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Exploration of the Sea

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REPORT OF THE STUDY GROUP ON SEABIRD/FISH INTERACTIONS

Copenhagen, 6-10 September 1993

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1 INTRODUCTION

1.1 Participation

The following nominated members of the Study Group participated in the meeting:

R.T. Barrett	Norway
P.H. Becker	Germany
R.W. Furness	UK
G.L. Hunt (Chairman)	USA
D. Latrouite	France
W.A. Montevecchi	Canada
B. Olsen	Denmark
H. Skov	Denmark
M.L. Tasker	UK
P.J. Wright	UK

The following members were not able to attend the meeting but contributed to the report: D.K. Cairns (Canada), S. Garthe (Germany), S.P.R. Greenstreet (UK), and O. Hüppop (Germany).

1.2 Terms of Reference

At the 80th Statutory Meeting, it was agreed (C.Res.-1992/2:29) that the Study Group on Seabird-Fish Interactions should produce a report, and that the study group should meet at ICES Headquarters 6-10 September 1993. The terms of reference were:

a) describe and quantify the interaction between seabird, fish and shellfish populations;

b) document the amount, species and age compositions of fish taken by seabirds in the North Sea, insofar as possible, broken down by seasons, years, and sub-divisions for use by the Multispecies Assessment Working Group;

c) review the status of seabirds in relation to trophodynamics and energy budgets of marine ecosystems in the ICES area.

1.3 Health Warning

The mandate and working time frame of our Study Group were such that data base manipulations and calculations were made over a few days with minimal time for rigorous checking and full discussion of input parameters. The values presented should be taken as working estimates that may be subject to refinement.

1.4 Overview

The prey of seabirds consists in many cases of species of finfish or shellfish that are harvested by humans or which are the prey of species taken in commercial harvests. There is now a considerable body of literature investigating the trophic ecology of seabirds and the potential for interactions with fisheries (e.g., see reviews in Nettleship *et al.*, 1984; Croxall, 1987). In recent years, growing attention has been paid to the inclusion of estimates of fish consumption by marine birds and mammals when multispecies models of fisheries interactions are developed for assessing catch limits (Croxall, 1989; Anon., 1991; Rice, 1992). Several modelling efforts have shown that localized consumption of prey by seabirds has the potential to remove significant amounts of biomass (Weins and Scott, 1975; Furness, 1978; Furness and Cooper, 1982; Duffy and Schneider, 1992), although when this impact is viewed over larger spatial scales, it represents only a small portion of the prey potentially available (e.g., Bailey, 1982; Duffy and Siegfried, 1987). If we assume that seabird populations are prey limited (Cairns, 1992b), then seabird consumption of prey taken by commercial harvests is of interest to marine scientists because of the potential for competition between seabirds and fisheries when prey stocks become depleted (e.g., Schaefer, 1970; Furness, 1982; Furness and Monaghan, 1987; Montevecchi *et al.*, 1987; Croxall and Prince, 1987; Nehls, 1989; Croxall, 1989; Vader *et al.*, 1990a). In other instances, fisheries activities can increase the availability of prey to birds by removing predatory fish (Springer, 1992) or by generating offal and discards (e.g., Wahl and Heinemann, 1979; Hudson and Furness, 1988; Furness *et al.*, 1988; Garthe, 1993).

The trophic linkages of seabirds to fish stocks are also of interest as they provide an alternative approach for monitoring changes in the distribution, abundance and age class structure of prey populations. Recent attempts to use seabirds as indicators of aspects of prey stocks include Hislop and Harris (1985), Berruti (1985), Cairns (1987, 1992a), Croxall (1989), Monaghan *et al.* (1989), Barrett *et al.* (1990), Hatch and Sanger (1992), Klages *et al.* (1992), Montevecchi and Myers (1992), Montevecchi (1993), see also Lilly (1991). Indices of changes in prey stocks determined from seabirds complement more traditional indices used in fisheries management and can provide information about age classes of fish and inshore populations and distributions frequently undersampled in conventional surveys (Barrett *et al.*, 1990; Barrett, 1991; Montevecchi and Berruti, 1991; Montevecchi and Myers, 1992). Implicit in this approach to monitoring prey stocks is the assumption that aspects of seabird behaviour and population biology are linked to prey stock size, but the reliability and nature of such links require documentation before such indices can be accepted (Cairns, 1987, 1992a; Hunt *et al.*, 1991). Nevertheless, it is clear that prey abundance influences seabird population biology at the extremes of stock size variation. A full understanding of the nature of interactions between seabirds and fisheries can only be gained when the relationship between seabirds and their food organisms on the one hand, and between fisheries and fish populations on the other, are understood.

What Seabirds Eat

Seabird species take a wide variety of prey in a diversity of marine habitats. For instance, waders typically exploit infaunal invertebrates in littoral and sublittoral zones, and many nearshore-foraging sea ducks, cormorants and shags take epibenthic prey in the neritic zone. Other marine birds include surface- and near-surface-foraging storm-petrels, fulmars, gannets, gulls and terns, and subsurface pursuit-diving auks that forage in nearshore and to a lesser extent in offshore waters.

The primary foods of most seabirds worldwide are densely-schooling, small, lipid-rich pelagic fishes, crustaceans and cephalopods that occur in the upper- to mid-water column (e.g. Furness, 1978; Anderson and Gress, 1984; Croxall *et al.*, 1984; Piatt and Nettleship, 1985; Montevecchi *et al.*, 1992). Seabirds also consume demersal fishes (during pelagic egg, larval and juvenile stages; Barrett *et al.*, 1990), inshore benthic fishes (Birt *et al.*, 1987), shellfish (Goudie and Ankney, 1988) and fish offal and discards (Hudson and Furness, 1988). At high northern latitudes, sandeels *Ammodytes* spp., herring *Clupea harengus*, capelin *Mallotus villosus*, walleye pollock *Theragra chalcogramma* and arctic cod *Boreogadus saida* dominate harvests of pelagic fishes by seabirds. Anchovies and sardines are primary prey for birds in temperate boundary currents (Rice, 1992). Cephalopods are mostly exploited by seabirds at mid- and low-latitudes; crustaceans can be important prey at any latitude. Because most seabirds eat small fish or the juvenile stages of large fish, in many cases it can be assumed that the period of highly variable fish mortality has passed, and that seabirds take prey after the size of the prey cohort has been set.

Most seabirds show seasonal variation in diet and varying degrees of prey selectivity. Many species are opportunistic, taking whatever mix of prey species is available, although in multi-species communities, seabird species show distinct, consistent preferences for particular prey. Prey preferences may be constrained by foraging behaviour and energy requirements. Energetic constraints include the costs of capturing and transporting food to chicks at colonies during breeding seasons, and the energy density of prey. The high metabolic demands of seabirds require frequent intake of energy-rich food. Seabirds are migratory and exhibit seasonal changes in distributions and concentrations. Waders and most species of sea ducks migrate to high latitude tundra or freshwater habitats to nest and rear offspring. Seabirds aggregate at insular and coastal colonies that tend to be very large at high latitudes, with higher numbers of large and moderately sized colonies in temperate areas. Foraging ranges around breeding colonies are usually in the order of 10s of km, and for the most part less than 100 km, with the exception of pelagic seabirds such as storm-petrels. Once young birds of the year leave the colony, many species shift to more pelagic habitats, though most species of gulls and terns continue to forage in nearshore habitats throughout the year.

Most species of marine birds capture their food independently of human activities, though others have learned to exploit fisheries offal and discards. Large-scale demersal trawler fisheries have provided massive quantities of artificial (naturally unavailable) food in the form of offal and discards (e.g., Wahl and Heinemann, 1979; Abrams, 1983; Tasker *et al.*, 1987; Hudson and Furness, 1988; Furness *et al.*, 1992; Camphuysen *et al.*, 1993; Garthe, 1993). This "new food" production may be responsible for increases in the numbers of many seabirds (e.g., Fisher, 1952; Burger and Cooper, 1984; Furness, 1992; Howes and Montevecchi, 1993).

How Much Seabirds Eat

Seabirds consume substantial tonnages of fish and other marine organisms. The most widely used and comparative index of fish consumption by seabirds is the proportion or percentage of pelagic fish production consumed (Wiens and Scott, 1975). Ratios of consumption to production are more useful indices than ratios of consumption to biomass for small, short-lived, rapidly growing prey like small pelagic fish, crustaceans and cephalopods (Duffy and Schneider, 1992). When assessing potential influences of predation by seabirds on fish populations, it is informative to consider harvests in terms of yield-at-age analyses and number of individual prey harvested because birds often take juvenile fish that otherwise might have had a high probability of entering a fishery (Cairns, 1992a). To date, there are few examples of this approach (Barrett *et al.*, 1990; Anker-Nilssen, 1992).

