging ranges. Terns, Kittiwakes, Fulmars and storm-petrels rely on the presence of prey near the water surface, while Gannets were not expected to dive deeper than 20-25m (Garthe *et al.* 2000). These differences in foraging capabilities have implications as to how prey stocks can be utilised by each predator and it was essential to see how our study species performed.

Observations that **Guillemots** from the Isle of May mainly utilised stratified waters were confirmed when breeding birds were equipped with PreciTD loggers. The maximum foraging depth of Guillemots from the Isle of May colony was between 60 and 70m and the birds tended to make shallower dives around sunrise and sunset. In stratified waters, primary production is typically concentrated at the thermocline (Mann & Lazier 1996). We found that Guillemot foraging effort was strongly targeted at the zone below the thermocline, while data collected concurrently by fixed moorings demonstrated that primary production was highest at the thermocline, lowest below the thermocline and intermediate above the thermocline. In 2003, Guillemot foraging distribution was very different with the area above the thermocline as well as below the thermocline extensively foraged in. As in previous years, the thermocline was not targeted. Once more, our data showed that the concentration of primary production was highest at the thermocline. Acoustic surveys demonstrated a higher density of sandeels below the thermocline than in the thermocline. Thus, the data appear to show that the mismatch between Guillemot and plankton distribution is partly explained by the distribution of their prey. Unfortunately, these surveys are unable to measure fish densities in the top 10m of the water column, so no estimates above the thermocline were available.

Shags, as benthic feeders, foraging at on average 20-27m depth, were expected to be affected by the tidal cycle, and were predicted to forage preferentially at low tide. However, there was no evidence that birds preferred to forage during low tide and we concluded that there are patterns in the behaviour of Shag prey (adult lesser sandeels) that are more important in determining the timing of foraging than the reduced distance between sea surface and the sea floor during low tide. There was no correspondence between the distributions of sandeels and foraging Shags, perhaps because the data were collected on different dates or because the acoustic survey recorded sandeels in the water column, whereas Shags appear to forage benthically, probably mainly targeting sandeels buried in the sand. Indeed, Shag foraging distributions appeared to be tied more closely to the distribution of sandy habitats (where sandeels settle).

From activity recorders attached to the **Gannets**, diving locations and 'shallow-feeding' locations could be pinpointed. After combining the results with observations of feeding behaviour from ship-based surveys, it became obvious 'shallow feeding' Gannets were tracked almost exclusively in areas where Gannets joined 'natural' MSFAs and foraged in a more pelican-like manner (scooping; see the images earlier in this Chapter). Deep diving Gannets were recorded within as well as beyond the areas where most Gannets were seen to participate in multi-species feeding frenzies. Analysis of dive depths indicated that birds made shallower dives inshore of the tidal front (mean depth = 2.07 ± 0.19 m) than offshore (mean = 4.31 ± 0.16 m). The phase of the tide was also important, with the deepest dives occurring during decreasing South and increasing North tides. Birds dived primarily in stratified water and only very occasionally penetrated the thermocline (most dives were <5 m). There was some evidence that dives were more numerous at locations exhibiting higher horizontal variation in sea surface temperature (SST). This may in part reflect variation in distance to land. However, at equal distances from the colony, locations with higher horizontal SST variation were also more often used for diving. Feeding events in 2003 had a preference zone covering the extent of the Shallow Sea front.

As stressed earlier, associations with marine mammals largely occurred at greater distances (>60 km) from the colony, and typically in stratified offshore waters over >50m deep. The frequency at which 'natural' MSFAs were joined by Gannets mirrors the possibilities at sea (Fig. 5.4.4). Cetaceans were widespread and occurred in similar numbers closer to colony and coast as they occurred far out at sea, but Gannets joined cetaceans preferably offshore.

Seabird feeding habitats

From a combination of observation techniques, our work has emphasised the importance of the Shallow Sea fronts for foraging seabirds and the results indicated that this also forms an outer 'barrier' for many birds breeding down the east coast of Britain (Camphuysen *et al.* 2006). Top predators frequently congregate around these Shallow Sea fronts that are normally associated with increased abundances of fish, larvae and zooplankton (Pingree *et al.* 1975; 1978; Richardson *et al.* 1986). The influence of tidal mixing fronts has been studied in the North Sea, Irish Sea, Bay of Biscay and the Bering Sea, where tidal mixing fronts have a profound effect on the dispersal of sub-surface foraging piscivorous seabirds (Pingree *et al.* 1974; Bourne 1981; Schneider 1982; Kinder *et al.* 1983; Hémery *et al.* 1986; Leopold 1987; Decker & Hunt 1996; Begg & Reid 1997). The offshore boundary of the area used by many seabirds and marine mammals, as this was repeatedly identified from peak abundances during at-sea surveys on board RV *Tridens* criss-crossing the area, typically coincided with an area where the stratification index ranged from 0.6-0.8. Closer to land, surface waters are cooler than over stratified waters further offshore and the outer boundary of the main (coastal) feeding zone (and the approximate location of the fronts separating the mixed waters along the coast and thermally stratified waters further offshore) could be visualised by using satellite images presenting sea surface temperatures (SST; Fig. 9.3.1). The exact location of the transition zone varied from day to day, but between 55°30'N and 57°30'N, the transition between mixed coastal waters and thermally stratified offshore waters occurred normally between 20 and nearly 70 km from the British east coast (Fig. 7.1.3). Beyond the Shallow Sea fronts, in central parts of the North Sea, of the four species studied, only breeding Gannets acquired a considerable part of energetic requirements. From combined data and modelling results, within the principal study area, we were able to describe the most commonly used, species-specific feeding habitats in more detail (see also Chapters 5 & 7):

Shags were exclusively found in freshwater influenced nearshore waters, mainly in the immediate vicinity of the breeding colony. They were benthic feeders, foraging at 20-27m depth, with foraging distributions tied closely to the distribution of sandy habitats (where sandeels settle).

Guillemots utilised perhaps the widest range of habitats within the principal study area, as they were most evenly distributed across the hydrographic/bathymetric regions (Chapter 7). The intriguing find however, that Guillemots nesting on the Isle of May were foraging much closer to the colony than expected from previous at-sea surveys, indicated that Isle of May breeding birds occupied only a part of the principal study area, with a range of 50km at most to the east of the island. Most of the principal study area was apparently occupied by a mix of non-breeders and breeding birds from colonies further to the south and north along the Scottish east coast (Fig.7.1.5). Incidentally, this suggested that the prime feeding habitats of Guillemots from the Isle of May were quite different from those utilised by birds from Kincardine & Deeside in the north (estimated range 110 km) and from East Lothian to Northumberland in the south (range 55-70km). While Guillemot feeding in the principal study area occurred mainly over and around the banks and in freshwater influenced areas, feeding habitats for the birds breeding on the Isle of May were distinctly closer inshore and probably more dominated by freshwater influenced waters than most other Guillemots in the area.

Kittiwakes from the Isle of May were distinctly further ranging according to the information obtained from individuals with data loggers and these data were in agreement with ship-based survey results, indicating that the Shallow Seas front region was within reach of breeding individuals. The offshore distribution of Kittiwakes overlapped with that of Guillemots, and it is likely that just as with the auks, proportionally fewer Kittiwakes at large distances from the Isle of May originated from that colony. In Kittiwakes, distribution patterns were generally more variable than in auks, with peak densities apparently developing in response to constantly changing, hydrographical conditions (see below).

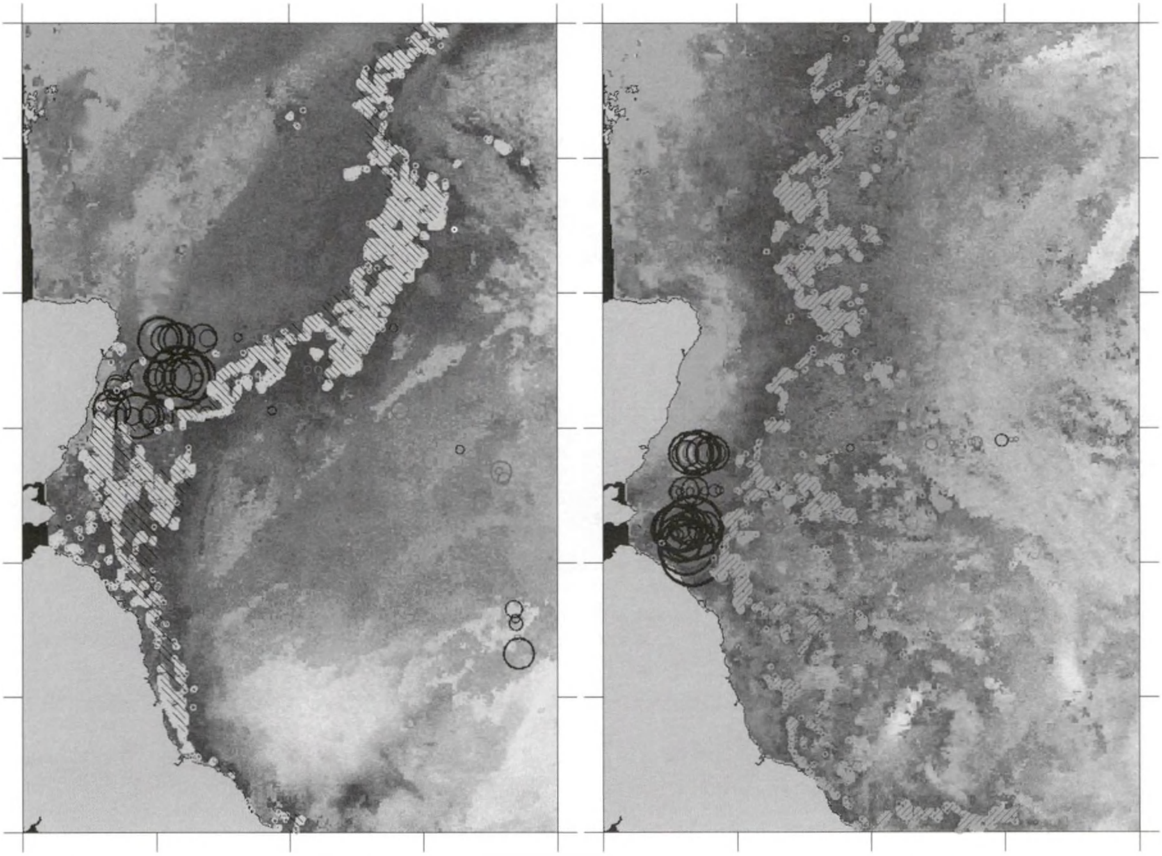


Figure 9.3.1. Examples of seabird feeding concentrations (Guillemots and Kittiwakes; circles) just inshore of the transition zone between thermally stratified central North Sea waters (SST relatively warm) and mixed coastal waters (SST cooler) in two subsequent weeks in 2002 off the Scottish east coast. The SST temperature scale runs from blue (cool) via dark blue and green to yellow and red (warm). The highlighted (pink and orange) pixels represented temperature values that were intermediate between surface temperatures on either side. Circle size is indicative for the size of the feeding flocks.

Well-mixed (nearshore) waters were the least preferred areas of the four study species during the *IMPRESS* project. During the dedicated cruise in 2003 hardly any feeding Gannets and Kittiwakes were found in that zone while 18.3% of the Guillemots were observed there (Table 7.2.2). The longer term data confirm that well mixed waters are generally avoided by feeding seabirds, although used by small numbers of all species (Fig. 5.4.13), and that multi-species feeding frenzies are both rare and particularly small (hence, short-lived) in that area (Fig. 5.4.10). Stratification, in any form, is a condition that seemingly enhances foraging conditions for all birds and therefore attracts relatively high densities. The offshore stratified zone, however, beyond the Shallow Seas fronts, is an area where species richness was consistently much lower, where the seabird community was dominated by Fulmars and Gannets, and with considerably lower densities of auks (Guillemots) and Kittiwakes that were also dubious with regard to their breeding status.

It is clear that Kittiwakes were foraging in more stratified water than Guillemots. The need for more stratified water implies that Kittiwakes are more limited in the locations in which they can forage than Guillemots and at times of greater mixing (i.e. very windy weather, spring tides) they may have to fly greater distances to deeper water where stratification is more likely to be present. Guillemots were found to be able to exploit a greater range of water mass characteristics. Gannets preferentially foraged in the strongly stratified waters seaward of the Shallow Sea front, but commonly joined multi-species feeding frenzies with surface feeding opportunities within the principal study area.

In conclusion, the study area at large could be characterised by a wide coastal strip separated from thermally stratified central North Sea waters by a Shallow Sea frontal zone. Species richness and overall seabird abundance was considerably higher within the coastal strip than in the offshore waters (Fig. 5.4.2-3). Within the coastal strip (within the principal study area), most seabird foraging occurred in freshwater influenced waters and in bank regions, while well-mixed (nearshore) waters were generally avoided (Fig. 5.4.10, 13, Figs 7.1.1-6; Table 7.2.2). The results of our study show that indeed the mixing properties (as indicated by stratification, i.e. the differences between the top and bottom of the water column, using either temperature or density differences) of the water column in which different species feed were significantly different. Gannets were found foraging in the most stratified water, while Kittiwakes used water that was less stratified than that of the Gannets, but more so than the water columns over which Guillemots mainly foraged. Shag were exclusively feeding nearshore in freshwater influenced waters.

Tidal influences on seabird foraging performance

Visual observations at sea and previous studies on the foraging ecology of seabirds indicated strong tidal effects on foraging opportunities, particularly for surface feeding seabirds (Galusha & Amlaner 1978; Vermeer *et al.* 1987; Frank 1992; Jürgens-Kammel *et al.* 1993; Irons 1998). Within an area in which birds are found foraging, the speed and direction of the tide can alter the physical characteristics of the water column in which the birds are feeding.

There was an obvious temporal effect on the location of Kittiwakes foraging during the different phases of the tide (Chapter 7.3). The majority of Kittiwakes were seen foraging in northern parts of the principal study area where the greatest change in topography occurred (depths increasing and decreasing from 65 to 45m over a hill) and foraged most strongly when the tidal current was flowing northward. Prey may be associated with either the bottom topography or the water column, but if prey is associated with water column characteristics, foraging birds should move with the tidal currents. Our observation of foraging activities of Kittiwakes at sea suggest that there is an association with both topography and water column characteristics. Observations elsewhere within the principal study area suggested that foraging was not enhanced only by tidal speed, but also by the direction of tidal currents over the change in slope of bottom topography and that the foraging of Kittiwakes may be affected by a combination of tidal speed and local topography (Chapter 7.3 for details). The observed phasing of the foraging is a potentially important result as it indicates that the favoured use of a particular phase of the tide by a species that is constrained to foraging in the surface waters can be at different phases of the tide in regions with very different topography, (i.e. regions with change in slope at different angles to the tidal current).

The influence of tidal currents was more pronounced on the feeding behaviour of Kittiwakes than on the behaviour of the other seabirds and Kittiwakes and Gannets responded significantly different at various tidal phases. Decreasing tidal speed during the ebb were the phases mostly used by Kittiwakes and Gannets targeting the maximal current speeds on both the ebb and flood tides in their preferred foraging region of the Shallow sea front. Guillemots showed almost no difference in foraging abundance with tidal phase. Assuming that internal wave action underlying these trends concentrated prey nearer the surface at distinct phases of the tide, Kittiwakes needed to adjust their activity, or their exact foraging location, continuously.

The speed and direction of the tidal currents appeared to influence the number of birds foraging. This may be because tidal currents are important forcing factors in the aggregation and movement of prey, especially in the case of very constrained predators. However, it may be the combination of local topography and tidal current which determines the exact conditions in which prey are aggregated or influenced in such a way as to be more easily predated upon. As these conditions are dependant on local attributes it is very difficult to generalise these findings over larger feeding areas. Suggestions that individual seabirds tend to specialise on certain conditions and study results demonstrating foraging area fidelity (*i.e.* Irons 1998) become quite understandable. Seabirds are likely to enhance their foraging efficiency by learning and remembering where and when they were successful and to use that knowledge to find prey on future trips.

In conclusion, the use of purpose built loggers greatly enhanced our knowledge of the foraging locations and behaviour of individual seabirds from colonies in the northwest North Sea. Advances were particularly marked for the Shag, Guillemot and Gannet. Because of the Kittiwake's more meandering flight path, the compass logger did not perform well and the GPS logger is currently too heavy for this species. Further work is required to develop an appropriate logger for this species.

The at-sea survey results (Chapter 5) corroborate earlier findings that the northwest North Sea is of vital importance for North Sea seabirds (Tasker *et al.* 1987; Skov *et al.* 1995; Stone *et al.* 1995) and illustrate the significance of the Wee Bankie/Marr Bank area. The importance of this particular area is partly due to the large breeding seabird population found along the coast (Mitchell *et al.* 2004), but has also to do with the large numbers of non-breeding seabirds summering in or visiting the area. The results suggest that apart from local breeding birds (i.e. individuals nesting in colonies within the principal study area), considerable numbers of non-breeders and adults nesting on colonies further to the north (Angus, Kincardine and Deeside) and to the south (Berwickshire and Northumberland) utilise these waters.