Estimates of the pelagic production consumed by seabird communities are generally inversely related to ocean area included in the energetics model (Table 1.1), suggesting possible competitive interactions with fisheries are more likely at the meso-scale (Furness, 1990; Bailey, 1991) than at larger scales. However, even in considerations of localized marine areas, these models miss the dynamics of pelagic prey movements through avian foraging ranges around colonies. Food supplies around colonies in highly dynamic regimes may depend more on the advection and in migration of prey than on its production locally (e.g., Cairns and Schneider, 1990; see also Springer *et al.*, 1987; Hunt, 1991). Low consumption rates by seabirds over large scales imply that seabirds are unlikely to compete with fisheries, but do not indicate that seabirds are unaffected by commercial fishing (Duffy and Schneider, 1992).

Seabird Life History Characteristics and Influences of Fluctuations of Prey Stocks on Seabird Populations

The behavioural ecology and life-history traits of marine birds act to buffer seabird populations from fluctuations in food supply (Montevecchi and Berruti, 1991; Cairns, 1992a). Seabirds display the classic K-selected characters of high annual survivorship, great longevity, delayed sexual maturity, and low annual reproductive rate. All seabirds are K-selected in relation to typical birds and mammals of similar size, but the intensity of K-selectedness increases with increasing distance of feeding habitat from shore. Lack (1968) classified seabirds as inshore feeders, foraging within sight of land and rearing several young per year, or offshore feeders that forage across the continental shelf and raise one young per year. Survivorship, longevity, and age of sexual maturity are greater in the offshore than in inshore feeders. One might add a third category; that of oceanic birds, which have exceptionally long lifespans but which may breed only in alternate years.

Fluctuations in fish stock recruitment are likely to affect the survival of adult seabirds and seabird reproduction differently. Except in extreme cases of a region-wide collapse of all available prey stocks, adult seabird survival is unlikely to be affected by the common interannual variability in prey stocks. This is because adults can shift to alternate prey or migrate to seek prey in other regions. In contrast, breeding birds are tied to their colonies, and local fluctuations in fish recruitment can have a dramatic effect on seabird reproduction by reducing the food supply below the amount needed to generate and incubate eggs, or by removing the prey of a specific species and size that is needed to feed chicks. Seabird reproductive output can, therefore, be expected to vary with fish recruitment, and the degree of linkage will depend on the narrowness of the species-size requirements of chick feeding and the availability of alternate prey. Seabird populations will not directly track recruitment fluctuations because seabird populations are typically composed of numerous year-classes. Over the long term seabird populations will respond to fish recruitment fluctuations if recruitment is consistently good or bad for several years.

In typical situations where seabirds harvest young teleost fishes, populations of adult seabirds and of adult fish will be relatively stable and numbers of young fish and young birds will be relatively unstable. However, in situations where seabirds feed on fish subject to environmental changes sufficiently intense to kill adult fish, both seabird populations and seabird reproduction may fluctuate greatly. The El Niño Southern Oscillation (ENSO) is the classic example, where physical phenomena severely reduce fish populations to the point that adult seabirds may starve. In such a case, seabird population recovery can be expected to lag behind population recovery of the fish, since the fish can reproduce much faster than the birds.

There are many demonstrations of positive associations between the reproductive performance of seabirds and independent estimates of prey abundance (Hunt and Butler, 1980; Anderson *et al.*, 1982; Springer *et al.*, 1986; Monaghan et al. 1989; see also Diamond, 1978; Gaston *et al.*, 1983; Furness and Birkhead, 1984; Birkhead and Furness, 1985; Hunt *et al.*, 1986; Birt *et al.*, 1987). There is also evidence for decreases in seabird populations in response to drastic changes in prey stocks (Lid, 1980; Duffy, 1983; Schreiber and Schreiber, 1989). Some of these food shortages are generated by mega-scale oceanographic events, such as ENSO warm water events. Surface-feeding seabirds are more vulnerable to thermal perturbations than are pursuit-divers that can access much more of the water column (Montevecchi, 1993). The higher vulnerability of surface feeders compared to pursuit-divers is reflected in the higher reproductive variability of the former.

Fisheries and Seabird Interactions

Fisheries probably always have greater effects on seabirds than vice versa. The most direct influences of human-induced changes of fish populations on seabirds occur when both the fishery and the birds exploit the same-sized prey of a particular species, usually small pelagic fishes. There are many examples of such interactions producing severe consequences for seabirds (Table 1.2; Montevecchi, 1993). Indirect, more complex trophic interactions can occur when fisheries are directed at larger prey than seabirds eat, i.e. when seabirds prey on smaller-sized fish than are captured by the fishery. Because most large-scale fishery technologies (e.g., trawlers, gill nets) target large demersal fishes, most of the effects of these fisheries are indirect and positive. By cropping large piscivorous predators and cannibals, these fisheries benefit seabirds by increasing the abundances of small fish and crustaceans (e.g., Sherman *et al.*, 1981; Alverson, 1991; Springer, 1992; see also May *et al.*, 1979). But recruitment overfishing may also be harmful to seabirds because availability of juvenile stages of the predatory species may be reduced. From a seabird's point of view, the ideal situation is removal of a competing predator which is never itself a prey. Overharvest of whales in the Southern Ocean has often been cited as being of benefit to penguins because of the removal of a competitor. The current depletion of many groundfish species in the Northwest Atlantic may provide a test of this notion. Seabirds, notably guillemots, eat some juvenile cod but their main prey is capelin, a major prey of cod. If fisheries aid seabirds by removal of competitors, seabird reproductive rates should be higher than normal in the next several years in areas where groundfish stocks are low and limiting. When seabirds prey on smaller fish than the fishery captures, then seabirds have a greater probability of influencing prey availability for human harvests (Bailey *et al.*, 1991; Cairns, 1992a).

Focus of Study Group

Over 4 million marine birds breed on the islands and along the coasts of the North Sea and, in winter, similar numbers forage here, but species composition differs due to seasonal migrations (Dunnet *et al.*, 1990). Additionally, particularly in autumn and winter, half a million seaducks forage in coastal waters and several million migrant waders forage in the intertidal zone. The objective of this Study Group is to evaluate the interactions that have been identified between seabirds and fish, and between seabirds and shellfish, in the North Sea and other nearby regions. Our analysis is not comprehensive for pelagic birds in the North Sea. We include examples of studies detailing consumption of shellfish by seaducks, but a careful examination of shellfish consumption will need to be covered at a subsequent Study Group meeting. Our results provide a first step in developing the information necessary for including seabird prey demands in multispecies assessments for fisheries management, and for understanding the interactions between seabirds and fisheries.

Acknowledgements

The Study Group wishes to thank the many scientists who have contributed unpublished data to the European Seabirds at Sea Data Base. Knowledge of seabird numbers at sea derive from studies carried out from the United Kingdom, the Netherlands, Denmark, Germany, Norway and Belgium. These studies were funded by a number of sponsors. The European Seabirds at Sea database was compiled with funding from the UK Department of the Environment. Information on seabird colony sizes was collected by many observers, who are also thanked. We also acknowledge unpublished sandeel data from the Marine Laboratory at Aberdeen. We thank Roger Bailey, Gudrun Hilgerloh and Georg Nehls who contributed to and made comments on subsections of the report. The staff of the ICES Secretariat provided pleasant and superb support in the production of our report, and we are very appreciative of their assistance. Finally, we thank Roger Bailey for efforts in getting the Seabird Study Group off the ground and into ICES.

2 FOOD CONSUMPTION BY SEABIRDS IN THE NORTH SEA

2.1 Introduction

To estimate the amount of fish eaten by seabirds in the North Sea, the Study Group constructed a simple model. This model required the following information:

1. seabird numbers in sections of the North Sea for each month of the year,

2. energy requirements of these birds,

3. diet composition by mass,

4. energy content of foods,

5. food utilisation efficiency (assimilation efficiency).

In this section, the data requirements for estimation of fish consumption by North Sea seabirds are examined and estimates of consumption of prey are calculated using the best data currently available. Deficiencies in the data set are highlighted, since improvements to the estimates could clearly be made.

2.2 Diets of Seabirds in the North Sea

2.2.1 Foraging methods of seabirds

Ashmole (1971) classified seabird feeding methods rather than birds, because individual species often exhibit multiple methods of feeding. He identified six categories: 1. wing-propelled underwater swimming; 2. foot-propelled underwater swimming; 3. plunging from the air using momentum to approach prey at high speed; 4. feeding while settled on the surface; 5. feeding when flying, capturing prey at or near the surface; and 6. piracy (kleptoparasitism). In the North Sea seabirds use each of these methods to differing degrees, and many species can make use of several methods (Table 2.1). The auks have particularly specialised feeding methods, though they differ in details of foraging and diets (Swennen and Duiven, 1977; Bradstreet and Brown, 1985; Piatt and Nettleship, 1985). Gulls show the greatest diversity of methods within and among species: differences among species are largely a function of body size and its implications for flight. Gannets and larger gulls are less agile in the air but more powerful and able to displace smaller gull species from food sources (Braune and Gaskin, 1982; Hudson and Furness, 1988; Garthe, 1993).

Many seabirds feed in flocks, and this is especially true of those that feed on fish shoals by plunge- or pursuit-diving. One reason for the development of flocks over shoals is the apparent reluctance of fish shoals to disintegrate when attacked by predators. Around Shetland, shoals of sandeels at the sea surface used to attract large flocks of seabirds.

The behaviour of seabirds in such foraging flocks in the North Sea has not been studied, but flock foraging has been investigated elsewhere, in terms of interspecific interactions and age-related feeding performance (Porter and Sealy, 1981, 1982).

2.2.2 Methods used to study seabird diets

Methods of sampling seabird diets and statistical considerations regarding necessary sample sizes and presentation of data have been reviewed by Duffy and Jackson (1986) and in the North Sea context by Dunnet *et al.* (1990). Food samples may be obtained by killing birds and dissecting the alimentary tract, by removal of stomach contents from living birds using stomach pumps, emetics, or the natural tendency of some species to regurgitate when disturbed or handled, by examination of waste products (faeces or regurgitated pellets) containing identifiable hard parts of prey, or by direct observation or filming of food being consumed, carried, fed to chicks, or dropped at colonies. Recent work on N-isotope ratios in seabird tissues has shown that analysis of isotopes can provide information on the trophic status, but not species composition of diet (Hobson and Montevecchi, 1991).

All of these methods have their advantages and disadvantages. All can be used at breeding colonies during summer, but the study of diets in other seasons is restricted to analysing pellets at resting places, to the killing of seabirds or to observing directly the consumption of fish which is practicable behind fishery vessels and has been used in recent years (e.g. Hudson and Furness, 1988; Camphuysen *et al.*, 1993; Garthe, 1993; Hüppop and Garthe, 1993). The problem of determining diets and foraging ecology is aggravated by the fact that some seabirds feed extensively or even predominantly at night. Seabirds found dead on coasts in winter can be examined to obtain some information on the foods recently consumed, but probably provide a biased picture. In general, knowledge of the diets of North Sea seabirds is poor for the non-breeding period (Blake 1983, 1984; Blake *et al.*, 1985), but moderate to very good for the breeding season, except for non-breeders.

2.2.3 Interspecific variation in diets

Many studies of the diets of seabirds have been made in recent years in the North Sea and adjacent areas (Table 2.10). These show a strong selection for sandeels as food during the breeding season (Tables 2.12 to 2.25). North Sea seabirds eat many other kinds of animals (Table 2.2). In addition to natural diets, anthropogenic sources such as discards, offal and garbage are used by seabirds, particularly gulls.

Fish and crustaceans are of special importance for seabirds (Table 2.2). Fish is taken by most of the North Sea seabirds, and about 50% of the species take predominantly fish. In comparison, the percentage of fish in the diet often differs among closely-related species, e.g. lesser black-backed and herring gull, Arctic and common tern or common and black guillemot.

2.2.4 The preferred fish species

The preferred fish families taken by piscivorous seabirds whose diet composition is well known are presented in Table 2.3. The most important fish for the nutrition of seabirds in the North Sea are sandeels and clupeids, especially during the breeding season. Owing to a high fat content, sprat and herring are of high caloric value per unit mass, and sandeels also have relatively high energy content (Harris and Hislop, 1978; Massias and Becker, 1990; Hislop *et al.* 1991). Clupeids and sandeels are small schooling fish. In other parts of the North Atlantic, the clupeids are replaced by the capelin. A few species of Gadidae are also important prey (Table 2.3), but together with other fish groups mentioned in Table 2.3, they are relatively rare in the diets of the smaller seabird species. They are supplementary prey to which the birds switch if sandeels and clupeids are not available in sufficient numbers to fulfil nutritional requirements (see Section 2.2.8).

The key prey of seabirds are also the object of the industrial fisheries. As a consequence, North Sea seabirds are in potential competition with fisheries and at risk if the stocks of prey fish are depleted (e.g., Furness, 1987b; Bailey *et al.*, 1991).

The quality of food can have major effects on the growth and survival of seabird chicks, although it appears to be less important for adults. In gulls and terns, chicks fed on fish grow better than those fed on marine invertebrates (Spaans, 1971; Murphy *et al.*, 1984; Massias and Becker, 1990), probably because fish have higher caloric and protein densities. Puffin chicks grow best on a diet of oily fish, their preferred prey, such as sprat or large sandeel (Harris and Hislop, 1978; Harris, 1984). Similarly, great skuas feed their chicks on sandeels in preference to other food items and the proportion of the diet comprising sandeels is much higher in chicks than in breeding adults or non-breeders at the same time in the season (Furness, 1987a). Dietary studies on Arctic terns at Sumburgh (Monaghan *et al.*, 1989) and puffins at Hermaness (Martin, 1989) indicated a marked decline in the size of 0-group sandeels brought back to the nest in the late 1980s. On the basis of a caloric value of sandeels, these changes in prey size represent a marked reduction in the energy content of fish fed to chicks (Hislop *et al.*, 1991).

Even within a prey species, quality can vary considerably. Capelin show large age class differences and seasonal changes in lipid water and protein content (Montevecchi and Piatt, 1984). Seabirds feeding on capelin in north Norway appear to select, or find more readily available, capelin that are ripe and energy rich rather than spent or immature fish (Furness and Barrett, 1985). Possibly the seasonal changes in chemical composition of prey fish in the North Sea are rather less pronounced than those in Arctic fish. However, variation in nutritional content is also found between individual lesser sandeels, herring and sprat at a given time and throughout the year (Hislop *et al.*, 1991). The calorific values and body mass of sandeels larger than 10 cm show marked seasonal trends. As a consequence, the total energy content of a sandeel of a given length in summer is approximately double the spring value. Thus selection by North Sea seabirds of nutritionally superior prey within fish species may occur.

2.2.5 The length of fish chosen by seabirds

The length of fish taken by the seabirds species corresponds to body and gape size of the bird; large species take larger fish, and small species take small fish to feed their young and themselves (Table 2.4; Pearson, 1968). In discard experiments this phenomenon can also be observed (Table 2.5; Hudson and Furness, 1988; Hüppop and Garthe, 1993). Garthe and Hüppop (in press) found positive correlations between body lengths of birds and the lengths of four out of six fish species. Most sandeels eaten by seabirds are 4-16 cm (Figures 2.1 and 2.2; Table 2.12), but sizes can vary among years.

Another factor to be considered is the shape of the fish. Discard experiments showed that, on average, only 30% (5 - 67%) of all flat fish (mainly dab, flounder and plaice) but 80% (58 - 92%) of all round fish (mainly cod, whiting and bib) were eaten by herring gulls, great black-backed and lesser black-backed gulls (Garthe and Hüppop, 1993). This is partly due to the necessity for more complicated handling of flatfish and partly to the higher survival rates of flatfish before being discarded (Kelle, 1976).

2.2.6 Seasonal variation in diets

The diet composition of seabirds varies seasonally due to fluctuations in prey species availability (due to prey movements, weather, tides, predation) and to changing food demands during the different phases of the annual breeding cycle (e.g., puffin: Barrett *et al.*, 1987; kittiwake: Pearson, 1968, sandwich tern: Veen, 1977). In terns, the food composition and length of fish fed varies between courtship feeding and the chick rearing period. Males feed females with fish longer than those they eat themselves (Taylor, 1979) or than they later feed to chicks (Ewins, 1985; Monaghan *et al.*, 1989). Younger tern chicks get smaller fish or different prey species than older chicks (Lemmetyinen, 1973; Ewins, 1985; Uttley, 1991; Frick, 1993).

Herring gulls in the Wadden Sea of Schleswig-Holstein feed predominantly on shore crabs *Carcinus maenas* and mussels *Mytilus edulis*. From autumn to winter, the proportion of these prey species change in favour of the mussels and towards smaller sized crabs (Dernedde, 1992).

2.2.7 Geographic variation in diets

The diet composition of seabirds varies greatly between localities. Thus, obtaining an accurate picture of the diets of seabirds throughout the North Sea requires studies at a wide variety of localities. This is largely fulfilled for herring gull, common tern, common guillemot and puffin whose diets have been studied at several breeding sites on the North Sea coast.

The diets of these seabird species vary geographically depending on the site-specific food availability. In the herring gull, which forages predominantly intertidally, marine invertebrates are the main food source. In the Firth of Forth, discards were preferred (Table 2.6). The studied sites differed also in the percentage of marine fish and garbage in the food taken by herring gulls.