From our surveys and work with instrumented seabirds on breeding colonies, where locational data were combined with detailed observations of (foraging) behaviour and diving performance of seabirds at sea to highlight the main feeding areas, it became clear that most energy is acquired in a broad zone along the coast, mostly to the north of 55°30'N (Fig. 5.4.12). The entire principal study area falls within that main feeding area, but with local hotspots such as around Wee Bankie and Marr Bank, around the Isle of May and off St Abbs Head (SE Scotland). Visual observations of foraging seabirds combined with hydrographical observations as discussed above provided further insight in the habitat peculiarities of our study species and the results matched often very well with foraging locations obtained using VHF telemetry, GPS loggers, PTTs and compass loggers. Most seabird foraging occurred in freshwater influenced waters and in bank regions, while well mixed (nearshore) waters are generally avoided. The results of our study show that indeed the mixing properties in which different species feed were significantly different. Gannets were found foraging in the most stratified water, while Kittiwakes used water that was less stratified than that of the Gannets, but more so than the water columns over which Guillemots mainly foraged. Shag were exclusively feeding in nearshore freshwater influenced waters.

9.5 Prey fish abundance and reproductive success in seabirds

Fish abundance, measured as stock size or density or some index, is probably not a very accurate indicator of prey availability for seabirds in general. Common sense dictates that a depleted stock would lead to low prey availability, but fluctuating levels of prey abundance are considerably more difficult to interpret. In previous studies, the effect of reduced prey availability on breeding success was often more pronounced in surface-feeding seabirds such as Kittiwakes and terns (Monaghan *et al.* 1992; Rindorf *et al.* 2000). Prey availability as a term was in fact rather loosely used, however. Monaghan (1992) used sandeel recruitment (number of 0 group fish estimated in 1 July) and sandeel biomass (1000t) as proxies of prey availability for Arctic Terns and Guillemots and derived these values from VPAs. Rindorf *et al.* (2000) used catch per unit effort statistics (CPUE) from the Danish sandeel fishery. Other attempts to relate breeding success of some seabird species with stock size relied on VPA estimates of total stock biomass from ICES research surveys.

Sensitivity of breeding seabirds to prey fish abundance fluctuations

Life history theory suggests that animals should balance their current investment in young against the chance to reproduce in the future, with long-lived species such as seabirds being more restrictive in any increase of their current investment (Stearns 1992). During poor breeding conditions (e.g. low prey availability, adverse weather), or when the adults arrive at colonies in sub-optimal body condition, maximum fitness (i.e. by maximising future reproductive success) is achieved either by not breeding at all, by abandoning the brood, or by adjusting clutch size or even the sex of offspring (Drent & Daan 1980; De Korte 1985; Houston *et al.* 1983; Bolton *et al.* 1993; Nager *et al.* 2000). It has been suggested that long-lived species have evolved a fixed level of investment in young in order to maximize their own adult survival. Recent experimental studies, however, showed that long-lived seabirds have a flexible reproductive performance and adjust their breeding efforts according to their own body condition and to the need and growth of the chick(s) (Erikstad 1997, 1998).

Furness & Tasker (2000) presented a quantitative index of the sensitivity of different seabird species' breeding success to reduced abundance of sandeels. The index was based on seabird size (smaller birds being more sensitive), cost of foraging (high if using flapping flight, low when adapted to economical gliding flight), potential foraging range (birds with a small feeding range being more sensitive), ability to dive (surface feeders being more restricted and therefore more sensitive), amount of 'spare' time in the daily budget (the amount of ‘off duty’ time during chick-rearing as a measure of flexibility), and ability to switch diet (specialist feeders being most sensitive). According to this sensitivity index, breeding success of Gannets (index score 5), Shags (8), and Guillemots (9) were least vulnerable to reduced sandeel abundance, while Kittiwakes (16) and all coastal nesting terns (4 species, scores 19-22) in the North Sea were ranked highest.

In a study in Alaska on Middleton Island, to determine if food availability was responsible for chronic breeding failures, Kittiwakes were supplementally fed Herring *ad libitum* to non-captive adults and nestlings in two seasons. Kittiwake productivity dramatically increased when birds were fed and this increase occurred through enhancements of breeding performance at all stages of the breeding season (Gill *et al.* 2002). This example confirms that breeding success can be a useful parameter as an indicator of low prey resources.

Prey fish abundance and breeding success in the principal study area: 1997-2003

Given the strikingly different foraging strategies, habitat preferences, at-sea distributions (feeding range) and reproductive success of the various seabird study species, prey ‘availability’ to them must have varied. However, Shags and Kittiwakes are sandeel specialists and reproductive success (chicks fledged nest^{-1}) correlated positively with sandeel stock size using most measurements (Table 9.1). The strongly positive correlation between Kittiwake and Shag breeding success and sandeel abundance estimates suggests that it may be just the size of sandeel stocks that influences the performance of these birds. However, strong positive correlations were found also with total Herring (from the acoustic survey), prey fish that are not known to be of great significance for these species during breeding on the Isle of May (Chapter 5). Examining the fish abundance data in more detail, and comparing each of the indices with (local) breeding success of our seabirds, a rather confusing pattern emerges. Sandeel abundance indices derived from the demersal trawl data correlated positively with Kittiwake breeding success, but no significant correlation was found with stock assessments from the acoustic survey, arguably a better indicator of prey fish in the water column.

Correlations between breeding success of Guillemots and any of the sandeel or Herring abundance estimates were either very weak or negative, but a positive correlation was found with total Sprat. Breeding success of Guillemots measured on the Isle of May gradually declined overall, and this may have been influenced by other factors than just prey availability.

Table 9.1 Correlation coefficients (r) between prey fish biomass estimates from acoustic surveys, demersal trawls and grab sampling (Chapter 4) and breeding success of study species (chicks fledged nest^{-1} in Shag and Kittiwake, chicks fledged pair^{-1} in Guillemot), 1997-2003 (Chapter 5). Values in bold denote significant correlations (= P<0.05, ** = P< 0.02).*

		Predator		
Prey stock	methods	Shag	Kittiwake	Guillemot
0 group sandeel	acoustic	0.63	0.28	-0.19
	demersal trawl	0.41	**0.72***	-0.13
	grab sampling	-0.15	0.41	0.24
1+ group sandeel	acoustic	**0.79***	0.38	-0.57
	demersal trawl	0.58	**0.88****	-0.28
	grab sampling	0.40	0.71	0.20
0 group sandeel	[total biomass]	0.79*	**0.77***	-0.23
1+ group sandeel	[total biomass]	0.66	**0.69***	-0.57
Total sandeel	[total biomass]	0.78*	**0.80***	-0.53
0 group herring	acoustic	0.09	0.25	-0.29
1+ group herring	acoustic	0.53	0.29	0.21
Total herring	acoustic	**0.75***	**0.70***	-0.16
Total sprat	acoustic	-0.13	-0.08	**0.73***

Although a link between prey stock and breeding performance seems logic, we prefer not to value these correlations very high, particularly so because they are not very insightful. Note that the difference in prey biomass in the late 1990s compared with the early 21st century was very large, so large that any subtleties in the relationship with seabird breeding success have gone. Threshold values of prey stock or prey density cannot be set with this kind of information and the fact that acoustic survey results tended to correlate rather weakly with the performance of surface feeding seabirds should be a reason for concern. During and prior to the *IMPRESS* project, while the reproductive success of sandeel specialists such as Kittiwakes and Shags fluctuated more or less in parallel ($r_S = 0.78$, $n = 14$, $P < 0.001$), their foraging habits and at-sea habitats differed most radically (Chapter 5; Camphuysen *et al.* 2006). In contrast, while at-sea distributions of Kittiwakes and Guillemots in this area overlap substantially, their breeding success was not correlated ($r_S = -0.05$, $n = 14$, n.s.).

Seabird breeding success, timing of spring bloom and industrial fisheries

After examining relationships between breeding performance and indices of the physical environment during a period of years with and without an industrial fishery, responses by seabirds were evaluated that might reflect differences in prey availability mediated by their foraging technique (Scott *et al.* 2006). Information on the breeding success for seabirds with contrasting foraging strategies in an area where an industrial sandeel fishery has operated intermittently, and which has experienced large climatic changes (Edwards *et al.* 2002), provided a rare opportunity to investigate the effects of both climate and fishing activities.

Breeding success of Kittiwakes increased by 0.13 chicks pair^{-1} for every five days delay in timing of the spring bloom (Chapter 8.3). Kittiwakes bred thus more successfully in the years when the spring bloom and stratification in either region occurred later, but the variability was considerable. There was no evidence that the effect of date of the spring bloom on breeding success was different in fishing and non fishing years, but breeding success was 0.66 ± 0.098 (SE) chicks higher in years without fishing than in years with fishing. The final model containing both the effects of spring bloom date and the sandeel fishery explained 74% ($P < 0.001$) of the variance in breeding success. Separating years with or without a fishery, the effect of climate alone explained 56% of the variance in breeding success in years without a fishery and 10% of the variance in years with a fishery. This suggests that important climatic variables are more easily identified in the absence of the confounding effects of a fishery.

The results suggested that breeding success of Kittiwakes is higher in years when the spring bloom occurs relatively late throughout the study area. The timing of stratification and spring bloom could be used as indicators of sandeel availability. Because Kittiwakes are surface feeders and are more dependent on prey being present in the upper water column, we speculate that a later spring bloom increases the availability of prey in the upper water column during the breeding season. The mechanism by which this is achieved may be through a slowing down in the growth of juvenile sandeels, possibly coupled with a delay in the emergence of adult sandeels. With elevated levels of food occurring relatively late in the season, the trade off between predation and feeding may force fish to take longer to acquire adequate levels of food needed to survive the next winter. Either the slowing of fish growth or the extension of the time window during which sandeels are feeding actively in the water column, could potentially provide an increase in prey availability, especially to surface feeders.

These results accord well with those of Rindorf *et al.* (2000) who found that breeding success of Isle of May seabirds was higher when sandeel abundance peaked later in the season. They also help interpret the findings of Frederiksen *et al.* (2004) that Kittiwake breeding success at the Isle of May was reduced when local winter sea temperature was high in the previous year. There is a weak negative correlation between winter sea temperature and the timing of the spring bloom in the current as well as the previous year (r_p = -0.22 and r_p = -0.27 respectively). Although spring bloom timing here is modelled rather than measured, it is a more proximate and thus a much more interpretable correlate of breeding success than a single weather variable such as sea temperature. The approach allowed Scott *et al.* (2006) to separately quantify fishing and climate effects and indicates that the presence of a local sandeel fishery decreases breeding success of Isle of May Kittiwakes by 0.33 chicks pair^{-1} whereas every 5 day delay in the date of the spring bloom increases breeding success by 0.13 chicks pair^{-1}.

For Guillemots, annual variations in breeding success were not explained by either the timing of spring blooms, stratification or the presence of a sandeel fishery. Guillemots are pursuit divers, less constrained in their foraging depths than Kittiwakes, which have access to sandeels in the whole water column. This helps explain why annual variations in breeding success of different species at the same colony may not be in phase, and also why breeding success fluctuates less from year to year for Guillemots than for Kittiwakes.

9.6 Prey harvesting and predator conservation

Prey availability

Two important issues remain: (1) what factors affect prey availability and can such factors be generalised over large spatial and temporal scales, and (2) how much fish is required. If availability would reflect absolute prey abundance, different species preying on the same prey population should show synchronised variation in breeding success. If species-specific foraging techniques coupled with prevailing oceanographic conditions result in differential access to prey, breeding success is more likely to vary asynchronously between species. In this case, for each species, long-term variations in breeding success should be predictable using appropriate oceanographic covariates. Currently, commercial fishing quotas are set on the assumption that prey abundance (*i.e.* stock size) is the only important factor for multi-species management. Therefore, it is essential to understand prey availability, preferably in the context of both climate change and fishing pressure.

Foraging energetics

Furness & Tasker (2000) were uncertain about the relative importance of some factors, such as foraging energetics. In Chapter 6.4 (Enstipp *et al.* 2006), the hypothesis was tested that the impacts of reduced sandeel availability on seabirds depend on energetic and behavioural constraints during foraging. This test highlighted the interactions between physiological and behavioural constraints that condition the different responses of seabirds in the Firth of Forth area to reduced sandeel availability. While Shags and Guillemots may have sufficient time and energy to allow them to increase their foraging effort considerably, Kittiwakes and Gannets appeared more constrained by time and energy respectively. As previously recognised by Furness & Tasker (2000), consideration of energetic constraints is essential to fully evaluate the capacity of species to cope with food, particularly sandeel, shortages. Gannets scored low for the criteria used by Furness & Tasker (2000) to establish vulnerability and sensitivity indices for seabirds in the North Sea and the authors concluded that this species was generally well buffered against change. However, the results of *IMPRESS* suggest that during chick-rearing, Gannets are working at the highest metabolic level of all species considered and hence, have the least physiological capacity to increase foraging effort. This indicates that Gannets could potentially be very sensitive to a reduction in prey availability. To compensate for their energetically costly life, however, Gannets might make use of a highly profitable foraging niche and their ability to switch to exploiting other prey types is probably larger than most other seabirds. Dietary information suggests that Kittiwakes and Shags may be less able to switch to alternative prey compared to Guillemots and Gannets. In the case of Kittiwakes this might be exacerbated by its surface feeding habit that limits its foraging abilities to prey items at, or close to, the surface.

Density dependence

Density dependent competition could also occur at sea. Lewis *et al* (2001) showed theoretically how interference competition could occur with foraging Gannets that temporarily disrupt prey, so that there is no need to invoke forage fish depletion (i.e. a major argument against density dependent exploitation competition). At-sea collected data confirm the patterns described in that paper, with Gannets generally feeding in areas with very low densities of conspecifics (Chapters 5, 7). After a long period of population increase and with very high numbers of birds at sea, it is possible that the same or a similar situation is currently developing in Guillemots. Density dependent (exploitation) competition could explain the decline in breeding success while the population as a whole was increasing. Fully understanding what is going on at sea is still challenging because not only the trophic interactions are an issue of significance, but also horizontal interactions among the predators, including facilitation, as the results of MSFA studies have pointed out. There is little doubt that seabirds compete for the same resource, even if they target different cohorts in different habitats. The benefits of facilitation, a very common side-effect of the foraging activity of several deep-diving diving top-predators on the foraging opportunities for surface feeding seabirds, are still very difficult to quantify.

Year to year variability

The results from the multi-year comparison in Chapter 8 showed that there was considerable inter-annual variability in most parameters measured and that few fluctuated entirely in concert. The year 1999 came out as an extreme season, with very low prey fish stocks, a low presence of sandeels in the water column, and a very low breeding success in

Shags, Guillemots and Kittiwakes, and low numbers of seabirds at sea in the principal study area. It was a late year (stratification), but spring bloom started more or less as normal, and there was no commercial fishery for sandeels of significance. By contrast, 2001 was a season in which rather high prey-fish stocks were found, with abundant sandeels in the water column, substantial amounts of other prey fish, with a again late development of stratification and spring bloom, very high densities of Guillemots and a strong tendency by Gannets and Kittiwakes to form 'natural' MSFAs over these auks. Note that 0 group sandeel stocks were rather low in 2001, but that these fish were relatively large and heavy.

Despite several significant correlations, the variability of the material collected from year to year is substantial and the predictive value of the parameters measured is relatively low. Mechanisms influencing prey availability are clearly species-specific, but other factors must have influenced breeding populations and reproductive success, given the contrasting trends in the seabird population monitored on the Isle of May. Sandeel biomass was significantly higher in 2000-2003 than it was in the three years prior to the project and the reproductive success of Shags and Kittiwakes was relatively high in these years, albeit variable in Kittiwakes.

How much fish is enough

When we started to study the seabird-sandeel case within the *IMPRESS* project, most evidence of a negative relationship between sandeel stock and the performance of seabird populations was based on correlative analyses ('statistical approach'). Within the *IMPRESS* project, we aimed to come up with the 'individual-based static approach' and thus with, as far as possible, a description of the daily ration and the true functional responses, while taking into account several of the complexities mentioned earlier. We further wanted to take into account the spatial aspects of the feeding process, to restrict our case to short term aspects of the functional response, to acknowledge that our study system is a multi-predator and multi-prey system, and to know the effects of the hydrographical conditions on the foraging process. These four issues were more fully discussed in Chapter 6.5, showing how our knowledge might contribute to answering the question "how many fish should be left in the sea".

Much information has been gathered to assess the daily rations and to compare these to the required information on available fish stocks. Estimates based on breeding populations sizes (from Kincardine and Deeside in the north to Northumberland in the south), on DEE for adults and chicks (as given in chapter 6), an energy content of 5 kJ per gram fish and an absorption efficiency of 0.8, reveal a total consumption for the period June-July of about 16 thousand tonnes (7430, 266, 2198, and 6231 tonnes for Gannet, Shag, Kittiwake and Guillemot, resp.). Estimates of numbers at sea in the principal study area based on at-sea observations in the study area yield a total of about 8 thousand tonnes (1978, 34, 648, 5510, respectively). Both these consumption estimates are small compared to the total stock estimate (of sandeel, herring and sprat combined) averaged over years: 197 thousand tonnes (1/12 to 1/25). Yet, they form a significant part of the minimum prey fish stock found between 1997 and 2003 of 27 thousand tonnes, which is only about 2 to 3 times larger than the estimated consumption of these four top-predator species alone.