Common terns also show intersite differences in diets (Table 2.7). In contrast to common terns on the Farne Islands, common terns in the Wadden Sea rarely feed on sandeels. Crustaceans were taken in high numbers only on Griend and Wangerooge (Boecker, 1967; Becker *et al.*, 1987). Common terns breeding on the coast of the Wadden Sea exploit smelt *Osmerus eperlanus* or fish caught inland, such as sticklebacks *Gasterosteus aculeatus*, as supplementary food (Becker *et al.*, 1987; Frank, 1992). Clupeids were an important prey in all colonies studied.

The proportion of clupeids in the diets of common guillemots varied from one colony to another (Table 2.8). Clupeids were of major importance only on Helgoland, and, to a lesser extent, on the Isle of May and the Farne Islands. At all colonies except Helgoland, sandeels were the most important food.

Sandeels are also the most common prey fed to young puffins in a number of colonies (Table 2.9). In contrast, on Runde and on the Isle of May (during the 1970s before the collapse of the sprat stock), clupeids or gadoids formed an important part of the diet during some of the breeding seasons studied. Along the coast of the southern North Sea clupeids are a preferred prey, and their share in chick diets often is greater than that of sandeels (Tables 2.7, 2.8).

2.2.8 Interyear variation in diets

Interyear variability in diets is a common phenomenon among seabirds. This may be caused by annual fluctuations in prey stocks, by the food availability changing due to environmental factors such as weather and ocean temperatures, by differences in prey migration behaviour or by interspecific food competition. Owing to the different energetic values of the prey species, this variation can significantly affect breeding biology, chick growth and condition, as well as breeding success.

In common guillemots and puffins (Tables 2.8, 2.9), the percentage of clupeids or other fish in the diet correlates negatively with the percentage of sandeels. For many seabird species of the Shetland Islands, Bailey *et al.* (1991) show that the switching from sandeels to other prey species is in approximate proportion to the abundance of sandeels, and that there is no evidence of a non-linear functional response. If sandeels dominate the food, the breeding success of seabirds is comparably good (Shetland seabirds: Bailey *et al.* 1991; puffin: Barrett *et al.*, 1987; Arctic tern: Uttley, 1991; common tern: Frank, 1992).

Between 1972 and 1988, considerable changes in the species of fish fed to young puffins were found on the Isle of May (Table 2.9; Harris and Wanless, 1991): Sandeels were the most common prey except 1974-1978, when sprats formed 50-86% of the diet (by mass). During the 1980s, the proportion of sprats declined and the importance of herring increased gradually. As on the Isle of May, the proportion of herring fed to chicks on Røst, Norway, rose during the 1980s.

On the Wadden Sea island of Terschelling, the ratio between the number of breeding pairs of herring and lesser black-backed gulls has changed in favour of the latter species between 1966 - 1987 (Noordhuis and Spaans, 1992). This was concomitant with a change in the diet of the breeding herring gulls. The proportion of marine invertebrates has increased over the years, while that of fish has decreased. In contrast, lesser black-backed gulls still ate primarily marine fish. Noordhuis and Spaans suggested that lesser black-backed gulls, which outmanoeuvre herring gulls when competing for discards behind fishing boats, and are better long distance flyers, have forced herring gulls to concentrate on food sources other than discards.

2.2.9 Diets used in model

For estimation of fish consumed by seabirds in the North Sea, we reviewed the published information on diets of seabirds in the North Sea and adjacent areas, including both seabird community studies and those of single-species (Table 2.10). From these data we present selected dietary information in a summary form (Table 2.11). This table includes for each major energy-consuming seabird species a best estimate of the fish species and sizes eaten. For some species it was necessary to separate sections IVa (west) and all other areas because diets clearly differed between areas. In general, sandeels were more strongly represented in the diet in IVa (west) than in other areas. The quality of the diet data varies considerably among species, being good for guillemot but poor for fulmar.

2.3 Seabird Numbers

Seabird numbers were obtained by combining data on densities of seabirds at sea (numbers on or above a unit area of sea) throughout the year and from data on numbers of breeding and non-breeding individuals attending colonies around the North Sea in different months. The following two sub-sections detail these model inputs.These numbers and much of the rest of the model are based on six divisions of the North Sea (Figure 2.3).

2.3.1 Seabirds at sea

Methods for counting birds at sea from ships in the North Sea are described by Tasker *et al.* (1984) and Webb and Durinck (1992). These methods, or slight variants, have been used by seabird counters from many countries around the North Sea. The data collected by these observers have been assembled into one database (the European Seabirds at Sea (ESAS) database), managed by the Joint Nature Conservation Committee in Aberdeen, Scotland. The majority of the data within the North Sea were collected between 1980 and 1987, but some substantial new data for some areas in some months of the year are included in the present model. All available data have been used in this modelling effort, regardless of year. Temporal trends in seabird distribution have been ignored. Much of the information held on the database was published in 1987 (Tasker *et al.* 1987). A further analysis is in progress which will include an analysis of any temporal trends (Webb *et al.*, in prep.).

Most observations were collected away from coasts due to the avoidance of nearshore waters by ships from which observations were made. This zone is used by a number of seabird species not considered in detail in this analysis. Survey effort farther offshore has not been uniform (Table 2.26). In general, there has been a reasonable amount of survey in all areas in all months, with the exception of ICES Sub-division IVa (east). Waters in this area have been surveyed adequately in July and August, but very poorly in January, March, October and December. As a rough guide, every 1 km² surveyed takes about 10 minutes; thus there have been many hours spent in some areas. The higher the ratio of ICES rectangles to the number of rectangles in each area, the better the distribution of effort. Hunt (pers. common.) estimates that between 500 and 1000 ten-minute counts are required in an area before the estimate of the mean number of birds in the area stabilizes satisfactorily.

Despite standardized observation procedures being used, different teams of observers produce some detectable variations between data sets. These variations have not been analyzed in depth; however, some data have been treated to minimize the effects of known variations and this will be described in detail in Webb *et al.* (in prep.). Estimates of the density of seabirds in the North Sea may change slightly once such analyses have been completed, and the outputs of the model constructed here may also change as a consequence.

Mean densities of each species in each ICES rectangle in each area were averaged to produce an average density of birds for each area for each month (Table 2.27). The low survey effort in ICES IVa (east) in January and December produced anomalous mean densities (for kittiwake and gannet) that were ignored, and a mean value interpolated between adjacent months' data was inserted. In addition, herring gull densities in ICES Division IVc seemed anomalously high, and this density was reduced to one-fifth.

2.3.2 Seabirds at colonies

Methods for counting birds at colonies vary with species. In general, surface nesting species have been counted by direct observation, while burrow nesting species have been censussed by counting burrows, either as a total count or in a set of samples. Methods used in the UK in the 1980s are described by Lloyd *et al.* (1991). In general, these or similar methods have also been used elsewhere around the North Sea. Totals of these counts, mostly from the early to mid-1980s are given in Table 2.28. There have been few recent major changes in numbers in any area, but overall numbers of breeding seabirds are probably at or close to historical highs in most areas.

To calculate total numbers of birds feeding, the estimates of birds temporarily at colonies have to be added to those at sea. Table 2.29 indicates the proportion of the birds that breed at a colony that are likely to be present on land during each month. Because most cormorants and shags occur in the poorly surveyed near-shore zone, and because they are resident in areas, colony numbers (counted in pairs) were used for them throughout the model. Numbers of terns should also have been treated in this way, but due to an error were not. Their contribution to the overall model would be negligible even if their input numbers were doubled; thus this input error is not important overall.

In addition to breeding birds, colonies are also attended by non-breeding and pre-breeding birds. Table 2.30 lists the proportions of numbers counted at colonies that need to be added to account for these non-breeding birds. The timing of breeding activities, age at first breeding and adult survival rates needed for input of the above parameters have been reviewed by Dunnet *et al.* (1990).

Input to the model of numbers at colonies was thus a multiplication of numbers counted at colonies. The exact multiplier depended on species and time of year. These colony figures were added to estimates of numbers at sea before further energetic modelling.

It should be noted that new information on population levels at colonies in the south and east North Sea has become available since the review of Dunnet *et al.* (1990). This information documents considerable increases in the numbers of gulls breeding on these coasts; however such increases are not thought to have a great effect on the results of the model. Future model refinements should take account of such population changes.

2.4 Seabird Food Consumption

2.4.1 Seabird energy requirements

The energy requirements of seabirds are very high relative to those of fish of the same mass. This is because, unlike fish, seabirds are endothermic and so use large amounts of energy to maintain high body temperatures. This requires seabirds to burn more calories to offset heat loss. Metabolic rates in birds usually scale with body mass to a power of between 0.6 and 0.8, such that the metabolism per gram is considerably higher in smaller animals than in large ones. It is thus essential for metabolic rates of each group of predators to be taken into account (Furness 1984).