Not enough knowledge has become available on the functional reponses to fully apply the 'individual based static approach'. Using the maximum intake rate (while foraging) observed in the experiments with the cormorants (which served as a substitute for the Shag), a prey density of about 40 mg m^{-3} is required. Acoustic surveys over the years 1997 until 2003 estimated the total biomass of 1+ group sandeel in the *IMPRESS* study area to be on average 135 thousand tonnes (Table 8.2.1). The study area is about 6000 km^2 large, approximately 60 m deep. Hence the estimated biomass was on average 18 g m^{-2}, the estimated biomass density when expressed per volume of water was about 300 mg per m^3. The estimate is much higher than the required 40 mg m^{-3}, that is the prey density at which for example the Shag should be able to meet its energy requirements.

Our field studies on feeding site choices in seabirds further suggested that the functional response parameters as measured under laboratory conditions might give a too optimistic view of the field situation. At the smaller spatial scales, most seabirds seem to respond more strongly to environmental/oceanographic conditions in choosing their feeding sites than on prey density itself. This might be due to a strong interaction between the foraging process and the environmental conditions. In other words, the effective searching rate (or volume of discovery) in the field might be strongly influenced by local environmental conditions. As it might be hard to mimic these conditions in an experimental laboratory setup, one of the great challenges for future studies (apart from more controlled experiments on foraging behaviour in response to food supply) is to obtain fine-scale measurements of both food intake rate, prey density and the relevant environmental conditions simultaneously in the field.

9.7 Discussion

It has been suggested that the fishing ban currently in place for industrial fisheries in the Wee Bankie area could be "switched" on and off on the basis of the performance of an ecological indicator. The indicator chosen was Kittiwake breeding success: should breeding success drop below 0.7 chicks per breeding pair for two years in succession, the situation prevailing in 1999, then the industrial fishery in the area should cease. Following such closure, should Kittiwake breeding success then exceed 0.7 chicks per pair for two years in succession, then the fishery could be reopened. Breeding success of Kittiwakes on the Isle of May was considerably higher during the fishing ban than in the late 1990s, but thus far did not reach above 0.7 chicks per pair in two consecutive years (Fig. 5.2.2). Irrespective of this, the EC declined to adopt the recommendation to use Kittiwake breeding success as an ecological indicator and instead proposed a fixed-term closure of three years duration, thereby banning commercial industrial fishing on the Wee

Bankie, Marr Bank and Berwick's over the period 2000 to 2002. In 2003, because of the absence of a clear mechanism to close the fishery once more should problems reoccur, the decision was taken to maintain the fishery closure. At present it therefore appears that commercial sandeel fishing in this area will remain prohibited until a formal management protocol for opening and closing the fishery in response to sandeel stock management issues or marine wildlife conservation concerns can be introduced.

The final year, being the write-up phase of the *IMPRESS* project, turned out to be a highly peculiar year. Breeding success on Orkney and particularly on Shetland, to the north of our study area, had been low for a series of years (Ratcliffe 2004), but were even worse in 2004. From our principal study area, few data exist for 2004, but widespread breeding failures became apparent along much of the Scottish east coast and the first signals had been received early in the season, when mature birds appeared to return exceptionally late. We have evidence that nesting was seriously delayed in some species (notably Guillemots), but with timing of nesting and fledging near normal in others (for example in Razorbills). On the Farne Islands, alternative prey fish were fed to terns, suggesting a scarcity of sandeels (Wilson 2004). In the North Sea as a whole, sandeel stocks were exceptionally low and substantial non-breeding (or breeding failures) of seabirds occurred at the Northern Isles of Britain. We observed very low breeding success in the absence of an industrial fishery, possibly as a result of significantly reduced prey stocks due to climatic changes (Edwards & Richardson 2004; Richardson & Schoeman 2004; Wanless *et al.* 2004). The signals received from our seabirds, delayed laying, reduced clutches, lower levels of parental care and the associated increase in depredation of eggs and chicks, slower chick growth, and reduced overall reproductive success, are all too familiar and indicative for a system under food stress. Even while some seabird populations on the west coast of Britain and in northwest Norway seemed to perform better in 2004 (Wilson 2004), the area affected is large and seemingly increased in size over the last few years. In the absence of a clear understanding as to what is currently going on and if this is a temporary effect or the beginning of a trend, a precautionary approach in fisheries management is required for the years to come (Frederiksen *et al.* 2004; RCEP 2004).

Changes in numbers of many North Sea seabirds over the last 15-20 years have varied from long-term increases e.g. in Puffins, Guillemots, Razorbills and Gannets, to declines in e.g. Kittiwakes, Terns and Shags (Mitchell *et al.* 2004). Given the increasing pressures on the North Sea ecosystem from both fisheries and climate change (Edwards & Richardson 2004; Huntington *et al.* 2004), using top predators to monitor ecosystem health is an attractive concept (Boyd & Murray 2001). Combining information on at-sea distribution and activity (both from visual observations and from data collected with instrumented individuals) with oceanographic data has highlighted the potentially complex interplay between seabird foraging success, feeding location and inter-specific competition. Thanks to multi-disciplinary projects such as *IMPRESS*, do we begin to understand the functional links between marine predators, their prey and the marine climate and may we thus come closer to ecosystem-based fisheries management. However, as the results presented here clearly indicate, we are still some way from having all the background knowledge required for such an approach. Simple signals such as the breeding success of one or few species to indirectly monitor the well being or prey availability of a complex and large community heavily relying on a single or few prey species do not provide sufficient insight necessary for an adequate management of ecologically important areas.

Prey fish stocks, notably sandeels, prior to and following the year 2000 in the principal study area were an order of magnitude different. It seems clear that many seabirds were under stress when sandeel stocks fell below 100 000 tonnes, irrespective of the relative large (but comparatively tiny) Sprat stocks and moderate (and tiny) Herring stocks. Breeding success of at least three study species was high, albeit variable, in 2000-2003, when prey stocks were on average well in excess of 250 000 tonnes (Tables 8.2.1-2, 8.5.1). Simple advice to stay on the safe side could thus read: sandeel stocks in excess of 250 000 would suffice for most seabirds breeding in the area.

However, environmental variation affects breeding and survival, and climate change is predicted to have an impact on population dynamics of seabirds, marine mammals and predatory fish in the northwest North Sea by influencing food quality or availability (Thomson & Ollason 2001). Global climate change is likely to cause shifts in the timing of peak food availability, and in order to adapt successfully to current and future climate change, animals need to be able to adjust the time at which they initiate breeding (Frederiksen *et al.* 2004b). We have no data for prey fish stocks in the principal study area for 2004, when breeding success generally crashed, apparently following a major decline in prey fish biomass or profitability (a combination of quality and availability), but in the absence of a (significant) fishery. It remains to be seen if this crash was an outlier and a rare exception, or part of a trend developing further to the north in the North Sea for at least a decade or two, with prey availability and breeding success seriously reduced for many seabird species. Richardson & Schoeman (2004) showed that sea surface warming in the Northeast Atlantic is accompanied by increasing phytoplankton abundance in cooler regions and decreasing phytoplankton abundance in warmer regions. This impact propagates up the food web (bottom-up control) through copepod herbivores to zooplankton carnivores because of tight trophic coupling. Future warming is therefore likely to alter the spatial distribution of primary and secondary pelagic production, and is eventually (if not already) likely to affect top-predators in the northwest North Sea. A study of populations of North Sea plankton suggested that annual phenological cycles such as migration and blooming are changing as the ocean warms (Edwards & Richardson 2004). The study found that not all species are affected in the same way, so that peaks that once occurred together or in close succession are now moving apart a breakdown of ecosystem synchronicity that could, warn the authors, have major consequences in years to come. Between 1973 and 2002, the average size of 0-group sandeels declined by 11.1 mm fish^{-1}. Over the same period, 1+ group sandeels showed an overall reduction in size of 19.4 mm fish^{-1} and in both cases, the change in length corresponded to a 40% decline in energy content. These long-term trends in size-at-age are likely to have had major demographic consequences for this aggregation in terms of delayed sexual maturity and lower age-specific fecundity (Wanless *et al.* 2004).

Long-term climatic and oceanographic cycles regulate seabird populations on decadal time-scales (Tyres 1979) and seabirds in the North Sea have been increasing for decades, apparently in response to a combination of reduced persecution and greatly enhanced prey availability (Camphuysen & Garthe 2000). Their success may be about to change, if we understand the signals well and the recent concerns about the impact of climate change on the North Sea ecosystem, coupled with the largely unexplained crash in North Sea sandeel stocks in 2002-2004 (ICES 2004) would call for extreme care with an important area such as the Wee Bankie/Marr Bank complex.

The scientific staff on the Pelagia cruise, June 2003, Wee Bankie area: mission completed

Chapter 10 Conclusions

In this concluding chapter, the main results of the preceding chapters are listed without further discussion, followed by suggestions and recommendations for future research in Chapter 11. The sequence of the conclusions follows the structure of the report.

- The objective of the project was to determine the relationship between sandeel population characteristics, hydrography, the foraging success and breeding performance of seabirds and the effect of fishing and the risk of overfishing in an ecologically important area.

Sandeel fisheries, sandeels and other prey fish

- Industrial fisheries for sandeels in the Wee Bankie/Marr Bank sandbank complex of the Firth of Forth in SE Scotland took off in the early 1990s. Sandeel landings from this area rarely constituted more than 10% of the total North Sea landings.
- Coincident with the increase in the removal of sandeels from areas close to the Scottish east coast, seabird breeding success at colonies along the coast started to decline.
- The fishery was closed in 2000, but fishing pressure was very low in 1999. Over the period 2000 to 2003 a limited amount of sandeel fishing was permitted in the area to allow the maintenance of a scientific catch. In 2003, the decision was taken to maintain the fishery closure.
- ICES classifies the North Sea sandeel stock as a whole as having reduced reproductive capacity and SSB in 2004 was estimated to be at a historic low value (325 000 t).
- Acoustic survey and demersal trawl data, collected 1997-2003, suggest that total biomass of sandeels in the study area was significantly higher in the four years when sandeel fishing was prohibited (250 000t-335 000t) than in the three previous years when they had been fished (25 000t-89 000t).
- Biomass estimates of Herring from acoustic surveys (1997-2003), were significantly higher during 2000-2003 (4000t-6400t) than in the three earlier years (1700t-3800t). The biomass of Sprats in all years was relatively low (<3000t).

Oceanography

- The water column for the principal study area was well mixed for most of the year and the onset of stratification was usually observed in April and reached a maximum in late July/ early August. The western and/or eastern extremes of the primary study area generally being the more strongly stratified regions. The western region, close to the coast, is influenced by fresh water while the eastern region away from the coast is deep enough for surface thermal stratification not to be mixed by tidal friction.
- Separate regions with different mixing and/or productivity characteristics and bathymetry were defined: Inner and Outer Banks, the Shallow sea front and the Offshore stratified region, the Outer Bank region, Mixed (nearshore) Waters and Freshwater Influenced Waters (Fig. 3.2.8).
- Tides play an important role in the foraging of seabirds.
- Over the last 30 years, meteorological variability drove most of the inter-annual variability of both the onset of stratification (86% of the variance) and the spring bloom (70% of the variance), with variability in the spring solar irradiance being more important than variability in wind stress. The North Atlantic Oscillation (NAO) played a significant role in generating inter-annual variability in the timing of spring stratification and the spring bloom.

Seabirds breeding: population trends, reproductive success and diet

- There were *c* 45 000-48 000 Apparently Occupied Sites (AOS) of Northern Gannets on the Bass Rock and counts carried out in 1994 and 2004 suggested a continuous increase. Counts of European Shag nests declined sharply in 1999 due to a large proportion of adults not breeding that year, but numbers subsequently increased. Breeding populations of Common Guillemots increased markedly, but there was a continuous decline in Black-legged Kittiwake numbers between 1997 and 2003.
- Shags showed a general increase in breeding success over 1997-2003, except for 1999 when success was low. Guillemot breeding success showed an overall decline. The number of chicks fledged per pair in Kittiwakes was very variable, with no clear trend. Breeding success of Gannets, only available for 2002 and 2003 was consistently high, as in previous years.

- Breeding success during 2001-2003 varied, with that in Shags being the highest recorded at the Isle of May, but with values for Guillemots being some of the lowest recorded. Kittiwake breeding success fluctuated, but was higher than during the late 1990s.
- Shags were almost completely dependent on sandeels, except in 1999 when a large proportion did not breed. Kittiwakes also depended heavily on sandeels. The main prey brought in by Guillemots for their chicks was Sprats, but adult birds were found to have been feeding substantially on sandeels. Gannets, took a wide variety of prey.
- The importance of sandeels in the diet of the seabird predators has been demonstrated and evidence of similarities in patterns of seasonal change has been provided with a consistent shift from 1+ group to 0 group.

Seabirds at-sea: distribution and foraging behaviour

- In the study area at large, the offshore seabird community comprised at least 37 different seabird species.
- In comparison with the study area at large, the overall abundance of Guillemots, Puffins, Kittiwakes, Razorbills and Gannets is relatively high, whereas the abundance of Northern Fulmars is fairly low. The number of Shags observed was very low as a result of their inshore distribution; sea-going research vessels seldom venture in these shallow waters.
- Clear-cut, generalised seabird distribution patterns were derived, with Gannets far-ranging, Guillemots and Kittiwakes highly concentrated in the western (nearshore) half of the study area at large, and with Shag concentrated in inshore waters.
- The main feeding area for auks and Kittiwakes was within approximately 100km from the coast, with peak densities usually slightly nearer the coast. Gannets occurred in the entire study area at large. Seabird densities and species richness declined and species composition altered with increasing distance to the UK coast. The principal study area was situated within the areas with highest mean top-predator densities and diversity.
- Shags breeding on the Isle of May used three main foraging areas: inshore, west and north of the colony; and close to the island.
- Guillemots with compass loggers were foraging much closer to the colony than expected from at-sea surveys, with the furthest distance from the colony estimated at 25.3 km.
- Kittiwakes carrying instruments used a wide variety of foraging areas, from inshore coastal areas in St Andrews Bay area out to the Wee Bankie/Marr Bank region. Mid-July foraging locations became more concentrated on the western edge of the Wee Bankie.
- Gannet locations extended to the Bergen/Viking Bank (West Norway), Halibut Bank (NE Scotland), Fisher Bank (north central North Sea), Dogger Bank (south central North Sea) and the Outer Silver Pit (southern North Sea).
- In biomass terms, the seabird community in the principal study area was dominated by auks (Guillemot, Puffin and Razorbill), Gannets and Kittiwakes (98.0% of all birds found in transect). The energy requirements of seabirds per unit area within the principal study area (118 380 kJ $\text{day}^{-1}\ \text{km}^{-2}$) were on average 3.9x higher than those in the study area at large (30 260 kJ $\text{day}^{-1}\ \text{km}^{-2}$).
- Feeding Gannets were mostly deep plunge-diving or scooping and the latter activity entirely associated with 'natural' MSFAs. Gannets associated with dolphins were typically deep plunge-diving and solitary Gannets were either shallow- or deep plunge-diving. Feeding Kittiwakes were dipping or shallow plunge-diving. Guillemots were observed pursuit diving from the surface mostly, but were occasionally pursuit plunging in attempts to keep up with fast moving fish shoals.
- In Shags, the commonest foraging depth was between 21-30 m. There was no significant difference in the number of dives per trip between years. In Guillemots, the number of dives per bout varied from 12.2 in 2001 to 4.8 in 2003. Depth distributions peaked between 41-60 m in 2001 and 2002, but was <20m deep in 2003. Comparing these data with results from 1997-98 indicated that dives were shorter, but surface times were longer, such that dive efficiency was generally lower in 2001-2003. Mean foraging depth was between 39m and 43m in all years except in 2003. In Gannets, dive depth did not differ between years (2002, mean = 2.50 ± 0.06 m; 2003, mean = 2.96 ± 0.10 m).
- Three major types of MSFAs were recognised: (1) human induced feeding flocks (birds associated with (fishing) vessels), (2) marine mammal-induced feeding flocks (birds attracted to hunting cetaceans or seals), and (3) 'natural' feeding flocks (seabirds, sometimes with marine mammals, jointly exploiting a shared resource).
- Most birds that were recorded as feeding participated in feeding flocks and most these flocks comprised several species (multi-species feeding associations, MSFAs). In the study area at large, in 12 out of 18 common species recorded, at least 80% of the feeding individuals were joining some sort of MSFA.
- Within the principal study area, relatively more birds joined 'natural' MSFAs in Guillemots (88.2%, $n = 6567$) and Gannets (56.0%, $n = 2913$), but Kittiwakes had a slightly stronger tendency to feed among conspecifics (49.4% in 'natural' MSFAs).
- 'Natural' MSFAs were generally formed in coastal waters of very high seabird density and were nearly all encountered within 100km from the nearest coast. Flock size varied with distance to the coast, with numerous

but relatively small MSFAs formed within 20km from the coast, fewer and larger flocks at 20-50km distance, and with numerous relatively small flocks at 50-70km distance.

- The proportions of seabirds in MSFAs were not accordance with the relative densities at sea and the most aerial species, surface feeding gulls (both Kittiwakes and larger species), had a greater tendency to become flock participants than expected on the basis of their overall abundance at sea.
- MSFAs formed around marine mammals mainly occurred in stratified offshore waters, and within c. 80km from the coast, cetaceans were largely ignored by seabirds.
- Shags made similar numbers of trips per day in 2001 and 2002, but the proportion of time spent foraging was greater in 2002, and less time was spent on land. There was no difference in the number of trips by Guillemots made per day between 2002 and 2003. Kittiwakes made more trips per day in 2003 than in 2002 or 2001, and birds spent a higher proportion of time in foraging flight and consequently less time on the water. The percentage time spent at sea in Gannets did not vary between years. Gannets spent 0.3%, 43.1%, and 56.6% of time respectively diving, flying and resting/swimming on the surface of the water.
- Dives of Gannets, as well as feeding events, occurred all along the foraging trips, with the first dive of a trip performed at a median distance of 137.8 km from Bass Rock (range 21.7 – 167.1 km) in 2002, and of 57.42 km (range 1.29 – 275.92 km) in 2003. Shags were successful on approximately 10% of dives and in 55-65% of bouts. In Guillemot, recorded success rate per dive (33%) was much higher than in Shags.

Seabird energetics

- Water temperature, dive depth, and digestive phase we demonstrated to be important factors that strongly affect the amount of energy which seabirds have to expend during foraging.
- European shags did not employ a strategy of regional hypothermia to prolong dive duration.
- Foraging success of cormorants foraging on live fish depended to a large degree on fish density, while fish behaviour had important consequences for predator performance.
- Prey size, light conditions, bird condition (body mass) and water temperature had little impact on cormorant foraging behaviour within the range tested. Dive depth greatly affected dive duration of cormorants but had little effect on the overall success rate of dives.
- Dietary information suggested that Kittiwakes and Shags may be less able to switch to alternative prey compared to Guillemots and Gannets. In the case of Kittiwakes this might be exacerbated by its surface feeding habit that limits its foraging abilities to prey items at, or close to, the surface.
- Shags and Guillemots were estimated to have sufficient time and energy to allow them to increase their foraging effort considerably, Kittiwakes and Gannets appeared more constrained by time and energy respectively and during chick-rearing Gannets are working at the highest metabolic level of all species and have the least physiological capacity to increase foraging effort.
- Total consumption for June-July for four study species within the principal study area based on breeding seabirds within and around the principal study area amounted to 16 thousand tonnes. Estimates based on numbers seen foraging at sea in the principal study area yield a total of at least 8 thousand tonnes. Both estimates are low compared to the total prey stock estimate averaged over the years: *c.* 197 thousand tonnes (1/12 to 1/25). Yet, they form a significant part of the minimum prey fish stock found between 1997 and 2003 of 27 thousand tonnes, which is only about 2 to 3 times larger than the estimated consumption of these four top-predator species alone.
- Using the maximum intake rate (while foraging) observed in the experiments with cormorants, a prey density of about 40 mg m^{-3} is required. Surveys during 1997-2003 estimated the total biomass of 1+ group sandeel in the *IMPRESS* study area to be on average 300 mg per m^{3}.

Seabirds, foraging habitat characteristics from a combination of methods

- The density of MSFAs per unit area were highest in Freshwater Influenced Waters and Offshore Stratified Waters. By far the largest MSFAs were found in the Bank Areas.
- Northern Gannets acquired 24% of their energy in Freshwater Influenced Waters, 11% in Mixed Waters (mostly in deeper waters), 59% over the Banks and 7% in Offshore Stratified Waters.
- Kittiwakes acquired 53% of their energy on the Banks, 18% in Offshore Stratified Waters, 27% in Freshwater Influenced waters and only 2% in Mixed Waters.
- Guillemots acquired 48% of the energy on the Banks, 20% in Offshore Stratified Waters, 24% in Freshwater Influenced Waters and only 8% in Mixed Waters.
- A combination of all data suggests that for these three species the Bank Areas are the most important foraging grounds (49% of the energy acquired) and that Mixed Waters near the coast were relatively unimportant (8%).
- All Shags were foraging in waters that have been categorised as Freshwater Influenced and this is the area where these birds acquired most energy required.
- Kittiwakes utilised a broad zone off the Scottish east coast, with peak densities to the shallow-sea front. Dipping, shallow plunge-diving, and surface pecking were characteristic types of feeding behaviour and

Kittiwakes were commonly seen to join 'natural' MSFAs in Freshwater-Influenced coastal waters and over the Banks. The foraging distance of instrumented Kittiwakes originating from the Isle of May accorded well with the distance from the breeding colony to the shallow sea front. The front appears an outer boundary for breeding Kittiwakes, and foraging occurred throughout the zone between the colony and the front.

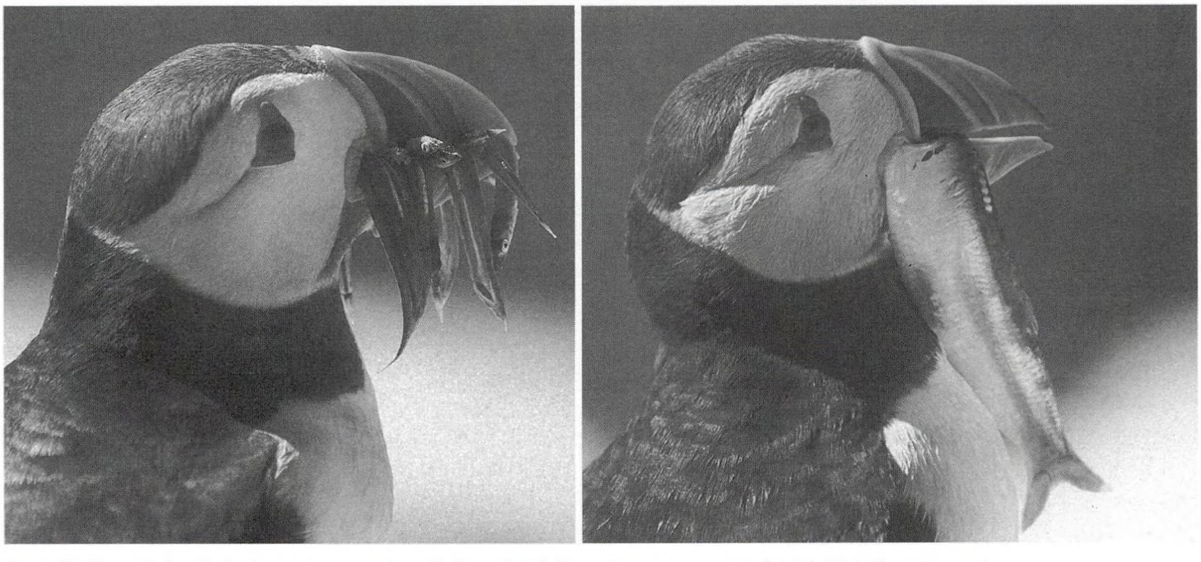
- The shallow sea front is important for mid-water divers too, but these species can exploit the entire water column. Guillemots were essentially highly widespread in a broad zone along the coast, with relatively lower concentrations of feeding individuals in mixed coastal waters and beyond the shallow sea front in offshore stratified waters. Foraging locations from Isle of May breeding birds equipped with compass loggers in 2002 and 2003 suggested that Guillemots from this colony foraged considerably nearer the colony than these overall densities would suggest. A subsequent analysis of directions of flight of birds carrying fish in the principal study area, suggested a high degree of overlap between logger data and at-sea data with regard to feeding range, such that birds flying towards the Isle of May were exclusively seen in and immediately around the area where instrumented birds were found foraging in 2002 and 2003.
- Adults Guillemots catching prey for their chick utilised only a small part of the principal study area and mainly the west side of the Wee Bankie/Marr Bank complex. The data suggest that the bulk of the (adult) Guillemots in the eastern part of the principal study area breed in Kincardine and Deeside and in East Lothian, Berwickshire and or Northumberland.
- Estimated maximum foraging ranges for Guillemots from the Isle of May from sightings were in the range of 50km, whereas those from St Abb's Head were estimated at *c.* 55 km, Guillemots nesting on the Farne Islands at 70 km, and birds nesting at Fowlsheugh at 110 km.
- In all three years, Shags were foraging inshore of the Isle of May and the water they foraged in was mixed. The lack of a preference for different phases of the tide by Shags suggests that there are patterns in the behaviour of (adult) sandeels that are more important in determining the timing of foraging than reduced distance between sea surface and foraging habitat apparent during low tide.
- Gannets were by far the furthest ranging species, foraging abundantly within and beyond the principal study area. Behavioural observations during ship-based surveys indicated that the foraging techniques, the tendency to participate in multi-species feeding frenzies, the tendency to join hunting cetaceans as well as the opportunities to scavenge at fishing vessels varied considerably between areas. 'Shallow-feeding' locations from activity recorders coincided with the areas where type 3 MSFAs were joined most frequently by Gannets and where scooping behaviour was observed during at-sea surveys.
- The continuous oceanographic data from the *Pelagia* 2003 cruise produced a detailed 'snapshot' of the water column characteristics underneath foraging birds. Gannets were found foraging in the most stratified water, while Kittiwakes used water that was less stratified than that of the Gannets, but more so than the water columns over which Guillemots mainly foraged. Within the principal study area, Guillemots were relatively evenly distributed across the regions, but were most abundant in the Inner Bank region. Nearly half of all Kittiwakes seen foraging were observed within the Outer Bank region and two thirds of all Gannets were found in the Offshore stratified region. This separation of bird species determined mainly by the difference in stratification (using top and bottom temperature differences) indicates that their foraging habitat can be defined using rather straightforward and predictable physical characteristic of the water column.
- The need for stratified water implies that Kittiwakes are more limited in the locations in which they can forage than Guillemots and at times of greater mixing they may have to fly greater distances to deeper water where stratification is more likely to be present.
- Kittiwakes and Gannets responded significantly different at various tidal phases. Decreasing tidal speed during the ebb were phases mostly used by Kittiwakes and Gannets targeting the maximal current speeds on both the ebb and flood tides in their preferred foraging region of the Shallow sea front. Guillemots showed almost no difference in foraging abundance with tidal phase.
- No clear absolute relationship between the density of any seabird species and the density of either sandeels, Herring or Sprats could be determined. High densities of each of the major sandeel, or small pelagic fish, predators could be linked to patches of one or other, or all three, of the prey species.

Inter-annual variability

- During 1997-2003, the onset of stratification occurred between 7 April and 30 April (23 d difference between seasons at most) and was very early in 2002 (7 April) and very late in 2001 (30 April) (Table 3.1). Spring bloom lasted between 5.8 (2001) and 7.5 weeks (2000) and commenced between 14 April (2002) and 1 May (2001), or a two-week difference between seasons.
- Breeding success of Kittiwakes increased by 0.13 chicks pair^{-1} for every five days delay in timing of the spring bloom. The model containing both the effects of spring bloom date and the sandeel fishery explained 74% ($P < 0.001$) of the variance in breeding success. Separating years with or without a fishery, the effect of climate alone explained 56% of the variance in breeding success in years without a fishery and 10% of the variance in years with a fishery, suggesting that important climatic variables are more easily identified in the absence of the confounding effects of a fishery.

- A later spring bloom may have increased the availability of prey in the upper water column during the breeding season for Kittiwakes through a slowing down in the growth of juvenile sandeels, possibly coupled with a delay in the emergence of adult sandeels.
- For Guillemots, annual variation in breeding success was not explained by the timing of spring blooms, nor stratification in either oceanographic region or the sandeel fishery.
- For Kittiwakes and Shags there is an interaction between the timing of egg-laying relative to the timing of spring bloom and the effect of the fishery. The results provide further evidence that the presence of a fishery in the area has an additional adverse effect on seabird reproductive output.
- Between years, in the study area at large, the density of Guillemots was four times the density of Kittiwakes which was in turn about twice the density of Gannets at sea. Within the principal study area, however, a rather erratic pattern in the relative abundance of Guillemots was found, probably caused by non-breeders that were more abundant within the principal study area in some years than in others.
- All species (except Shag) showed a remarkable variability in their tendency to forage within natural MSFAs in the principal study area, with very high values for all three species in 1997 and 2001 and a high figure for Guillemots and Kittiwakes in 2004.
- There was considerable inter-annual variability in most parameters measured. The year 1999 came out as an extreme season, with very low prey fish stocks and much reduced breeding success in Shags, Guillemots and Kittiwakes, low numbers of seabirds at sea but there was no commercial fishery for sandeels of significance. By contrast, 2001 was a season in which rather high prey-fish stocks were found, with abundant sandeels in the water column, substantial amounts of Herring and Sprat, with a late development of stratification and spring bloom, high densities of Guillemots and a very strong tendency by Gannets and Kittiwakes to join these birds in natural MSFAs.
- Sandeel biomass was significantly higher in 2000-2003 than it was in the three years prior to the project and the reproductive success of Shags and Kittiwakes was relatively high in these years, albeit variable in Kittiwakes.
- In 2004 breeding success and prey stocks were seriously reduced in the study area at large.
- Breeding success of seabirds on the Isle of May was very low in Shags, and in all three auks. Kittiwakes reproduced less than the long-term average, and Fulmar production was the lowest ever recorded. These results should be put into the context of a much larger area with the productivity for most species being the lowest in recent history and sandeel shortages were evident from dietary studies in several areas.

Prey fish stocks, notably sandeels, prior to and following the year 2000 in the principal study area were an order of magnitude different. Many seabirds were under stress when sandeel stocks fell below 100 000 tonnes in the late 1990s, while breeding success was generally high in 2000-2003, when prey stocks were on average well in excess of 250 000 tonnes. Long-term climatic and oceanographic cycles regulate seabird populations on decadal time-scales and seabirds in the North Sea have been increasing for decades, apparently in response to a combination of reduced persecution and greatly enhanced prey availability. Their success may be about to change, if we understand the signals currently received from large parts of the northwest North Sea well and the recent concerns about the impact of climate change on the North Sea ecosystem, coupled with the largely unexplained crash in North Sea sandeel stocks in 2002-2004, would call for extreme care with an important area such as the Wee Bankie/Marr Bank complex.



Atlantic Puffin with Sandeels Ammodytes marinus (left) and with Sprat Sprattus sprattus (right) (C.J. Camphuysen)

Chapter 11 References

Aebischer N.J. 1986. Retrospective investigation of an ecological disaster in the Shag, *Phalacrocorax aristotelis* - a general method based on long-term marking. J. Anim. Ecol. 55:613-629.

Anonymous 2004a. Report of the Working Group on Seabird Ecology, FRS Marine Laboratory, 29 March -2 April 2004. Oceanography Committee, ICES Marine Habitat Committee ICES CM 2004/C:05 Ref. ACME, ACE, International Council for the Exploration of the Sea, Copenhagen, Denmark.

Anonymous 2004b. Report of the Planning Group for Herring Surveys. ICES CM 2004/G:05 Ref. D.

Ashmole N.P. 1971. Sea bird ecology and the marine environment. In: Farner D.S. & King J.R. (eds). Avian Biology, 1: 224-286. Academic Press, New York.

Avery M. & Green R. 1990. Sad story of Shetland's seabirds. New Scientist 13 Oct 1990: 50-51.

Bailey R.S. 1986. Food consumption by seabirds in the North Sea in relation to the natural mortality of exploited fish stocks. ICES C.M. 1986/G: 5.

Bailey R.S. 1989. Interactions Between Fisheries, Fish Stocks and Seabirds. Mar. Poll. Bull. 20(9): 427-430.

Bailey R.S., Gauld J.A. & Kunzlik P.A. 1989. Recent changes in the population of the Lesser Sandeel, *Ammodytes marinus* Raitt, at Shetland and their effect on the food supply of predatory seabirds. J. Fish Biol. (Suppl.)

Ballance L.T., Pitman R.L. & Reilly S.B. 1997. Seabird community structure along a productivity gradient: importance of competition and energetic constraint. Ecology 78(5): 1502-1518.

Barrett R.T., Røv N., Loen J., Montevecchi W.A. 1990. Diets of shags *Phalacrocorax aristotelis* and cormorants *P. carbo* in Norway and possible implications for gadoid stock recruitment. Mar. Ecol. Progr. Ser. 66: 205-218.

Beaugrand G. 2004. The North Sea regime shift: Evidence, causes, mechanisms and consequences. Progress in Oceanography 60: 245-262

Begg G.S. & J.B. Reid 1997. Spatial variation in seabird density at a shallow sea tidal mixing front in the Irish Sea. ICES Journ. Mar. Sci. 54: 552-565.

Bennet D.C. & Hart L.E. 1993. Metabolizable energy of fish when fed to captive Great Blue Herons (*Ardea herodias*). Can. J. Zool. 71: 1767-1771.

Birt-Friesen V.L., Montevecchi W.A., Cairns D.K., Macko S.A. 1989. Activity-specific metabolic rates of free-living Northern Gannets and other seabirds. Ecology 70(2): 357-367.

Blaxter J.H.S. & Hunter J.R. 1982. The biology of the clupeoid fishes. Advances in Marine Biology 20: 3-203

Bolton M., Monaghan P. & Houston D.C. 1993. Proximate determination of clutch size in Lesser Black-backed Gulls: the roles of food supply and body condition. Can. J. Zool. 71: 273-279.

Bourne W.R.P. 1981. Some factors underlying the distribution of seabirds. In J. Cooper (ed.) Proc. Symp. birds Sea and Shore, 1979. African Seabird Group, Cape Town, South Africa.

Boyd I.L., S. Wanless & C.J. Camphuysen (eds) 2006. Top predators in Marine Ecosystems. Cambridge University Press, Cambridge.

Boyd I.L. & T. Arnbom 1991. Diving behavior in relation to water temperature in the Southern elephant seal – foraging implications. Polar Biology 11: 259-266

Boyd I.L. & W.A. Murray 2001. Monitoring a marine ecosystem using responses of upper trophic level predators. J. Anim. Ecol. 70: 747-760.