Energy requirements of seabirds can be assessed in two independent ways. One involves the use of allometric equations (Croxall 1982; Adams and Brown, 1984; Ellis, 1984; Gavrilov, 1985; Bennett and Harvey, 1987; Gabrielsen *et al.*, 1988, 1993; Birt-Friesen *et al.*, 1989; Koteja, 1991; Bryant and Furness, submitted) or directly determined laboratory or captive metabolic rates extrapolated to the field situation by applying correction factors or by combining laboratory measurements of metabolic costs of activities with field studies of time-activity budgets (Wiens and Scott 1975; Furness, 1978, 1990; Croxall and Prince, 1982, 1987; Furness and Cooper, 1982; Croxall *et al.*, 1984, 1991; Abrams, 1985; Gaston, 1985; Bailey, 1986; Cairns *et al.*, 1986, 1991; Briggs and Chu, 1987; Duffy *et al.*, 1987; Brown, 1989; Bailey *et al.*, 1991; Crawford *et al.*, 1991; Diamond *et al.*, 1993).

The other method uses measurements of rates of turnover of isotopes (usually of hydrogen and oxygen; Nagy, 1980, 1987) in free-living seabirds in order to assess energy expenditure over the period between release of an injected individual and its recapture, usually a day or two later (Kooyman *et al.*, 1982, 1992; Davis *et al.*, 1983, 1989; Flint and Nagy, 1984; Nagy *et al.*, 1984; Adams *et al.*, 1986, 199x; Costa *et al.*, 1986; Ricklefs *et al.*, 1986; Roby and Ricklefs, 1986; Gabrielsen *et al.*, 1987, 1991; Obst *et al.*, 1987; Pettit *et al.*, 1988; Birt-Friesen *et al.*, 1989; Cairns *et al.*, 1990; Gales and Green, 1990; Green and Gales, 1990; Montevecchi *et al.*, 1992).

2.4.2 Time-activity budget models

Many of the papers describing the energy requirements of seabird populations have used detailed species, time-activity budgets and estimates of the energy costs of incubation (Croxall, 1982; Grant and Whittow, 1983; Brown 1984; Brown and Adams, 1984; Pettit *et al.*, 1988), resting (Birt-Friesen *et al.*, 1989), walking (Ellis, 1984), flying (Ellis, 1984; Flint and Nagy, 1984; Birt-Friesen *et al.*, 1989), swimming (Ellis, 1984), diving (Kooyman *et al.*, 1982, 1992), or foraging (='at-sea metabolism') (Adams *et al.*, 1986; Costa and Prince, 1987; Birth-Friesen *et al.*, 1989; Cairns *et al.*, 1990); moulting (Croxall, 1982; Brown, 1985), chick growth (Brown, 1987) and other activities to produce a more detailed energy budget for seabirds (Furness, 1978; Burger, 1981). Such a procedure is possible only if detailed data exist for each species, and so is beyond the scope of this study. In particular, we lack information on the time-activity budgets of all North Sea seabirds outside the breeding season, and have little data for most species even during breeding. An alternative to this detailed time-budget approach is to use a direct measurement of energy expenditure as described in the next subsection.

2.4.3 Isotopic analyses of Daily Energy Expenditures (DEE)

The doubly-labelled water technique has recently been used widely on seabirds to measure field metabolic rates (FMRs) and hence average daily energy expenditures of free-living individuals. In some cases this has been combined with the use of devices to record time-activity budgets so that costs of components of the daily budget can be assessed. The technique is simple in principle, requiring birds captured and injected with deuterium (or tritium) and oxygen-18 to be recaptured, usually 24 or 48 hours after release, to obtain a second blood sample to measure the rate of turnover of each heavy isotope. The principles and limitations of analysis are reviewed by Nagy (1980) and Birt-Friesen *et al.* (1989). In theory, this direct approach to the study of seabird energy demands seems optimal in that it avoids uncertainties in the reliability of complex models based on large numbers of inputs of uncertain accuracy. In practical terms the doubly labelled water method has limitations which may make it no better than the indirect modelling approach. In particular, the fieldwork is difficult and so sample sizes using labelled water tend to be small. Variances in measurements obtained tend to be very large, giving mean estimates of energy expenditure with wide confidence intervals. Furthermore, the results may be biased. The method requires that the behaviour of the birds caught and injected is normal during the 24 or 48 hour study period. In practice, birds may not behave normally. Birt-Friesen *et al.* (1989) showed that injected gannets spent longer away from the nest than did control birds. The same result was obtained with gannets by Furness and Bryant (unpubl.), and they also found striking deviations from normal behaviour in fulmars. Such effects are often not reported, and may not have been looked for. These results do not necessarily invalidate the procedure, but they do mean that the data produced need to be viewed with caution.

Only one study has examined the extent of agreement of results achieved by activity budget and by labelled water approaches. Nagy *et al.* (1984) obtained measurements of jackass penguin FMRs only 3% higher than those produced by the bioenergetics model of Furness and Cooper (1982). Nagy *et al.* (1984) said that this close agreement lends confidence in both methods, which differ considerably in their approaches and assumptions. Kooyman *et al.* (1992) also compared results from labelled water estimation of the energy expenditure at sea with an estimate based on at sea activity budget data and model estimation from costs of resting and diving. Results from the two methods were within 7% of each other.

2.4.4 BMR multiples

Basal Metabolic Rate is the lowest rate of energy expenditure by a bird, in the thermoneutral zone, post-absorptive and at rest. Thus BMR is less than the 'Field Metabolic Rate' (FMR) (=DEE 'Daily Energy Expenditure', =AMR 'Active Metabolic Rate') which includes energy costs of thermoregulation, digestion, moult, reproduction and activity. Drent and Daan (1980) argued that birds and mammals are unable to sustain a work rate in excess of about 4.5 BMR, and most studies of the energy expenditure of birds and mammals using labelled water have found FMRs that are less than 4.5 BMR, though exceptions do exist (Birt-Friesen *et al.*, 1989).

Thus it is reasonable to assume that for most seabirds FMR will fall within the range >1 BMR to 4.5 BMR.

Furness (1990) suggested that in cases where the data are not very precise and a simple model is to be preferred, it is best to take a multiple of BMR as a measure of the FMR, rather than to attempt a complex analysis of the energy costs of a time-activity budget. Similarly, Birt-Friesen *et al.* (1989) estimated that FMR of free-ranging breeding seabirds averaged 3.3 BMR (n=18). FMR can also be extrapolated from body mass in regressions calculated for birds of different foraging modes and in different oceanographic regions (Birt-Friesen *et al.*, 1989).

Bennett and Harvey (1987) showed that for the 47 species of birds for which estimates of FMR and BMR were available (but pooling breeding and nonbreeding period data), the slope of FMR was significantly shallower (0.61) than the slope of BMR (0.68) in relation to body mass (log-log plots). Such a trend would make the use of a constant multiple of BMR invalid, but Koteja (1991) analysing a larger data set which included the data used by Bennett and Harvey (1987) found that for breeding birds as a whole (n=23) and for breeding seabirds (n=12) the slopes of BMR and FMR on body mass were equal. Furthermore, residuals of FMR and BMR from regression lines were significantly correlated for breeding birds ($r=0.48$, $n=23$, $p<0.02$), the subsample of breeding seabirds giving the same correlation ($n=12$, $r=0.51$). The implication is that species with high BMRs have high FMRs, the ratio of FMR to BMR being somewhat consistent among species, as predicted by the Drent and Daan (1980) model of maximum working capacity. These findings support the use of a single ratio of FMR to BMR. Bennett and Harvey (1987) found that birds had higher FMR to BMR ratios during breeding than at other stages of the annual cycle.

2.4.5 Diet composition by mass

Diets of seabirds in the North Sea were reviewed in Section 2.1. Diets are only very poorly known outside the breeding season, and probably vary in detail from place to place and from year to year, especially in relation to changes in fish stocks (Crawford *et al.*, 1985; Hislop and Harris, 1985; Springer *et al.*, 1986; Montevecchi *et al.* 1988; Barrett and Furness, 1990; Hamer *et al.*, 1991; Bailey *et al.*, 1991; Wanless and Harris, 1992). For this model we have used the dietary summary data Table 2.11 as representing the best estimates of diets of North Sea seabirds at different times of year. We note here the uncertain nature of these data, especially with regard to seabird diet outside the breeding season. This is identified as one of the weakest aspects of the analysis. Another concern is the way in which many seabirds can switch diet according to food availability (Barrett and Furness, 1990; Hamer *et al.*, 1991). It is clear that in recent years many of the larger seabirds have obtained large amounts of food from fishing vessels, scavenging on offal and discards (Hudson and Furness, 1988, 1989; Furness *et al.*, 1992; Camphuysen *et al.*, 1993). The possible effects on scavenging seabirds of increases in net mesh size, decreases in fishing effort and increases in minimum landing size regulations in North Sea fisheries have been reviewed by Furness (1992).