Briggs K.T., D.G. Ainley, L.B. Spear, P.B. Adams & S.E. Smith 1988. Distribution and diet of Cassin's Auklet and Common Murre in relation to central California upwellings. In: Oulett H. (ed.) Proceedings of the 19th International Ornithological Congress, Ottawa, 1986: 982-990. University of Ottawa Press, Ottawa.

Bryant D.M. & R.W. Furness 1995. Basal metabolic rates of North Atlantic seabirds. Ibis 137: 219-226.

Cairns D.K. 1987. Seabirds as indicators of marine food supplies. Biol. Oceanogr. 5: 261-271.

Cairns D.K. 1992. Bridging the gap between ornithology and fisheries science: use of seabird data in stock assessment models. Condor 94: 811-824.

Camphuysen C.J. 1996. De verspreiding van zeevogels in de Noordzee: naar een beter begrip van patronen en verbanden. Sula 10: 41-88.

Camphuysen C.J. 2001a. Seabirds and fisheries interaction. In: Steele J.H., Thorpe S.A. & Turekian K.K. (eds) Encyclopedia of Ocean Sciences: 2677-2686. Academic Press, London.

Camphuysen C.J. 2001b. Food of an adult breeding female Common Guillemot *Uria aalge* drowned off the scottish east coast, summer 2001. IMPRESS Report 2001-003, Internal Report Netherlands Institute for Sea Research, Texel.

Camphuysen C.J. 2005. Seabirds at sea in summer in the NW North Sea. British Birds 98: 2-19.

Camphuysen C.J., C.M. Berrevoets, H.J.W.M. Cremers, A. Dekinga, R. Dekker, B.J. Ens, T.M. van der Have, R.K.H. Kats, T. Kuiken, M.F. Leopold, J. van der Meer & T. Piersma 2002. Mass mortality of Common Eiders (*Somateria mollissima*) in the Dutch Wadden Sea, winter 1999/2000: starvation in a commercially exploited wetland of international importance. Biological Conservation 106(3): 303-317.

Camphuysen C.J., B. Calvo, J. Durinck, K. Ensor, A. Follestad, R.W. Furness, S. Garthe, G. Leaper, H. Skov, M.L. Tasker & C.J.N. Winter 1995. Consumption of discards by seabirds in the North Sea. Final report to the European Comm., study contr. BIOECO/93/10, NIOZ-Report 1995-5, Netherlands Institute for Sea Research, Texel.

Camphuysen C.J., A.D. Fox, M.F. Leopold & I.K. Petersen 2004. Towards standardised seabirds at sea census techniques in connection with environmental impact assessments for offshore wind farms in the U.K. Report commissioned by COWRIE for the Crown Estate, London. Royal Netherlands Institute for Sea Research, Texel.

Camphuysen C.J. & S. Garthe 2000. Seabirds and commercial fisheries: population trends of piscivorous seabirds explained? Chapter 11 In: Kaiser M.J. & S.J. de Groot (eds). Effects of fishing on non-target species and habitats: Biological, Conservation and Socio-Economic Issues: 163-184. Blackwell Science, Oxford.

Camphuysen C.J., B. Scott & S. Wanless 2006. Distribution and foraging interactions of seabirds and marine mammals in the North Sea: multi-species foraging assemblages and habitat-specific feeding strategies. In: Boyd I.L., S. Wanless & C.J. Camphuysen (eds). Top predators in Marine Ecosystems: 82-97. Cambridge University Press, Cambridge.

Camphuysen C.J. & A. Webb 1999. Multi-species feeding associations in North Sea seabirds: jointly exploiting a patchy environment. Ardea 87: 177-198.

Cochran W.W. 1980. Wildlife telemetry. In: Schemnitz S.D. (ed.) Wildlife Management Techniques Manual 4th edition: 507-520. Wildlife Society, Washington.

Constable A.J., W.K. de la Mare, D.J. Agnew, I. Everson & D. Miller 2000. Managing fisheries to conserve the Antarctic marine ecosystem: practical implementation of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR). ICES Journal of Marine Science 57: 778-791.

Cooper J. 1978. Energetic requirements for growth and maintenance of the cape gannet (Aves: Sulidae). Zool. Afr. 13: 305-317.

Coulson J.C. 2002. Black-backed Kittiwake *Rissa tridactyla*. In: Wernham C., Toms M., Marchant J., Clark J., Siriwardena G. & Baillie S. (eds) The migration atlas: movements of the birds of Britain and Ireland. British Trust for Ornithology, T. & A.D. Poyser, London.

Cowx I.G. (ed.) 2003. Interactions between fish and birds: implications for management. Fishing News Books, Blackwell Science, Oxford.

Coyle K.O., Hunt G.L. Jr, Decker M.B. & Weingartner T.J. 1992. Murre foraging, epibenthic sound scattering and tidal advection over a shoal near St George Island, Bering Sea. Mar. Ecol. Progr. Ser. 83: 1-14

Cramp S., Bourne W.R.P. & Saunders D. 1974. The Seabirds of Britain and Ireland. Collins, London.

Croll D.A. & McLaren E. 1993. Diving metabolism and thermoregulation in Common and Thick-billed Murres. J. Comp. Physiol. B 163: 160-166.

Croxall J.P. (ed.) 1987. Seabirds: feeding ecology and role in marine ecosystems. Cambridge Univ. Press, Cambridge.

Daan N. 1989. Database Report of the Stomach Sampling Project 1981. ICES Cooperative Research Report 164: 1-144.

Daan N., P.J. Bromley, J.R.G. Hislop & N.A. Nielsen 1990. Ecology of North Sea fish. Neth. J. Sea Res. 26: 343-386.

Daunt F. 2000. Age-specific breeding performance in the European Shag *Phalacrocorax aristotelis*. Unpubl. PhD-thesis, Univ. Glasgow, Glasgow.

Daunt F., Benvenuti S., Harris M.P., Dall'Antonia L., Elston D.A., Wanless S. 2002. Foraging strategies of the Black-legged Kittiwake *Rissa tridactyla* at a North Sea colony: evidence for a maximum foraging range. Mar. Ecol. Progr. Ser. 245: 239-247.

Daunt F., Peters G., Scott B., Grémillet D. & Wanless S. 2003. Rapid-response recorders reveal interplay between marine physics and seabird behaviour. Mar. Ecol. Progr. Ser. 255: 283-288.

Davoren G.K., Montevecchi W.A. & Anderson J.T. 2003. Distribution patterns of a marine bird and its prey: habitat selection based on prey and conspecific behaviour. Mar. Ecol. Progr. Ser. 256: 229-242.

Decker M.B. & G.L. Hunt Jr. 1996. Foraging by murres (*Uria* spp.) at tidal fronts surrounding the Pribilof Islands, Alaska, USA. Mar. Ecol. Prog. Ser. 139: 1-10.

Drent R.H. & S. Daan 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68: 225-252.

Duffy D.C. 1983. Environmental uncertainty and commercial fishing: effects on Peruvian guano birds. Biol. Conserv. 26: 227-238.

Duffy D.C., Wilson R.P., Ricklefs R.E., Broni S.C. & Veldhuis H. 1987. Penguins and Purse Seiners: Competition or Coexistence? Nat. Geogr. Res. 3(4): 480-488.

Edwards M. & A.J. Richardson 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature 430: 881-884.

ELIFONTS 1999. The Effect of Large Scale Industrial Fisheries on Non-Target Species. Final Report to the EC on ELIFONTS Project Contract 95/78 to DG XIV of the European Commission.

Enstipp M.R., R.D. Andrews & D.R. Jones 2001. The effect on the cardiac and behavioural responses of double-crested cormorants (*Phalacrocorax auritus*) during voluntary diving. J. Exp. Biol. 204: 4081-4092.

Enstipp M.R., F. Daunt, S. Wanless, E.M. Humphreys, K.C. Hamer, S. Benvenuti & D. Grémillet 2006. Foraging energetics of North Sea birds confronted with fluctuating prey availability. In: Boyd I.L., S. Wanless & C.J. Camphuysen (eds) Top predators in Marine Ecosystems: 191-210. Cambridge University Press, Cambridge.

Erikstad K.E., P. Fauchald, T. Tveraa & H. Steen 1998. On the cost of reproduction in long-lived birds: the influence of environmental variability. Ecology 79(5): 1781-1788.

Erikstad K.E., M. Asheim , P. Fauchald , L. Dahlhaug, T. Tveraa & P. Dahlhaug 1997. Adjustment of parental effort in the puffin; the roles of adult body condition and chick size. Behav. Ecol. Sociobiol. 40(2): 95-100.

Frank D. 1992. The influence of feeding conditions on food provisioning of chicks in Common Terns *Sterna hirundo* nesting in the German Wadden Sea. In: Spaans A.L. (ed.). Population dynamics of Lari in relation to food resources. Ardea 80: 45-55.

Frederiksen M., Wanless S., Harris M.P. Rothery P., Wilson L.J. 2004. The role of industrial fisheries and oceanographic change in the decline of North Sea Black-legged Kittiwakes. J. Appl. Ecol. 41: 1129-1139.

Frederiksen M., Harris M.P., Daunt F., Rothery P. & Wanless S. 2004b. Scale-dependent climate signals drive breeding phenology of three seabird species. Global Change Biology 10(7): 1214-1221(8).

Freeman S., Mackinson S., & Flatt R. 2004. Diel patterns in the habitat utilisation of sandeels revealed using integrated acoustic surveys. J. Exp. Mar. Biol. and Ecol. 305: 141-154.

Frost B.W. & S.M. Bollens 1992. Variability of diel vertical migrations in the marine planktonic copepod *Pseudocalanus newmani* in relation to its predators. Can. J. of Fish. Aq. Sc. 49: 1137-1141

Furness R.W. 1990. A preliminary assessment of the quantities of Shetland sandeels taken by seabirds, seals, predatory fish and the industrial fishery in 1981-83. Ibis 132: 205-217.

Furness R.W. 1996. A Review of Seabird Responses to Natural or Fishery-Induced Changes in Food Supply. In Greenstreet S.P.R. & M.L. Tasker (eds) Aquatic Predators and Their Prey. Fishing News Books. Blackwell Science, Oxford.

Furness R.W. 1999. Does a million tonne per year harvest of sand lance from the North Sea threaten seabird populations? AK-SG-99-01 Proceedings Ecosystem Approaches in Fisheries Management Alaska Sea Grant College Program: 407-424, Anchorage.

Furness R.W. 2002. "Management implications of interactions between fisheries and sandeel-dependent seabirds and seals in the North Sea." ICES J. Mar. Sc. 59: 261-269.

Furness R.W. 2002. Management Implications of Interactions Between Fisheries and Sandeel-Dependent Seabirds and Seals in the North Sea. Ices J. Mar. Sc. 59: 261-269.

Furness R.W. 2003. Impacts of fisheries on seabird communities. Sci. Mar. 67 (Suppl. 2): 33-45.

Furness R.W. & C.J. Camphuysen 1997. Seabirds as monitors of the marine environment. Ices J. Mar. Sc. 54: 726-737.

Furness R.W. & M.L. Tasker 1997. Seabird consumption in sand lance MSVPA models for the North Sea, and the impact of industrial fishing on seabird population dynamics. Proc. Forage Fishes in Marine Ecosystems, Alaska Sea Grant College Program, AK-SG-97-01: 147-169.

Furness R.W. & Tasker M.L. 2000. Seabird-fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. Mar. Ecol. Prog. Ser. 202: 253-264.

Gabrielsen G.W., Klaassen M. & Mehlum F. 1992. Energetics of Black-legged Kittiwake (*Rissa tricactyla*) chicks. Ardea 80: 29-40.

Galusha J.G. & Amlaner C.J. 1978. The effects of diurnal and tidal periodicities in the numbers and activities of Herring Gulls, *Larus argentatus*, in a colony. Ibis 120: 322-328.

Garthe S. 1997. Influence of hydrography, fishing activity, and colony location on summer seabird distribution in the south-eastern North Sea. Ices J. Mar. Sc. 54: 566-577

Garthe S., Benvenuti S. and Montevecchi W. A. 2003. Temporal patterns of foraging activities of Northern Gannets, *Morus bassanus*, in the northwest Atlantic Ocean. Can. J. Zool. 81: 453-461.

Garthe S., Camphuysen C.J. & Furness R.W. 1996. Amounts of discards in commercial fisheries and their significance as food for seabirds in the North Sea. Mar. Ecol. Progr. Ser. 136: 1-11.

Garthe S., Gremillet D. & Furness R. W. 1999. At sea-activity and foraging efficiency in chick-rearing Northern Gannets *Sula bassana*: a case study in Shetland. Mar. Ecol. Progr. Ser. 185: 93-99.

Gauld J.A. & Hutcheon R. 1990. Spawning and Fecundity in the Lesser Sandeel *Ammodytes marinus* (Raitt) in the North-Western North Sea. J. Fish Biology 36: 611-613.

Genstat C. 1993. Genstat 5 reference manual, release 3. Clarendon Press.

Gill V.A., Hatch S.A. & Lanctot R.B. 2002. Sensitivity of breeding parameters to food supply in Black-legged Kittiwakes *Rissa tridactyla*. Ibis 144: 268-283.

Girsa I.I. & Danilov A.N. 1976. Defensive Behaviour of Sandlance (*Ammodytes hexarterus*) of the White Sea. J. Ichthyol. 16: 862-865.

Gislason H. 1993. Report of the study group on ecosystem effects of fishing activities. Copenhagen, 7-14 April 1992, ICES C.M. 1992/G: 11, Ref.: Session T.

Glantz S.A. & B.K. Slinker 1990. Primer of applied regression and analysis of variance. McGraw-Hill Inc., New York.

Goss-Custard J.D, R.A. Stillman, A.D. West, R.W.G. Caldow, S. McGrorty 2002. Carrying capacity in overwintering migratory birds. Biol. Conserv. 105: 27-41.

Goss-Custard J.D., R.A. Stillman, A.D. West, R.W.G. Caldow, P. Triplet, S.E.A. le V. dit Durell, S. McGrorty 2004. When enough is not enough: shorebirds and shellfishing. Proc. Royal Soc. London, B 271: 233-237.

Greenstreet S.P.R. & M.L. Tasker (eds) 1996. Aquatic predators and their prey. Fishing News Books, Oxford.

Greenstreet S.P.R., J.A. McMillan & E. Armstrong 1998. Seasonal variation in the importance of pelagic fish in the diet of piscivorous fish in the Moray Firth, N.E. Scotland: a response to variation in prey abundance? ICES J. Mar. Sc. 55: 121-133.

Gremillet D. & Plos A. L. 1994. The use of stomach temperature records for the calculation of daily food intake in cormorants. J. Exp. Biol. 189: 105-115.

Grémillet D., Argentin G., Schulte B. & Culik B.M. 1998. Flexible foraging techniques in breeding Cormorants *Phalacrocorax carbo* and Shags *Phalacrocorax aristotelis*: benthic or pelagic feeding? Ibis 140: 113-119

Grémillet D., Wright G., Lauder A., Carss D.N. &Wanless S. 2003. Modelling the daily food requirements of wintering great cormorants: a bioenergetics tool for wildlife management. J. Appl. Ecol. 40: 266-277.

Grémillet D., I. Tuschy & M. Kierspel 1998. Body temperature and insulation in diving Great Cormorants and European Shags. Funct. Ecol. 12: 386-394.

Griffiths R., M.C. Double, K. Orr & R.J.G. Dawson 1998. A DNA test to sex most birds. Mol. Ecol. 7: 1071-1075.

Hamer K.C., R.A. Phillips, S. Wanless, M.P. Harris & A.G. Wood 2000. Foraging ranges, diets and feeding locations of gannets *Morus bassanus* in the North Sea: evidence from satellite telemetry. Mar. Ecol. Progr. Ser. 200: 257-264.

Hamer K.C., R.W. Furness & R.W.G. Caldow 1991. The Effects of Changes in Food Availability on the Breeding Ecology of Great Skuas in Shetland. J. Zool. 223: 175-188.

Hamer K.C., S. Lewis, S. Wanless, R.A. Phillips, T.N. Sherratt, E.M. Humphreys, J. Hennicke & S. Garthe 2006. Use of gannets to monitor prey availability in the NE Atlantic Ocean: colony size, diet and foraging behaviour. In: Boyd I.L., S. Wanless & C.J. Camphuysen (eds) Top predators in Marine Ecosystems: 236-248. Cambridge University Press, Cambridge.

Hamer K.C., P. Monaghan, J.D. Uttley, P. Walton & M.D. Burns 1993. The influence of food supply on the breeding ecology of Kittiwakes in Shetland. Ibis 135: 255-263.

Hamer K.C., R.A. Phillips, S. Wanless, M.P. Harris & A.G. Wood 2000. Foraging ranges, diets and feeding locations of Gannets *Morus bassanus* in the North Sea: evidence from satellite telemetry. Mar. Ecol. Progr. Ser. 200:257-264.

Hamer K.C., Phillips R.A., J.K. Hill, S. Wanless & A.G. Wood 2001. Contrasting foraging strategies of Gannets *Morus bassanus* at two North Atlantic colonies: foraging trip duration and foraging area fidelity. Mar. Ecol. Progr. Ser. 224: 283-290.

Handrich Y., R.M. Bevan, J-B. Charrassin, P.J. Butler, K. Puetz, A.J. Woakes, J. Lage, Y. Le Maho 1997. Hypothermia in foraging King Penguins. Nature 388: 64-67.

Haney J.C. 1991. Influence of pycnocline topography and water-column structure on marine distributions of alcids (Aves: Alcidae) in Anadyr Strait, Northern Bering Sea, Alaska. Mar. Biol. 110: 419-435.

Harris M.P. & H. Galbraith 1983. Seabird population of the Isle of May. Scott. Birds 12: 174-180.

Harris M.P. & B. Swann 2002. Common Guillemot *Uria aalge*. Wernham C., Toms M., Marchant J., Clark J., Siriwardena G. & Baillie S. (eds) The migration atlas: movements of the birds of Britain and Ireland: 397-400. T. & A.D. Poyser, London.

Harris M.P. & Wanless S. 1985. Fish fed to young guillemots, *Uria aalge*, and used in display on the Isle of May, Scotland. J. Zool. Lond. 207: 441-458.

Harris M.P. & Wanless S. 1988. The breeding biology of Guillemots *Uria aalge* on the Isle of May over a six year period. Ibis 130: 172-192.

Harris M.P. & Wanless S 1991. The importance of the Lesser Sandeel *Ammodytes marinus* in the diet of the Shag *Phalacrocorax aristotelis*. Orn. Scand. 22: 375-382

Harris M.P. & Wanless S. 1997. Breeding success, diet and brood neglect in the Kittiwake (*Rissa tridactyla*) over an 11 year Period. ICES J. Mar. Sc. 54: 615-623.

Hémery G., E. Pasquet & P. Yesou 1986. Data banks and population monitoring in France. In: Medmaravis & Monbailliu, X. (eds) Mediterranean Marine Avifauna. Population Studies and Conservation: 163-177. Springer-Verlag. Berlin.

Hennig V. 2004. Brutpaaraufstellung aus unseren Schutzgebieten 2003. Seevögel 25: 4-8.

Heubeck M. & Shaw D. 2004. Shetland's seabird meltdown. Brit. Birds 97(8): 425.

Hilton G.M., Furness R.W. & Houston D.C. 2000b. A comparative study of digestion in North Atlantic seabirds. J. Avian Biol. 31: 36-46.

Hilton G.M., Ruxton G.D., Furness R.W. & Houston D.C. 2000a. Optimal digestion strategies in seabirds: a modelling approach. Evol. Ecol. Res. 2: 207-230.

Hislop J., Bromley P.J., Daan N., Gislason H., Heesen H.J.L., Robb A.P., Skagen D., Sparholt H. & Temming A. 1997. Database Report of the Stomach Sampling Project, 1991. ICES Coop. Res. Rep. 219: 1-421.

Hislop J.R.G., Harris M.P. & Smith J.G.M. 1991. Variation in the calorific value and total energy content of the lesser sandeel (*Ammodytes marinus*) and other fish preyed on by seabirds. J. Zool. Lond. 224: 501-517.

Hoffman W., Heinemann D. & Wiens J.A. 1981. The ecology of seabird feeding flocks in Alaska. Auk 98: 437-456.

Houston A.I. 1992. The cost imposed on a fishery by a seabird population. J. theor. Biol. 158: 313-327.

Houston D.C., Jones P.J. & Sibly R.M. 1983. The effect of female body condition on egg laying in Lesser black-backed gulls *Larus fuscus*. J. Zool., Lond. 200: 509-520.

Humphreys E.M. 2002. Energetics of spatial exploitation of the North Sea by Kittiwakes breeding on the Isle of May, Scotland. Unpubl. PhD-thesis, Universty of Stirling, Stirling.

Hunt G.L. Jr & Harrison N.M. 1990. Foraging habitat and prey taken by Least Auklets at King Island, Alaska. Mar. Ecol. Prog. Ser. 65: 141-150.

Hunt G.L. Jr, Harrison N.M. & Cooney R.T. 1990. The influence of hydrographic structure and prey abundance on the foraging of Least Auklets. Avian Biol. 14: 7-22.

Hunt G.L. Jr, Mehlum F., Russell R.W., Irons D., Decker M.B. & Becker P.H. 1999. Physical processes, prey abundance, and the foraging ecology of seabirds. In: Adams N.J. and Slotow R. (eds) Proc. 22nd Int. Ornithol. Congr.: 2040-2056, BirdLife South Africa, Johannesburg

ICES 1998. Report of the Working Group on Seabird Ecology. ICES CM 1998 C:5: 1-37.

ICES 2002. Report of the Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak. ICES CM 2002 ACFM:01: 1-555.

ICES 2004a. Report of the Working Group on Seabird Ecology, Rep. No. ICES CM 2004/C:05. International Council for the Exploration of the Sea, Copenhagen.

ICES 2004b. Report of the Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak. ICES CM 2004 ACFM:07: 1-650.

ICES 2004c. The advisory committee on fishery management. Report International Council for the Exploration of the Sea, October 2004, www.ICES.dk.

ICES 2005. Report of the Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak. ICES CM 2005 ACFM:07.

Ichii T., Naganobu M. & Ogishima T. 1996. Competition between the krill fishery and penguins in the South Shetland Islands. Polar Biol. 16: 63-70.

Irons D.B. 1998. Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. Ecology 79: 647-655

Jackson J.B.C., Kirkby M.X., Berger W.H., Bjorndal K.A., Botsford L.W., Bourque B.J., Bradbury R.H., Cooke R., Erlandson J., Estes J.A., Hughes T.P., Kidwell S., Lange C.B., Lenihan H.S., Pandolfi J.M., Petersen C.H., Steneck R.S., Tegner M.J. & Warner R.R. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293: 629-638.

Jennings S., Kaiser M.J. & Reynolds J.D. 2001. Marine fisheries ecology. Blackwell Science, Oxford.

Jensen H., Tasker M.L., Coull K.D., & Emslie D. 1994. A comparison of the distribution of seabirds and prey fish stocks in the North Sea and adjacent areas. European Union.

Jensen H., Wright P.J. & Munk P. 2003. Vertical distribution of the pre-setttled Sandeel (*Ammodytes marinus*). in the North Sea in relation to size and environmental variables. ICES J. Mar. Sci. 60: 1342-1351

Jones R. 1983. The decline in Herring and Mackerel and the associated increase in other species in the North Sea. In: Sharp G.D. & Csirke J. (eds) Proc. Expert Cons. to Examine Changes in Abundance and Species Composition of Neritic Fish Resources. FAO Fish. Rep. 291(2): 507-519.

Jürgens-Kammel M.E., Schmidt U., Peter, H.U. & Funke W. 1993. Gantztagbeobachtung am Eissturmvogel (*Fulmarus glacialis*) und an der Dreizehnmöwe (*Rissa tridactyla*) in der Vorlegeperiode am Helgoländer Vogelfelsen, 19. April 1990, 5.40 bis 20.40 Uhr. Seevögel 14(1): 8-13.

Kacelnik A. J.R. Krebs & C. Bernstein 1992. The ideal free distribution and predator-prey populations. TREE 7(2): 50-55.

Kaschner K. & Pauly D. 2004. Competition between marine mammals and fisheries: food for thought. The Humane Society of the United States, Washington, 28pp.

Kendeigh S.C., V.R. Dol'nik, V.M. Gavrilov 1977. Avian energetics. In: Pinowski J. & S.C. Kendeigh (eds) Granivorous birds in ecosystems: 127-204. Cambridge Univ. Press, Cambridge.

Kenward R.E. 2001. A manual for wildlife radio tagging. Academic Press.

Kinder T.H., G.L. Hunt Jr., D. Schneider & J.D. Schumacher 1983. Correlations between seabirds and oceanic fronts around the Pribilof Islands, Alaska. Est. Coast. Shelf Sci. 16: 309-319.

Kokko H., Harris M.P. & Wanless S. 2004. Competition for breeding sites and site-dependent population regulation in a highly colonial seabird, the Common Guillemot *Uria aalge*. J. Anim. Ecology 73: 367-376.

Korte J. de 1985. Ecology of the Long-tailed Skua, *Stercorarius longicaudus* Vieillot, 1819, at Scoresby Sund, East Greenland. Part three: Clutch size, laying date and incubation in relation to energy reserves. Beaufortia 36(6): 93-127.

Leopold M.F. 1987. Seabird concentrations at a tidally induced front in the southern North Sea. NIOZ Internal Reports 1987-2, Netherlands Institute for Sea Research, Texel.

Lewis S., S. Benvenuti, L. Dall'Antonia, R. Griffiths L. Money T.N. Sherratt, S. Wanless & K.C. Hamer 2002. Sex-specific foraging behaviour in a monomorphic seabird. Proc. Royal Soc. Lond. Ser. B. 269: 1687-1693

Lewis S., Hamer K.C., Money L., Griffiths R., Wanless S. & Sherratt T.N. 2004. Brood neglect and contingent foraging behaviour in a pelagic seabird. Beh. Ecol. & Sociobiol. 56: 81-88.

Lewis S., Sherratt T.N., Hamer K.C. & Wanless S. 2001. Evidence of intra-specific competition for food in a pelagic seabird. Nature 412: 816-819.

Lewis S., Sherratt T.N., Hamer K.C., Harris M.P. & Wanless S. 2003. Contrasting diet quality in Northern Gannets *Morus bassanus* at two different colonies. Ardea 91: 167-176

Lewis S., Wanless S., Wright P.J., Harris M.P., Bull J. & Elston D.A. 2001. Diet and breeding performance of Black-legged Kittiwakes *Rissa tridactyla* at a North Sea colony. Mar. Ecol. Prog. Ser. 221: 277-284.

Liu K., Ollason J.G. & Ren N. 2002. A parameterisation of the individual-based model of the Common Guillemot (*Uria aalge*). IMPRESS Report 2002-002; 29/03/2002

Lloyd C., Tasker M.L. & Partridge K. 1991. The Status of Seabirds in Britain and Ireland. T. & A.D. Poyser, London.

Lohse L., E.H.G. Epping, W. Helder & W. van Raaphorst 1996. Oxygen pore water profiles in Continental Shelf sediments of the North Sea: turbulent versus molecular diffusion. Mar. Ecol. Progr. Ser. 145: 63-75.

Macer C.T. 1966. Sandeels (Ammodytidae) in the South-Western North Sea: Their Biology and Fishery. MAFF Fisheries Investigation London 2 24 (6): 1-55.

Mann K.H. & Lazier J.R.N. 1996. Dynamics of marine ecosystems. Blackwell Science, Oxford.

Mavor R., Parsons M., Heubeck M., Pickerell G. & Schmitt S. 2002. Seabird numbers and breeding success in Britain and Ireland 2001. Joint Nature Conservation Committee, Peterborough.

Mavor R.A., Parsons M., Heubeck M. & Schmitt S. 2004. Seabird numbers and breeding success in Britain and Ireland, 2003. UK Nature Conservation No. 28, Joint Nature Conservation Committee, Peterborough.

Meyer T.L., Cooper R.A. & Langton R.W. 1979. Relative abundance, behaviour and food habits of the American Sand Lance, *Ammodytes americanus*, from the Gulf of Maine. Fishery Bulletin 77: 243-254.

Miller G.B. 2004. Biological Oceanography. Blackwell Science, Oxford.

Mitchell P.I., S.F. Newton, N. Ratcliffe & T.E. Dunn 2004. Seabird populations in Britain and Ireland. T. & A.D. Poyser, London.

Monaghan P. 1992. Seabirds and Sandeels: The Conflict between Exploitation and Conservation in the Northern North Sea. Biodiversity Conservation 1: 98-111.

Monaghan P., Uttley J.D. & Burns M.D. 1992. Effect of changes in food availability on reproductive effort in Arctic Terns *Sterna paradisaea*. Ardea 80: 71-81.

Monaghan P., Uttley J.D., Burns M.D., Thaine C. & Blackwood J. 1989. The relationship between food supply, reproductive effort, and breeding success in Arctic Terns *Sterna paradisaea*. J. Anim. Ecol. 58: 261-274.

Monaghan P., Wright P.J., Bailey M.C., Uttley J.D., Walton P. & Burns M.D. 1996. The influence of changes in food abundance on diving and surface-feeding seabirds. Can. Wildl. Serv. Occ. Pap. 91: 10-19.

Montevecchi W.A. 1993. Birds as indicators of change in marine prey stocks. In: Furness R.W. & J.J.D. Greenwood (eds) Birds as monitors of environmental change: 217-265. Chapman and Hall, London.

Montevecchi W.A., Birt V.L. & Cairns D.K. 1988. Dietary changes of seabirds associated with local fisheries failures. Biol. Ocean. 5: 153-161.

Murawski S.A. 2000. Definitions of overfishing from an ecosystem perspective. ICES J. Mar. Sc. 57: 649-658.

Murray S. & Wanless S. 1997. The status of the gannet in Scotland in 1994-5. Scottish Birds 19:10-27.

Nager R.G., Monaghan P. & Houston D.C. 2000. Parental condition, brood sex ratio and differential young survival: an experimental study in gulls (*Larus fuscus*). Beh. Ecol. Soc. 48(6): 452-457.

Nelson J.B. 2002. The Atlantic Gannet. Fenix Books Ltd, Norfolk.

Nelson J.B. 1978. The Gannet. T. & A.D. Poyser, Berkhamsted.

Nielsen J.R. & C. Mathiesen 2002. Stakeholder preferences for management of the Danish protein fisheries in the North Sea. Institute for Fisheries Management and Coastal Community Development (IFM), Hirtshals.

Ollason J.G. (ed.) 2000. Modelling the Impact of Fisheries on Seabirds. Final Report CFP 96-079, University of Aberdeen, Aberdeen.

Ollason J.G. & Ren N. 2002a. Taking the rough with the smooth: foraging for particulate food in continuous time. Theoretical Population Biology 62: 313-327

Ollason J.G. & Ren N. 2002b. Simulations of the interactions of a diving predator feeding and the prey it feeds on distributed in three-dimensional patches underwater. IMPRESS Report 2002-008; 05/12/2002

Ollason J.G. & Ren N. 2004. A general dynamical theory of foraging in animals. Discrete and Continuous Dynamical Systems. Series B 4(3): 715-722.

Ollason J.G., Ren N. & Yearsley J.M. 2002. Corrigendum. Theoretical Population Biology 61: 249-250

Ollason J.G., Ren N., Scott B.E. & Daunt F. 2003. A model of the foraging behaviour of a diving predator feeding underwater at a patch of food (Revision 2003.4.0). IMPRESS report 2003-014, pp. 37; 29/10/2003.

Ollason J.G., Yearsley J.M., Liu K. & Ren N. 2006. Modelling the behaviour of individuals and groups of animals foraging in heterogeneous environments. In: Boyd I.L., S. Wanless & C.J. Camphuysen (eds). Top predators in Marine Ecosystems: 249-309. Cambridge University Press, Cambridge.

Ollason J.G. & Yearsley J.M. 2001. The approximately ideal, more or less free distribution. Theoretical Population Biology 9: 87-105

Parrish J.K. & Zador S.G. 2003. Seabirds as indicators: an exploratory analysis of physical forcing in the Pacific Northwest coastal environment. Estuaries 26: 1044-1057

Patterson H.D. & R. Thompson 1971. Recovery of interblock information when block sizes are unequal. Biometrika 58: 545-554

Pauly D., Christensen V., Dalsgaard J., Froese R., Torres Jr. T. 1998. Fishing down marine food webs. Science 279: 860-863.

Pauly D. & J. Maclean 2003. In a perfect ocean: the state of fisheries and ecosystems in the North Atlantic Ocean. Island Press, Washington,.

Pedersen J. 1999. Diet comparison between pelagic and demersal Whiting in the North Sea. J. Fish Biol. 55: 1096-1113.

Pedersen J. & Hislop J.R.G. 2001. Seasonal variations in the energy density of fishes in the North Sea. J. Fish. Biol. 59: 380-389.

Pedersen S.A., Lewy P. & Wright P. 1999. Assessments of the Lesser Sandeel (*Ammodytes Marinus*) in the North Sea based on revised stock divisions. Fish. Res. 41: 221-241.

Pennycuick C.J. 1987. Flight of auks (Alcidae) and other northern seabirds compared with southern Procellariformes: ornithodolite observations. J. Exp. Biol. 128: 335-347.

Pennycuick C.J. 1989. Bird flight performance: a practical calculation manual. Oxford Univ. Press, Oxford.

Pennycuick C.J. 1997. Actual and 'optimum' flight speeds: field data reassessed. J. Exp. Biol. 200:2355-2361

Pettifor R.A., W.G. Caldow, J.M. Rowcliffe, J.D. Goss-Custard, J.M. Black, K.H. Hodder, A.I. Houston, A. Lang & J. Webb 2000. Spatially explicit, individual-based, behavioural models of the annual cycle of two migratory goose populations. J. Appl. Ecol. 37: 103-135.

Piatt J.F. 1990. The aggregative response of Common Murres and Atlantic Puffins to schools of Capelin. In: Sealy S.G. (ed.). Auks At Sea. Studies in Avian Biology No. 14: 36-51.

Pierce G.J., Boyle P.R. & Thompson P.M. 1989. Diet Selection by Seals. In: Barnes M. & Gibson R.N. (eds) Trophic Relationships in the Marine environment. Proc. 24th Europ. Mar. Biol. Symp., Oban, Scotland.

Pierce G.J., Thompson P.M., Miller A., Diack J.S.W., Miller D. & Boyle P.R. 1991. Seasonal variation in the diet of Common Seals (*Phoca vitulina*) in the Moray Firth area of Scotland. J. Zool. 223: 641-652.