2.4.6 Energy content of foods

Calorific values of foods can be determined and have been listed in the literature, but values can differ between samples obtained in different ways. For example, seabirds appear to have selected ripe female capelin rather than catching fish at random near to Hornøy, north Norway, and so will be taking fish of higher calorific content than obtained by random sampling (Barrett and Furness, 1990). For this iteration of this model we have assumed the following calorific values of foods: sandeels, sprats and young herring 6.5 kJ/g; crustaceans 4 kJ/g; squid 3.5 kJ/g; gadid and flatfish discards 4 kJ/g, offal 10 kJ/g (Harris and Hislop, 1978; Hudson, 1986; Croxall *et al.*, 1991; Camphuysen *et al.*, 1993;). We are aware of the enormous variation in calorific value of 0-group sandeels (a major part of the seabird diet in summer) but it seems that, unless sandeels are particularly scarce, seabirds select the larger 0-group fish which have high lipid content. Further work is needed on the assignment of energy values to fish prey.

2.4.7 Food utilisation efficiency

Assimilation efficiency varies among food types, and for fish it varies according to the lipid content of the fish, being higher when lipid content is higher. However, in general, assimilation efficiency is around 75-85% for fish diets and around 70% for other marine prey (Nagy *et al.*, 1984; Jackson, 1986; Gabrielsen *et al.*, 1987; Brown, 1989; Crawford *et al.*, 1991). In view of the relatively small variation in assimilation efficiency, in relation to other errors in this calculation, use of a constant value of 75% seems satisfactory for our model.

2.4.8 Energetics model

Although there are more labelled water studies of seabirds than there are for other avian groups, most species have been studied at only one location in one or a short series of years. Thus we lack information on the extent of variation in energy expenditures as a consequence of variations in food availability and other environmental factors. It would be unwise to assume that measured FMRs for one site in one season represent figures that can be applied to that seabird species at all sites (Montevecchi *et al.*, 1992). Indeed, Koteja (1991) was able to explain only 25% of variance in FMRs of birds (or of seabirds) as a consequence of species-specific physiology (reflected by deviations of BMR from the allometric prediction). Much of the remaining variance may be due to environmental conditions affecting the birds sampled for FMR determinations rather than to species-specific characteristics. For example, Furness and Bryant (unpubl. data) found that the at-sea metabolism of fulmars decreased with increasing wind speed (this accounting for nearly 50% of the variance in individual FMRs), while Gabrielsen *et al.* (1991) found that higher wind speed caused higher at-sea metabolism of little auks. Thus, it makes as much sense to use the mean of all labelled water studies with seabirds as a BMR multiplier, as to use each individual species FMR estimates in a model based on individual species determinations summed for the community. This is particularly so when the seabird community in question (that of the North Sea) shares few species in common with the set of seabird species for which doubly labelled water estimates of FMR have been made.

A total of 34 species-measurements of seabird energetics using labelled water or using allometric equations and activity budgets gave daily energy expenditures mostly in the region of 3 to 4 x BMR during the breeding season, with medians of 2.9 BMR during incubation and 3.5 BMR during chick-rearing (Furness, 1990). Tabulation of labelled water studies of seabird FMR and measured BMR of the same populations (Table 2.31) shows that the FMR/BMR ratio varied among studies from 1.8 to 6.6, with a mean of 3.6 for a sample of 27 studies. Three of these studies were of albatrosses, which have especially efficient flight and thus lower than average at-sea energy expenditures (Birt-Friesen *et al.*, 1989), so that the appropriate multiples of BMR for North Sea seabirds are probably higher than these. For seabirds other than albatrosses the mean FMR/BMR ratio during the breeding period was 3.8, while for the small sample of six studies on seabirds that are numerous in the North Sea, the mean FMR/BMR ratio was 4.2. FMR outside the breeding season must be greater than 1 x BMR, but less than that during breeding (as shown by Bennett and Harvey, 1987). Thus we have decided to use an FMR of 3.9 BMR during the breeding season and 2.5 BMR during other periods in the model.

BMR for each species was estimated from the allometric equation derived by Bryant and Furness (submitted) for North Sea seabirds. In that study, the BMRs of individual species were found to deviate from the common regression by relatively small amounts, and some species considered to have 'above average' BMRs fell below the regression and vice versa. Thus the view that the BMR of individual species should be taken into account in modelling was not strongly supported; for ease of computation the predicted BMRs have been used; this will have very little effect on the overall total energy demands of the community since some species fall above and others below the regression. Estimated and measured BMR data are listed in Table 2.32.

Dietary data used are taken from Section 2.1 of this report and are summarised in Table 2.11.

Food consumption figures are calculated by combining the figures in the above tables and assuming a value of assimilation efficiency of 75%.

2.4.9 Model output

Monthly figures for food consumption in terms of energy requirement in each area of the North Sea by 18 seabird species were computed from the above data (Table 2.33). These figures are summarized as annual energy requirements in Table 2.34. Two species, northern fulmar and common guillemot are responsible for more than half of the energy requirements of the seabird species. Only one other species, herring gull, requires more than 10% of the total seabird energy requirement. The largest energy requirement is in ICES Division IVa (west).

These energy requirements were converted to food consumption needs using the data outlined in Section 2.3. The results of this are presented in Table 2.35 for the eight greatest consumers of energy in the North Sea (responsible for 94% of the energy demand), and the shag. This latter species, although only requiring 1.2% of the total seabird energy demand, is included as it consumes mostly sandeel. The mackerel and large herring sections of this table are truncated as they are consumed only by gannets.

Consumption by seabirds is further summarized by food species and by quarter and area in Table 2.36, and quarterly food requirements for the entire North Sea in Table 2.37. These show a very large proportionate demand of Division IVa (west) and the large demand for sandeel (33% of total food usage of seabirds), and waste products from fisheries (30% comprising 12% from offal, and 18% discards).

2.5 Discussion

The results of the modelling can be compared with those by other studies of the North Sea, and from further afield. The results of all but one of these other studies have been based on populations of breeding seabirds in an area, with suitable extrapolation to allow for non-breeding birds. In an area such as the North Sea, where there is substantial immigration, emigration and passage of seabirds through the area the assumption that only local populations of birds use an area does not hold. This study and that of Tasker *et al.* (1988) are the only studies to use at sea information from the North Sea to derive the bird population input.

Bailey (1986) used breeding population data from around the North Sea, and estimated about 1.9 x 10^{12} kJ of energy was required by seabirds. This is about half that estimated by the current model (3.9 x 10^{12}), but Bailey's seabird population data were from 1969/70, and there has been a substantial increase in breeding numbers since then (Lloyd *et al.*, 1991). Tasker *et al.* (1988) used at sea data and estimated 2.7 x 10^{12} kJ was consumed by seabirds; this earlier data set did not adequately allow for numbers of birds in some unsurveyed areas of the North Sea.

All of the above studies, and those of Furness (1978, 1984) indicate that food consumption is not uniform across the North Sea, but is distinctly heterogeneous, with particular "hot-spots" in the western northwestern North Sea and around seabird colonies. These areas of high food consumption are not confined to colonies and their environs, but can occur elsewhere in the North Sea, particularly outside the summer breeding season. The present analysis was not sufficiently spatially disaggregated to identify these hot-spots.

Sandeels and waste products from fisheries clearly dominate as foods consumed. There are, though, from the seabird point of view, some important temporal and spatial variations in foods consumed. Temporally, sandeels fulfil just under a half of the total food supply of seabirds in the early part of the breeding seasons (April to June); this ratio declines to about 35% in July to September, and about 20% for the remainder of the year. During the period that sandeels are not taken, presumably through being unavailable while buried in the sediments, sprats, young herring and gadids become much more important as food (from a total of 4% of total food in April/June to about 20% in October/December. Other studies have also shown substantial emigration of birds from the study area in winter. Guillemots, for instance, are found in substantial numbers in the Skagerrak/Kattegat area in winter (H. Skov, unpubl. data) and the English Channel (Webb *et al.*, unpubl. data). These areas are not used by guillemots to any great extent during the summer. Use of offal and discards is also considerably more important during the winter than in spring or summer. In this case, most of the diet switching is by fulmars. However, the evidence for fulmar diet composition (and any changes) is, as outlined above, not great.

Estimated consumption by seabirds can be compared to the figure previously used in the MSVPA. Consumption by seabirds is quite small relative to fish stock biomass and annual production, and relative to the mass of prey taken by the main MSVPA predatory fish. Our estimate of total live prey consumed (270,000 tonnes per year) is similar to that previously estimated in the MSVPA (230,000 tonnes per year). However, the species composition of seabird prey is very different from that of the MSVPA predatory fish, and hence from the prey spectrum for seabirds assumed in the MSVPA (Table 2.38). The seabirds feed highly selectively, especially on sandeels and small clupeids, and consume virtually no benthic invertebrates ("an important other food of predatory fish") in Table 2.38. Thus, the mortality of sandeels due to seabirds is much greater than in the MSVPA model. Moreover, seabird predation on sandeels is highly concentrated in a small portion of the North Sea.

2.5.1 Further research priorities

To refine this model, several areas need to be addressed. The most important of these is the relative lack of knowledge of seabird diet outside the breeding season, and in areas away from land. The major energy demands during this period are those of fulmar and guillemot, and better information on their winter diets must be a high priority, especially for fulmar where few data currently exist. The serious logistic problems of obtaining representative samples in offshore areas in winter are obstacles that will be difficult to overcome.

Further work should be undertaken to refine the population estimates, both of at-sea and breeding birds for input to the model. These refinements would undoubtedly improve the model, but it is thought that they would not substantially alter its findings. Further model refinements could include estimation of food demand by nestlings.

3 SEADUCK CONSUMPTION OF SHELLFISH: EIDERS AND SCOTERS IN THE WADDEN SEA

3.1 Introduction

In the North Sea the most important shellfish consumption by seabirds occurs on the southeastern and southern coasts, in and offshore the Wadden Sea (Fig. 3.1). In these areas the high shellfish biomass is used primarily by eiders *Somateria mollissima* and common scoters *Melanitta nigra*. Both species occur in substantial numbers and have high food demands. The distribution of eiders in the Wadden Sea and common scoter in the offshore zone corresponds largely with the harvesting area of the shellfish fisheries. As these seaducks mainly take the same molluscs as the shellfish fisheries, fishermen are concerned about competition from these seaducks. Owing to this conflict some research on duck feeding ecology has been carried out, and the knowledge of shellfish consumption by these seaducks is relatively good.

3.2 Population Development and Distribution

The breeding population of eiders in the Wadden Sea is relatively small, about 7000 pairs (Swennen *et al.*, 1989), but increasing (Becker, 1992). Much larger numbers of non-breeders, however, use this area in summer, autumn and winter. These birds originate from the Baltic Sea population (Swennen, 1976), which has increased during the last 20 years, from 250,000 pairs in the 1970s (Almkvist *et al.*, 1974) to 600,000 pairs in 1980 (Stjernberg, 1982). Numbers wintering in the Wadden Sea may be between 243,000 and 331,000; numbers moulting between 228,000 and 282,000 eiders (Swennen *et al.*, 1989, Table 3.1).

Although total numbers in fall and winter are similar, their distribution within the Wadden Sea changes seasonally. Highest numbers are found in the Danish and Dutch parts in winter, and in the German part during the moult period in late summer (Swennen *et al.*, 1989).

The numbers of birds per km^2 do not traditionally differ much between the different parts of the Wadden Sea (Swennen *et al.*, 1989). During the 1980s, however, the spatial distribution of wintering eiders between different areas of the Wadden Sea changed dramatically (Table 3.1), with the former centre of distribution in the western part moving towards the central parts of the Wadden Sea. As a result of poorer feeding conditions in the Danish and Dutch parts, eiders now concentrate in Germany.

Swennen *et al.* (1989) studied the percentage of the eider population near mussel culture plots (Table 3.3). However, there was no apparent relation to the presence or absence of mussel cultures. In Schleswig-Holstein the large concentrations of moulting birds stay away from the mussel cultures, and eiders increased mainly in areas without mussel cultures (Nehls *et al.*, 1988). Also in the Dutch Wadden Sea, eiders concentrate far from the mussel culture plots during the breeding and moulting period.

Non-breeding common scoters use the extensive shallow area in front off the Wadden Sea, approximately delimited by the 5 and 20 m depth contours (Laursen *et al.*, unpubl. data). The staging, wintering and moulting populations of common scoters off the Wadden Sea total to 200,000 birds (Laursen and Frikke, 1987a; Offringa, 1991; Laursen *et al.*, unpubl. data; Leopold, unpubl. data). As the entire habitat of the species offshore of the Wadden Sea has only recently been surveyed, little is known about trends in numbers of wintering birds.

Large concentrations of common scoters (> 100,000 individuals) have so far only been found on Terschelling bank (Leopold *et al.*, unpubl. data) and offshore of the Danish Wadden Sea islands. However, during cold winters parts of the very large population of the western Baltic Sea and Kattegat may be forced by ice cover to move into the coastal areas of the eastern North Sea, thereby increasing the population of common scoters considerably. In total, the Baltic Sea holds at least 5 million seaducks during winter (Table 3.2). Translocation of large seaduck populations from the Baltic to the North Sea during adverse weather conditions is especially relevant for common and velvet scoters *Melanitta fusca*, while the substantial population of long-tailed duck *Clangula hyemalis* (Pihl *et al.*, 1992; Durinck *et al.*, 1993;) remains within the Baltic Sea.

3.3 Diets and Foraging

Both the eider and common scoter feed on marine invertebrates, mainly molluscs, throughout the year. In the Wadden Sea the mussel *Mytilus edulis* and the cockle *Cerastoderma edule* are the most important food items. In the Dutch Wadden Sea, mussels and cockles each comprise 40% of the eiders' food (Swennen, 1976). Investigations in Schleswig-Holstein by Nehls (1989) showed that cockles contributed about 75% of the food during summer, when eider numbers are highest. At Königshafen, Sylt, eiders preferred mussels from May to December, except during October, when cockles predominated (Ketzenberg, 1991).

Eiders use various feeding techniques on tidal and subtidal areas (Nehls, 1991; Ketzenberg, 1991). They prefer feeding by head-dipping at low water levels, during the rising or falling tide, depending on the position of the feeding grounds. In winter, when the food demand of eiders is highest, they tend to feed at mussel beds close to the low water line, where feeding is not restricted during low tide. Eiders may dive to depths of more than 30 m and are thus able to reach any area of the Wadden Sea.

Ketzenberg (1991) found that the foraging intensity increased from summer to autumn, as did the length of the mussels consumed (32 mm median length in May, 47 mm median length in November).

Off the Wadden Sea, as well as in areas along the Danish westcoast, the bivalve *Spisula subtruncata* seems to be the most important food source for common scoters. This species dominated the food in a sample of oiled specimens from the Netherlands (Offringa, 1991), and in a sample of scoters from the northern west coast of Denmark (Durinck *et al.*, in press).

Within the main depth range used by common scoters along the continental coast of the North Sea, *S. subtruncata* is a very widespread and abundant species, reaching densities of 8,000 individuals per m^2 (Thorson, 1979).

3.4 Food Consumption in Relation to Biomass

The food consumption of eiders in the Wadden Sea was estimated by Swennen *et al.* (1989) to be 60,000 tonnes per year, based on a value of the daily food demand found by Swennen (1976, Table 3.4). This estimation is rather rough, however, as neither the seasonal variation in the number of birds using the Wadden Sea (Swennen *et al.*, 1989) nor variation in their energy and food demands (Laursen and Frikke, 1987b) were considered.

Using values of daily energy demands for common scoters given by Offringa (1991, 60 g AFDW (ash free dry weight)/day), the annual food consumption of common scoters occurring off the Wadden Sea can be roughly estimated at 25,000 - 30,000 tonnes mainly of *S. subtruncata*.

Studies of the impact of food consumption on the biomass of macrozoobenthos in the Wadden Sea region have only been carried out for eiders. In comparison with the biomass of the macrozoobenthos on the tidal flats of the Wadden Sea the food consumption of the Eider per m^2 is relatively low (3-5%, Table 3.5; Nehls, 1989, Swennen *et al.*, 1989). Also the consumption in relation to the available food resources of mussels and cockles (12.5 %, Table 3.5) is much lower than reported from other areas. In the Ythan estuary eiders are estimated to consume 39 % of the annual mussel production which is 20 % of all zoobenthos production (Milne and Dunnet, 1972). In the St. Lawrence estuary, Canada, eiders take 10-30 % of their preferred prey, a *Littorina* species, during summer (Cantin *et al.*, 1974). In the Schleswig-Holstein area, eiders eat 34 % of the total food taken by carnivorous birds (Nehls, 1989), and are therefore important consumers.

Based on the percentage of eiders near cultivated mussels (Table 3.3), Swennen *et al.* (1989) estimated that over the year eiders in the Dutch Wadden Sea take about 50 % of their mussel food (see Table 3.4) from culture plots (30 x 10^6 kg). This relation is much lower in the other areas of the Wadden Sea.

3.5 Development of Shellfish Populations and Shellfish Fishery

Owing to the eutrophication of the North Sea, the biomass of benthic invertebrates has increased during the last decades in the western part of the Wadden Sea (Beukema 1989). However, the populations of molluscs and other benthic organisms in the Wadden Sea fluctuate markedly in response to weather conditions. Losses are especially severe in cold winters (e.g. Michaelis, 1992) and during storms (Nehls & Thiel, in press). Spatial variation in the environmental conditions may cause regional differences in the mussel stock; Michaelis (1992) recorded small, reduced populations in some parts of the Wadden Sea of Niedersachsen from 1985-1990.