Pingree R.D, G.R. Forster & G.K. Harrison 1974. Turbulent convergent tidal fronts. J. Mar. Biol. Ass. U.K. 54: 469-479.

Pingree R.D. & Griffiths D.K. 1978. Tidal fronts on the shelf seas around the British Isles. J. Geoph. Res. 83 C9: 4615-4622.

Pingree R.D., P.R. Pugh, P.M. Holligan & G.R. Forster 1975. Summer phytoplankton blooms and red tides along tidal fronts in the approaches to the English Channel. Nature 258:672-677.

Pinto J.M., Pearson W.H. & Anderson J.W. 1984. Sediment preferences and oil contamination in the Pacific Sand Lance *Ammodytes hexapterus*. Mar. Biol. 83: 193-204.

Proctor R., Wright P.J. & Everitt A. 1998. Modelling the transport of larval sandeels on the North-West European Shelf. Fish. Oceanogr. 7: 347-354.

Quinn T. & Schneider D.E. 1991. Respiration of the Teleost fish *Ammodytes hexapterus* in relation to its burrowing behaviour. Comp. Biochem. & Physiol. 98A: 71-75.

Ragozin D.L. & G. Brown 1985. Harvest policies and non-market valuation in a predator-prey system. J. Envir. Econ. & Manage. 12: 155-168.

Ratcliffe N. 2004. Cause of seabird population change. In: Mitchell P.I., S.F. Newton, N. Ratcliffe & T.E. Dunn (eds) Seabird populations in Britain and Ireland: 407-437. T. & A.D. Poyser, London.

Reay P.J. 1970. Synopsis of biological data on North Atlantic Sandeels of the genus *Ammodytes*. FAO Fish. Synop. No. 82, Rome.

Regehr H.M. & Montevecchi W.A. 1997. Interactive effects of food shortage and predation on breeding failure of Black-legged Kittiwakes: indirect effects of fisheries activities and implications for indicator species. Mar. Ecol. Progr. Series 155: 249-260.

Richardson A.J. & D.S. Schoeman 2004. Climate impact on plankton ecosystems in the Northeast Atlantic. Science 305(5690): 1609-1612.

Rindorf A., Wanless S. & Harris M.P. 2000. Effects of changes in sandeel availability on the reproductive output of seabirds. Mar. Ecol. Progr. Ser. 202: 241-252.

Robards M.D., Willson M.F., Armstrong R.H. & Piatt J.F. 1999. Sandlance: a review of biology and predator relations and annotated bibliography. U.S. Department of Agriculture, Portland, Oregon.

Robinson, A., Sale, R. & Morrison, J. 1978. Elements of cartography. John Wiley and Sons, New York.

Ross S. 1976. A first course in probability. Macmillan, New York

Royal Commission on Environmental Pollution (RCEP) 2004. Turning the tide: addressing the impact of fisheries on the Marine Environment. 25th Report of the Royal Commission on Environmental Pollution, presented to Parliament by Command of Her Majesty, December 2004.

Russell R.W., Harrison N.M. & Hunt G.L. Jr 1999. Foraging at a front: hydrography, zooplankton, and avian planktivory in the northern Bering Sea. Mar. Ecol. Progr. Series 182: 77-93

Ryan P.G. & Moloney C.L. 1988. Effect of trawling on bird and seal distributions in the southern Benguela region. Mar. Ecol. Progr. Ser. 45: 1-11.

Santos M.B. & Pierce G.J. 2003. The diet of Harbour Porpoise (*Phocoena phocoena*) in the Northeast Atlantic. Oceanogr. Mar. Biol. 41: 355-390.

Schmidt-Nielsen K. 1997. Animal physiology: adaptation and environment. 5^{th} edn. Cambridge Univ. Press, Cambridge.

Schneider D.C. 1982. Fronts and seabird aggregations in the southeastern Bering Sea. Mar. Ecol. Prog. Ser. 10: 101-103.

Schneider D.C. & Piatt J.F. 1986. Scale-dependent correlation of seabirds with schooling fish in a coastal ecosystem. Mar. Ecol. Progr. Ser. 32: 237-246.

Schweder T., Hagen G.S. & Hatlebakk E. 2000. Direct and indirect effects of minke whale abundance on cod and herring fisheries: A scenario experiment for the Greater Barents Sea. In: Víkingsson G.A. & Kapel F.O. (eds) Minke Whales, Harp and Hooded Seals: Major Predators in the North Atlantic Ecosystem. NAMMCO Sci. Publ. 2: 120-132.

Scott J.S. 1973. Food and inferred feeding behaviour of Northern Sand Lance *Ammodytes dubius*. J. Fish. Res. Brd Canada 30: 451-454.

Sharples J., Ross O.N., Scott B.E., Greenstreet S.P.R. & Fraser H (submitted). Inter-annual variability in the timing of stratification and the spring bloom in a temperate shelf sea. J. Mar. Systems

Sibly R.M., Nott H.M.R., Fletcher D.J. 1990. Splitting behaviour into bouts. Anim. Behav 39:63-69.

Skov H. & J. Durinck 2000. Seabird distribution in relation to hydrography in the Skagerrak. Cont. Shelf Res. 20: 169-187.

Skov H., Durinck J., Leopold M.F. & Tasker M.L. 1995. Important bird areas for seabirds in the North Sea, including the Channel and the Kattegat. Birdlife International, Cambridge.

Slater P.J.B. & Lester N.P. 1982. Minimising errors in splitting behaviour into bouts. Behaviour 79: 153-161.

Stefanson G., J. Sigurjonsson & G.A. Vikingsson 1997. The dynamic interations between some fish resources and cetaceans off Iceland based on a simulation model. J. NW Atl. Fish. Sc. 22: 357-370.

Stenhouse I.J. & Montevecchi W.A. 1999. Indirect effects of the availability of capelin and fishery discards: gull predation on breeding storm-petrels. Mar. Ecol. Prog. Ser. 184: 303-307.

Stephens P.A., J. Fuller, R.G.H. Bunce, J.C. Duckworth & M. Shrubb 2003. Predicting the response of farmland bird populations to changing food supplies. J. Appl. Ecol. 40: 970-983.

Stone C.J., Webb A., Barton C., Ratcliffe N., Reed T.C., Tasker M.L., Camphuysen C.J. & Pienkowski M.W. 1995. An atlas of seabird distribution in north-west European waters. Joint Nature Conservation Committee, Peterborough.

Stroebele W.J. & H. Wacker 1995. The economics of harvesting predator-prey systems. J. Econ. 61: 65-81.

Swartzman G. & Hunt G. 2000. Spatial association between murres (*Uria* spp.), puffins (*Fratercula* spp.) and fish shoals near Pribilof Islands, Alaska. Mar. Ecol. Progr. Ser. 206: 297-309.

Tasker M.L. & R.W. Furness 1996. Estimation of food consumption by seabirds in the North Sea. In: Hunt G.L. & Furness R.W. (eds) Seabird/Fish Interactions, with particular reference to seabirds in the North Sea. ICES Cooperative Research Report No. 216, Copenhagen.

Tasker M.L., C.J.Camphuysen, J.Cooper, S.Garthe, W.A. Montevecchi & S.J.M. Blaber 2000. The impacts of fishing on marine birds. ICES J. Mar. Sc. 57: 531-547.

Tasker M.L., A.Webb, A.J.Hall, M.W. Pienkowski & D.R. Langslow 1987. Seabirds in the North Sea. Nature Conserv. Council, Peterborough.

Thompson P.M. & J.C. Ollason 2001. Lagged effects of ocean climate change on Fulmar population dynamics. Nature 413: 417-420.

Tollit D.J., S.P.R. Greenstreet & P.M. Thompson 1997. Prey Selection by Harbour Seals, *Phoca vitulina*, in relation to variations to prey abundance. Can. J. Zool. 75: 1508-1518.

Trites A.W., V. Christensen & D. Pauly 2004. Effects of fisheries on food chains. Oral presentation Zoological Society of London Conference "Management of Marine Ecosystems: monitoring change in upper trophic levels", London, 22-23 April 2004.

Tyres M.T. 1979. Long-term climatic and oceanographic cycles regulating seabird distributions and numbers. In: Bartonek J.C. & D.N. Nettleship (eds). Conservation of Marine Birds of Northern North America: 3-7. Wildlife Research Report 11. Fish & Wildlife Service, Washington DC.

Van der Meer J. 2004. Foraging games between prey and predators: grouping behaviour of prey as an anti-predation strategy. IMPRESS report 2004-017.

Veit R.R., Silverman E.D. & Everson I. 1993. Aggregation patterns of pelagic predators and their principal prey, Antarctic krill, near South Georgia. J. Anim. Ecol. 62: 551-564.

Vermeer K. Szabo I. & Greisman P. 1987. The relationship between plankton-feeding Bonaparte's and Mew Gulls and tidal upwelling at Active Pass, British Columbia. J. Plankton Res. 9: 483-501.

Víkingsson G.A. & Kapel F.O. (eds) 2000. Minke Whales, Harp and Hooded Seals: major predators in the North Atlantic Ecosystem. NAMMCO Scientific Publications, 2. Tromsø.

Visser G.H. 2002. Chick growth and development in seabirds. In: Schreiber E.A. & Burger J. (eds) Biology of Marine Birds: 439-465. CRC Press, Boca Raton.

Votier S.C., Furness R.W., Bearhop S., Crane J.E., Caldow R.W.G., Catry P., Ensor K., Hamer K.C., Hudson A.V., Kalmbach E., Klomp N.I., Pfeiffer S., Phillips R.A., Prieto I. & Thompson D.R. 2004. Changes in fisheries discard rates and seabird communities. Nature 427: 727-730.

Walsberg GE and Wolf BO (1995). Variation in the respiratory quotient of birds and implications for indirect calorimetry using measurements of rate of carbon dioxide production. J. Exp. Biol. 198: 213-219.

Walsh P.M., Avery M. & Heubeck M. 1990. Seabird numbers and breeding success in 1989. NCC CSD Report No. 1071, Nature Conservancy Council, Aberdeen.

Walsh P.M., Halley D.J. Harris M.P., del Nevo A., Sim I.M.W. & Tasker M.L. 1995. Seabird monitoring handbook for Britain and Ireland. JNCC/RSPB/ITE/Seabird Group, Peterborough, UK.

Wanless S. 2002. Northern Gannet *Morus bassanus*. Wernham C., Toms M., Marchant J., Clark J., Siriwardena G. & Baillie S. (eds) The migration atlas: movements of the birds of Britain and Ireland: 130-132. T. & A.D. Poyser, London.

Wanless S., Corfield T., Harris M.P., Buckland S.T. & Morris J.A. 1993. Diving behaviour of the Shag *Phalacrocorax aristotelis* (Aves: Pelicaniformes) in relation to water depth and prey size. Journal of Zoology 231: 11-25

Wanless S. Grémillet D. & Harris M.P. 1998. Foraging activity and performance of Shags *Phalacrocorax aristotelis* in relations to environmental characteristics. J Avian Biol 29:49-54.

Wanless S., Finney S.K., Harris M.P. & McCafferty D.J. 1999. Effect of the diel light cycle on the diving behaviour of two bottom feeding marine birds: the Blue-eyed Shag *Phalacrocorax atriceps* and the European Shag *P. aristotelis*. Mar. Ecol. Progr. Ser. 188: 219-224.

Wanless S., Grémillet D., Harris M.P. 1998. Foraging activity and performance of Shags *Phalacrocorax aristotelis* in relation to environmental characteristics. J. Avian Biol. 29: 49-54.

Wanless S., Harris M.P. & Morris J.A. 1991b. Foraging range and feeding locations of Shags *Phalacrocorax aristotelis* during chick rearing. Ibis 133:30-36.

Wanless S., Harris M.P., Greenstreet S.P.R. & Rindorf A. 1999. Avian predators. In: The effect of large scale industrial fidheries on non-target species (ELIFONTS). Final report contract 95/78, Directorate General Fisheries DGXIV, European Commission, Brussels.

Wanless S., M.P. Harris & S.P R. Greenstreet 1998. Summer sandeel consumption by seabirds breeding in the Firth of Forth, south-east Scotland. ICES J. Mar. Sc. 55: 1141-1151.

Wanless S., Monaghan P., Uttley J.D., Walton P. & Morris J.A. 1992. A radio-tracking study of Kittiwakes (*Rissa tridactyla*) foraging under suboptimal conditions. In: Priede I.G. & Swift S.M. (eds) Wildlife telemetry. Remote monitoring and tracking of animals: 580-590. Ellis Horwood, New York

Wanless S., Murray S., Evans S. & Harris M.P. 2004. Scottish Gannet Survey 2004. Unpublished report, Scottish Natural Heritage.

Wanless S., P.J. Wright, M.P. Harris, D.A. Elston 2004. Evidence for decrease in size of Lesser Sandeels *Ammodytes marinus* in a North Sea aggregation over a 30-yr period. Mar Ecol. Progr. Ser. 279: 237-246.

Weiner J. 1992. Physiological limits to sustainable energy budgets in birds and mammals: ecological implications. TREE 7(11): 384-388.

Wilson L. 2004. Seabird season summary 2004. Seabird Group Newsletter 98: 1-5.

Wilson L.J., Daunt F. & Wanless S. 2004. Self-feeding and chick provisioning diet differ in the Common Guillemot *Uria aalge*. Ardea 92(2): 197-208.

Wilson R.P., Burger A.E., Wilson B.L.H., Wilson M.-P.T. & Noldeke C. 1989. An inexpensive depth gauge for marine animals. Mar. Biol. 103:275-283.

Wilson R.P., Gremillet D., Syder J., Kierspel M.A.M., Garthe S., Weimerskirch H., Schafer-Neth C., Scolaro J.A., Bost C.A., Plotz J., Nel D. 2002. Remote-sensing systems and seabirds: their use, abuse and potential for measuring marine environmental variables. Mar. Ecol. Progr. Ser. 228: 241-261

Wilson R.P., Putz K., Gremillet D., Culik B.M., Kierspel M., Regel J., Bost C.-A., Lage J. & Cooper J. 1995. Reliability of stomach temperature changes in determining feeding characteristics of seabirds. J. Exp. Biol. 198: 1115-1135.

Winslade P. 1974a. Behavioural studies of the Lesser Sandeel *Ammodytes marinus* (Raitt) I. The effect of food availability on activity and the role of olfaction in food detection. J. Fish Biology 6: 565-576.

Winslade P. 1974b. Behavioural studies of the Lesser Sandeel *Ammodytes marinus* (Raitt). II. The effect of light intensity on activity. J. Fish Biology 6: 577-586.

Winslade P. 1974c. Behavioural studies on the Lesser Sandeel *Ammodytes marinus* (Raitt) III. The effect of temperature on activity and the environmental control of the annual cycle of activity. J. Fish Biology 6: 587-599.

Withers PC (1977). Measurement of $\dot{V}o_2$, $\dot{V}co_2$, and evaporative water loss with a flow-through mask. J. Appl. Physiol. 42: 120-123.

Withey J.C., Bloxton T.D. & Marzluff J.M. 2001. Effects of tagging and location error in wildlife radiotelemetry studies. In: Millspaugh J.J. & Marzluff J.M. (eds) Radio tracking and animal populations: 43-75. Academic Press, San Diego, California.

Wright P.J. & Begg G.S. 1997. A spatial comparison of Common Guillemots and sandeels in Scottish Waters. ICES J. Mar. Sc. 54: 578-592.

Wright P.J. 1996. Is there a conflict between sandeel fisheries and seabirds? A case study at Shetland. In: Greenstreet S.P.R. & Tasker M.L. (eds) Aquatic predators and their prey: 154-165. Fishing News Books, University Press, Cambridge.

Wright P.J., H. Jensen & I. Tuck 2000. The influence of sediment type on the distribution of the Lesser Sandeel, *Ammodytes marinus*. J. Sea Research 44: 243-256.

Wright P.J., H. Jensen & S. Wanless 2002. The European Commission's annual report on the impact of the northeast sandeel fishery closure and status report on the monitoring fishery in 2000 and 2001. STECF Report.

Wright P.J., Pedersen S.A., Donald L., Anderson C., Lewy P. & Proctor R. 1998. The Influence of physical factors on the distribution of Lesser Sandeels and its relevance to fishing pressure in the North Sea. C.M. ICES 1998/AA: 3.

Chapter 12 Glossary

Apex predators – or top-predators, carnivorous predators at the top of a food chain.

Bank regions - large banks in the seabed topography off SE Scotland, typically rising 20 - 40 metres above the surrounding seabed, and measuring 10 - 30 km east-west and 50 - 100 km north-south.

Bass Rock - A precipitous island lying 2.5 km off the East Lothian coast, 5.5 km north east of North Berwick at the entrance of the Firth of Forth on the east coast of Scotland (56°06'N, 02°36'W; Figure 1.5.3), where work on Northern Gannets was carried out. The Bass Rock rises sharply to 107m. Geologically, the Rock is a volcanic plug of Lower Carboniferous age. Whole colony counts of gannets on the Bass Rock were carried out in 1994 (Murray & Wanless 1997) and 2004 (Wanless *et al.* 2004) and indicated that numbers increased from 39,751 to 48,065 apparently occupied sites (AOSs). Assuming a constant rate of increase over the period indicated that there were *c* 45,000-48,000 AOSs on the Bass Rock during the *IMPRESS* project.

Black-legged Kittiwake *Rissa tridactyla* - Family Laridae. Small to medium-sized and essentially pelagic gull, wingspan 95-120cm, body mass 350-460g. Breeding North Pacific and North Atlantic, including Iceland, Svalbard, Norway, Faeroe Islands, British Isles, northern France, Helgoland (Germany) and Iberian Peninsula. West Palearctic breeding population winters from NW Africa to the Norwegian and Barents Seas (migratory). Mean adult annual survival >81%. Surface feeder, feeding entirely on marine fish and invertebrates obtained offshore.

B_{lim} – Lowest acceptable biomass (biological reference point)

B_{MSY} – Biomass corresponding to the maximum sustainable yield (biological reference point)

Cephalopods - Any of various marine mollusks of the class Cephalopoda, such as the octopus, squid, cuttlefish, or nautilus, having a large head, large eyes, prehensile tentacles, and, in most species, an ink sac containing a dark fluid used for protection or defense.

Common Guillemot *Uria aalge* - Family Alcidae. Commonest large auk in west Palearctic, wingspan 64-70cm, body mass 800-1100g. Breeding North Pacific and North Atlantic, including Iceland, Norway, Faeroe Islands, British Isles, France, Helgoland (Germany), Iberian Peninsula and Baltic. West Palearctic breeding population winters from Portugal to the Norwegian Sea (migratory). Mean adult annual survival *c.* 88%. Wing-propelled mid-water pursuit diver, almost entirely piscivorous.

Critical depth - if phytoplankton are continuously mixed between the sea surface and the critical depth, the light energy they receive is just sufficient to compensate for respiratory losses. If they are mixed in a region shallower than the critical depth, then growth exceeds respiratory losses and biomass can increase. If they are mixed deeper than the critical depth, then respiratory losses exceed growth and phytoplankton begin to die.

Crustaceans - Any of various predominantly aquatic arthropods of the class Crustacea, including lobsters, crabs, shrimps, and barnacles, characteristically having a segmented body, a chitinous exoskeleton, and paired, jointed limbs.

Demersal fish - The demersal fish fauna is diverse, consisting of numerous species occupying the bottom habitats, and include species such as flatfish, gadoid fish, and dragonets. Demersal fish are relatively sedentary and as a result have an increased exposure to accumulated contaminants in sediment and low levels of oxygen in near-bottom waters. Because demersal fishes respond to changes in the benthic environment, they have been monitored for many years to assess impacts resulting from human activities.

ELIFONTS project - (Effects of Large-scale Industrial Fisheries on Non-target species)

European Shag *Phalacrocorax aristotelis* - Family Phalacrocoracidae. Medium-sized, slender-billed marine cormorant, with a wingspan of 90-105cm, body mass 1600-1900g. Breeding Iceland, Norway, Faeroe Islands, British Isles, France and Iberian Peninsula (race *desmarestii* in Central Mediterranean and Black Sea). Dispersive, but adults largely resident in southerly breeding areas. Mean annual survival after 1st year *c.* 85% (variable from year to year). Foot-propelled surface diver: pursuit diving benthic feeder, almost entirely piscivorous.

Fresh water influenced - Region in the primary study area that has a strong influence of fresh water that follows the coastline in the southern portion of the primary study area. It also has deeper topography than either of the bank regions. (see Chapter 3)

Gannet – see Northern Gannet

Guillemot – see Common Guillemot

Industrial fisheries - Industrial fisheries catch fish not for direct human consumption. Fish from industrial fisheries are converted into fish meal, which is used in animal feed, and oil, which is used largely in the production of margarine. Industrial fisheries predominantly target small, bony fish such as sandeels, sprats or anchovy. Fishing for small fish for industrial purposes rather than human consumption in the North Sea commenced in the 1970s, and expanded rapidly during the 1980s. Sandeels are the principal species targeted by this fishery. In recent decades annual landings of sandeels have topped one million tonnes on occasion, and have rarely dropped below ½ million tonnes (ICES 2004). This makes sandeels the target of the largest single species fishery in the North Sea. These fisheries are occasionally termed *Protein Fisheries* by Danish fisheries managers (e.g. Nielsen & Matthiesen 2002).

Inner Bank - Region in the primary study area with greater mixing (mostly due to shallower depth) than outer banks and no access to nutrient rich cool bottom water. (see Chapter 3)

Isle of May – lying at the entrance of the Firth of Forth on the east coast of Scotland (Fife; 56°11'N, 02°33'W; Figure 1.5.2), where colony-based work on European Shags, Common Guillemots and Black-legged Kittiwakes was carried out. Scottish National Nature Reserve. Grid reference NT644999, 356.75 ha, SAC EU code UK0030172. General site character: 87% marine areas and sea inlets, 11.3% saltmarshes, salt pastures and salt steppes, 1.7% shingle, sea cliffs and islets.

Kittiwake – see Black-legged Kittiwake

Lesser Sandeel *Ammodytes marinus* – [also Raitt's Sandeel] Sandeels are numerically one of the most abundant fish species in the North Sea where they sustain a large industrial fishery. Of five species of sandeel that occur in the North Sea, *Ammodytes marinus*, is much more abundant than the others and accounts for over 90% of sandeel catches. Sandeels are relatively short-lived (the maximum age reached is around 8 years) and the fishery is mainly composed of sandeels less than three years old. The size of sandeel stocks each year is strongly influenced, therefore, by the number of young sandeels born in that, and the previous, year. There is increasing evidence that sandeels in the North Sea do not constitute a single homogenous stock, but may consist instead of several discrete stocks (Proctor *et al.* 1998; Pedersen *et al.* 1999). Fishing effort for the species is also patchily distributed and there is some concern that over-exploitation of sandeel stocks may have occurred at local spatial scales.

MIFOS project - (Modelling the Impact of fisheries on seabirds)

Northern Gannet *Morus bassanus* - Family Sulidae. Largest indigenous seabird in west Palearctic, wingspan 165-180cm, body mass 2500-3600g. Breeding Quebec and Newfoundland, Iceland, Norway, Faeroe Islands, British Isles (including Channel Islands), northern France, Helgoland (Germany) and incidentally in the Mediterranean. West Palearctic breeding population winters from NW Africa to the North Sea (migratory). Mean adult annual survival *c.* 94%. Plunge pursuit diver and surface feeder, almost entirely piscivorous.

Nutritious value - The nutritional value of fish is high. In the first place, fish contains unsaturated fat (low cholesterol content). In addition to protein and fat, fish provide vitamin B (in particular B12), vitamins A and D, iodine and selenium.

Omnivorous - Eating both animal and vegetable foods.

Outer Bank - Region in the primary study area with evidence of greater mixing than in Shallow sea front region but less mixing than inner banks area or Shallow well mixed region. This region is influenced by the presence of the Shallow sea front and has access to nutrient rich cool bottom water which leads to a difference in the seasonal productive regime as compared with the Inner Bank region. (see Chapter 3)

Pelagic fish - pelagic fish species such as herring, mackerel, horse mackerel, sardinella, blue whiting, sardine and silversmelt, swim together in shoals and often migrate over large distances in the sea'.

Piscivorous - Habitually feeding on fish; fish-eating.

Planktivorous – Habitually feeding on plankton, usually zooplankton; plankton-feeder.

Primary production - the growth of phytoplankton in the ocean. Phytoplankton are single-celled plants, typically between 5 and 100 microns in size, and requiring both sunlight and nutrients in order to photosynthesise and grow. They are the ocean's primary producers, forming the base of the marine food chain.

Primary study area - The *IMPRESS* primary study area was bounded by 56°00'N to the south, 56°30'N to north, 3°00'W to the west and 1°00'W to the east (Figure 1.5.1).

Protein fishery – see Industrial fisheries.

Sandeel - Sandeel is a collective term for a number of species in the family Ammodytidae. These 20-25cm long fish are slim, with an eel-like body. The fish are silvery with a darker dorsal region. The head is pointed with a distinctly outthrust lower jaw, the dorsal and tail fins are long and low, there is no ventral fin. The tail fin is deeply split. Sandeels are schooling fish which usually occur in coastal and shallow open-ocean waters. Five species occur in the North Sea, of which the Lesser Sandeel *Ammodytes marinus* is most abundant.

Shag – see European Shag

Shallow sea front area - Region in the primary study area with strongest gradient in density at the pycnocline and with coolest bottom temperatures, both of which are characteristics of the combination of greater depths and lack of mixing of bottom water with surface layers. (see Chapter 3)

Shallow Sea Fronts - also known as Tidal Mixing fronts or Shelf Sea fronts. These fronts separate areas of shelf sea that are permanently vertically mixed (shallow and/ or strong tidal currents) from areas that thermally stratify during summer (deeper water and/or weaker tidal currents). They mark the boundary where the tendency towards summer stratification driven by solar heating is just countered by the tendency to redistribute heat through the water column by tide-induced turbulent mixing.

Shallow-well mixed region - Region in the primary study area of strong tides and some shallow topography (with some amount of fresh water influence). This region shows the greatest amount of primary production throughout the vertical water column relative to the other regions. (see Chapter 3)

Spring bloom - as the solar irradiance increases in spring there is more light available for phytoplankton photosynthesis and more heat available for stratifying the water column. If the tendency towards stratification is able to overcome the mixing by tides and winds, the development of a warm surface layer isolates some phytoplankton, along with dissolved nutrients, in the surface layer. The stratification prevents these phytoplankton from being mixed into the deeper, darker water, and with ample light and nutrients they grow (bloom) rapidly. The bloom peaks quickly, but while the light in the surface layer continues to increase, the nutrients are used up and cannot be easily re-supplied from the deeper water because of the inhibiting effect that the stratification has on mixing. The phytoplankton become nutrient-limited and, along with losses to grazing by herbivorous zooplankton, the bloom decays.

SSB – spawning stock biomass

Stratification - a water column is stratified when the density of the water has some vertical variability. This could be because the surface water has been warmed (reducing its density compared to the deeper water), and/or because the surface water has a lower salinity. Stratification inhibits vertical mixing of heat, nutrients, phytoplankton etc. and is a key process in controlling the light and nutrient environments experienced by phytoplankton.

Study area at large - Ship-based surveys were conducted within and beyond the primary study area (indicated above and in Chapter 1), with surveys on board FRV *Tridens* (1991-2004) concentrating on a much larger area (54°N-59°N, 3°W-2°E; Figure 1.5.4). This second area, the larger area around the primary study area, will be referred to as the study area at large, throughout this report.

VPA – Virtual population analysis. VPA uses commercial catch data to calculate stock sizes and mortality rates of age-based or length-based cohorts. VPAs essentially describe the past and may be refined annually with better quality data (Jennings *et al.* 2001).

European Shag Phalacrocorax aristotelis with large chicks (C.J. Camphuysen)

Chapter 13 Acknowledgements

A very large number of people has contributed to the project and it is impossible to name them all. Contributions, large and small have made this project what it turned out to be: a major undertaking and a highly inspiring exercise. We thank all and everyone, named or 'anonymous', who have made the IMPRESS project to a success.

Very much on the background, but vital for a project like this, were the financial and administrative people. Each and every partner has been relying on them, on people that could answer questions ordinary folk didn't think could be asked. For the overall administration, we would like to thank Maarten van Arkel and Irene Wernand for their patience and understanding, and obviously for the difficult, if not near-impossible, task completed.

Otherwise in a more or less random order,

We thank personal from Fishery Research Services Marine Laboratory Aberdeen, in particular Eric Armstrong, John Dunn, Mike Heath, Gayle Holland, Sarah Hughes and George Slessor and the crew of the HMV *Clupea* for support with collection and analysis of the mooring and acoustic data.

We would also like to thank the crew of the *Pelagia* and volunteers Suzan van Lieshout, Luc Meeuwisse, Damien Nixon, Jackie Smith, Philipp Schwemmer, and Nicole Sonntag who were invaluable on the *Pelagia* cruise. Martin Laan and Santiago Gonzalez were both a great pleasure to have on board and were an invaluable help during the cruise.

Russell N. Arnott deserves thanks for his efforts with Polpred (Polpred Software, Proudman Oceanographic Laboratory) and Kerstin Geitner for GIS productions of the Scanfish data.

We thank Mike Harris, Sue Lewis, Linda Wilson, Debbie Russell, Genevieve Jones, Morten Frederiksen, Mark Newell, Dave Stevens, Sheila Russell, Aki Takahashi, Yutaka Watanuki, Laurent Crespin, Maggie Hall, Suki Finney, Liz Humphreys, Ailsa Reid, Jos Milner, Julia MacPherson and Steve Redpath for providing help with fieldwork on the Isle of May and Bass Rock. Jared Wilson, Ian Parkinson, Mareike Möller-Holtkamp and Yvonne Charras of SNH for logistical support. David Bryant, Liz Humphreys, Phil Bacon and Donnie Littlejohn for help with radiotracking on the mainland. Jenny Bull, Linda Wilson, Debbie Russell, Liz Wickens, Darren Edwards and Adam Boulton for help with post-processing of logger data. Gerrit Peters for help and support with all aspects of the logger work.

Andy Easton is thanked for providing transport to the Isle of May and the Marr family for providing transport to the Bass Rock throughout the season. Scottish Natural Heritage and Sir Hew Hamilton-Dalrymple for access to Isle of May and Bass Rock respectively.

We thank Svein-Håkon Lorentsen, Claus Bech, Geir Håvard Nymoen, Hans Jakob Runde and Magali Grantham for help with the captive work on Shags and Guillemots. The Norwegian Animal Research Authority granted research permits for this study (ref no: 7/01 and 1997/09618/432.41/ME). Thanks also to the many people who helped with fieldwork particularly Stefan Garthe, Mike Harris, Janos Hennicke, Sue Lewis, Gerrit Peters, and Linda Wilson. Scottish Natural Heritage and Sir Hew Hamilton-Dalrymple granted permission to work on the Isle of May and the Bass Rock respectively. Luigi dall'Antonia and Alberto Ribolini developed the flight activity sensors used on kittiwakes and provided software for data analysis.

Thanks to Nils Hammer and his co-workers for the IMPRESS logo and for the logistics surrounding the first international conference in Hamburg.

Thanks to Ian Boyd and his co-workers for the organization and scientific planning of the conference in London in 2004 and for his editing skills used to referee and improve papers submitted by IMPRESS partners following that event.

The Norwegian Animal Research Authority granted research permits for the part of this study that was conducted in Norway (ref no: 7/01 and 1997/09618/432.41/ME), while all experimental work in Vancouver, Canada, was approved by the UBC Animal Care Committee (Animal Care Certificate # A02-0122) and in compliance with the Canadian Council on Animal Care. Canadian Wildlife Service (CWS) issued catching permits for the capture of 10 common guillemot chicks from the Triangle Island breeding colony and BC Parks authorized the capture. The BC Ministry of Environment granted holding permits for the double-crested cormorants, while CWS issued holding permits for the common guillemots.

We wish to thank Dr. Svein-Håkon Lorentsen of the Norwegian Institute for Nature Research (NINA) and Dr. Claus Bech, Dept. of Zoology, Norwegian University of Science and Technology (NTNU), both in Trondheim, Norway, for their indispensable help with setting up the captive work with shags and guillemots at Sletvik Feltstasjon in Norway. Thanks to Geir Håvard Nymoen and Hans Jakob Runde for their help with bird collection at the Runde colony. We are indebted to Magali

Grantham for her enthusiastic help with animal care, experimentation and preliminary data analysis throughout the project. Sissel Smistad kindly shared her property and provided space for our research facility at Sletvik. Francis Daunt, besides helping with statistical questions, kindly provided the stomach temperature loggers, while Gerrit Peters was always available for advice on how to fix them.

We would like to thank Dr. D.R. Jones of the Department of Zoology at UBC in Vancouver for letting us use the Animal Care and diving facilities at South Campus. Arthur Vanderhorst and Sam Gopaul of the Animal Care Centre provided support in caring for the birds and so did Kim Borg. Bruce Gillespie and Don Brandies of the UBC Zoology Mechanical Workshop were of great help for technical questions. Thanks to Ron Ydenberg and his research team at Simon Fraser University in Burnaby and Mark Hipfner of the CWS for arranging the capture of the guillemot chicks and to Eric Davies, who actually caught them. Kevin Fort and his car helped with the chick transport. David Hancock generously shared his expertise and knowledge about raising alcid chicks in captivity and was a great source of inspiration. Dr. Anne McDonald of the Night Owl Bird Hospital and Dr. Tamara Godbey at the UBC Animal Care Centre in Vancouver provided veterinary support. Thanks to Ken Scheer from the Fraser Valley Trout Hatchery for generously providing us with live rainbow trout and to Andrew Lotto (UBC Forestry) for his fish transportation tank. Tom Hoeg was indispensable in setting up the Underwater Camera System within the deep dive tank and generously donated knowledge, expertise and time. Thanks to Dr. John Gosline (UBC Zoology) for providing the video date time generator and to Dr. Robin Liley (UBC Zoology) for tolerating the takeover of his fish holding tanks and access to video equipment. Gunna Weingartner helped with preliminary analysis of the energetic trials, while Lovena Toolsy is thanked for getting the video analysis started.

We thank the European Commission, notably the Directorate-General of Fisheries for advice, support and even patience during the various phases of the project from the very beginning to the very end.

Finally, we appreciate the remark of an unnamed industrial fisheries manager that "bird people are perhaps not that stupid after all".

Northern Gannet Morus bassanus (C.J. Camphuysen)

Chapter 14 Table of contents

For economic reasons, this report has been printed in black-and-white, despite numerous coloured figures. The CD accompanying this report contains PDFs in colour of all chapters.