An increase in the bivalve biomass resulted also from the commercial culture of mussels. It started in the Netherlands in the fifties and increased rapidly to 70 km^2 (Drinkwaard, 1987; Veer, 1989). In the Dutch Wadden Sea about 60 % of the mussel biomass is found on cultivated musselbeds (Dekker, 1989). Since 1960 the mussel culture has also increased markedly in the German part of the Wadden Sea (example: Figure 3.2). In the Danish Wadden Sea mussel culture banks are banned (Dahl, 1992).

According to the increasing practice of cultivating mussels, the annual mussel harvest grew strongly. In the German Wadden Sea the yield increased fivefold between the 1940s and the 1980s (Table 3.6). In the Danish Wadden Sea, an intensive fishery on natural mussel beds has developed since 1983 (Dahl, 1992). The total yield of mussels in the Wadden Sea per year is about 100,000 tonnes (Table 3.7), a higher mass than that consumed by the eider (60,000 tonnes) (Tables 3.4, 3.7).

Some restrictions of the shellfish fishery in the German Wadden Sea were caused by the foundation of the national park in Lower Saxony in 1986, "Nationalpark Niedersächsisches Wattenmeer", where the cockle fishery was banned in 1992. The fishery argues that the cockle catch was halved during the 1980s due to the restrictions by the national park (Meixner, 1992). In the national park of Schleswig-Holstein, "Nationalpark Schleswig-Holsteinisches Wattenmeer" which was founded in 1985, the harvest of cockles is not allowed. The fishermen are requested to transfer mussel culture plots from the strictly protected zone to other areas (Franz, 1992).

The shellfish fishery in Denmark has been under strict regulation since the severe decline in the mussel stock in the Danish Wadden Sea in 1988 (Dahl, 1992). In contrast, the Dutch fishery has been unregulated.

3.6 Possible Interactions of Shellfish Fishery and Seaduck-Consumption

Dramatic changes in the spatial pattern of winter distribution of eiders in the Wadden Sea indicate a possible competition between eiders and the shellfish fishery. In the mid-1980s, during a period with increasing intensity of mussel fishery by Dutch vessels in Danish waters, the number of wintering eiders in the Danish Wadden Sea has decreased (Laursen and Frikke, 1987a). Due to overfishing and ice damage in winter 1986/1987, only 3,000 tonnes of mussels were caught during the following 2.5 years, and the eider population was also much affected. Since 1987, the numbers of eiders in the Danish Wadden Sea have not increased (Table 3.1). Concurrent with the decrease in Denmark, the numbers of eiders decreased in the Netherlands and increased in the

German Wadden Sea. Swennen (1991) attributes the heavy decreases in the Dutch Wadden Sea to overfishing of the populations of cockles and mussels. The shift of eiders towards Germany possibly may be favoured by high mussel populations in the East-Frisian Wadden Sea (Nehls, pers. comm.).

Due to the lack of seabird monitoring in offshore regions in the German Bight, changes in the numbers of common scoters found off the Wadden Sea are not well known. Recent research carried out off the Frisian island Terschelling, in the Netherlands, indicates a possible conflict with the Dutch fishery targetting for *Spisula subtruncata* comparable to that between eiders and the shellfish fishery in the Wadden Sea (Leopold *et al.*, unpubl. data). During one month of fishery in 1993 the total biomass of *S. subtruncata* on the Terschelling bank was reduced by 50% (Leopold *et al.*, unpubl. data).

The same order of consumption per year by the shellfish fishery and eiders (Tables 3.4, 3.7) indicates, that conflicts are probable. Pehrsson (1984) has shown, that the availability of food is the key factor regulating the number of eiders. The eider consumption in relation to the available food resources (12.5%) (Table 3.5) is very low in the Wadden Sea, however, and there is no clear evidence that eiders reduce mussel populations in the Wadden Sea although some reduction of preferred sizes is apparent (Ketzenberg, 1991). The mussel harvest has actually increased despite the growing numbers of eiders.

Mussels harvested by the fishery are usually larger than 5 cm. Eiders, however, prefer mussels 3-5 cm long (Ketzenberg, 1991). The situation is different for the cockle, as harvested cockles are within the range preferred by the Eider. The exploitation of mussel beds by seaducks and shellfish fishery are different processes (Nehls, pers. comm.). The consumption by seaducks is a long-term process, directed to the more abundant smaller sizes of a mussel population, and very likely to be compensated by production in most cases. Exploitation by fisheries may completely remove a mussel bed within a few days. Removals may be compensated by new recruitment. In this way an impact of fisheries on eiders and common scoters appears to be more likely than *vice versa*. In Schleswig-Holstein, Nehls and Thiel (in press) identified storms as being a main factor limiting the distribution of mussel beds to the sheltered parts of the Wadden Sea, where beds may persist over long periods. On the other hand, beds in exposed parts are highly dynamic, and are removed frequently. The impact of the fishery will vary accordingly (Nehls and Thiel, in press). Fishing on persistent beds in sheltered areas may remove the crucial food reserve needed by mussel-feeding birds in times of low mussel populations.

Competition between fishermen and eiders/common scoters will occur mainly in years with low cockle or mussel populations, either due to natural fluctuations caused e.g. by severe winters, or by overfishing as documented in the 1980s in the Wadden Sea (see above).

3.7 Research Needs

The interactions of shellfish fishery and eiders/common scoters are not yet clearly understood, and further research on the mussel beds in the Wadden Sea and on the offshore banks of the German Bight is much needed. Eider and common scoter feeding ecology, their possible effects on the mussel beds and the relation between the mussel harvest of these birds and the shellfish fishery need to be studied, as do influences of the shellfish fisheries on the seaduck populations and their temporal and spatial distribution (Nehls, 1989).

4 SEABIRD-FISH INTERACTIONS IN THE EASTERN ATLANTIC

4.1 Introduction

As outlined in Section 1, the stability of seabird populations is far more sensitive to changes in mortality rates than in reproductive output. Fluctuations in fish stocks are likely to affect both parameters but the former is less likely to be affected by the usual range of interannual changes in fish availability. While seabirds are generalists in their choice of diet, some populations are nevertheless dependent on few or even one prey species at certain times of the year. This makes them particularly vulnerable to fluctuations in that particular stock.

This is demonstrated by several case studies within the ICES area where collapses in stocks of sandeels, capelin, and herring have had dramatic consequences for local populations of seabirds on Shetland, the Faroes and in Norway as summarized below.

4.2 Shetland

4.2.1 Background

The Shetland Isles are an internationally important area for breeding seabirds, the colonies of 13 species forming between 25 and 100% of their total breeding populations within the North Sea (Tasker *et al.*, 1987). Many seabirds breeding in the Shetland Isles are largely dependent on a single prey species, the lesser sandeel *Ammodytes marinus* particularly during the breeding season (e.g. Martin, 1989b; Monaghan *et al.*, 1989). For most seabird species no other suitably sized, energy-rich prey occurs near Shetland (Kunzlik, 1989; Hislop *et al.*, 1991).

Seabird species with relatively large chicks tend to provision them with larger (and generally older) sandeels than species with small chicks. For example, Arctic terns, kittiwakes and puffins tend to feed their chicks on O-group sandeels (young of the year), whilst large pursuit diving birds, such as shags and guillemots tend to feed on large (1 year old and older) sandeels (Martin, 1989b).

During the 1980s, the breeding success of several seabirds at Shetland declined markedly. This was coincident with a marked decline in landings of sandeels (mainly *Ammodytes marinus*) from an industrial fishery that operated close to the Shetland and Fair Isle coast. Due to the proximity of the fishery grounds to areas where seabirds foraged, many have argued that the fishery competed for the same resource as the seabirds, and was responsible for the decline in sandeel availability to seabirds. However, fishery studies carried out by the Scottish Office Agriculture and Fisheries Department indicated that the decline in both landings and sandeel abundance was the result of a decline in recruitment to the Shetland stock (recruitment here defined as the number of young surviving to 1 July from each year's spawning), which preceded any change in the spawning stock (Kunzlik, 1989). The Scottish Office maintained that natural fluctuations in sandeel survivorship prior to exploitation by the fishery were the main cause of the decline in fishery landings and prey for seabird chicks. Nevertheless, despite these arguments, there was still considerable controversy over the impact of the fishery, and in particular the possibility that local depletions near seabird colonies were not detected by fishery assessments (see Monaghan, 1992). Further, regardless of any direct impact on sandeel stocks that the fishery may have had, it was also not clear whether the decline in sandeel abundance alone was sufficient to explain the extent of seabird breeding failures since the breeding success of large pursuit diving species, which preyed on sandeels, did not decline to the extent seen in surface feeding seabirds (Heubeck, 1989; Okill, 1989).

4.2.2 The Shetland sandeel fishery

The Shetland sandeel fishery was established in 1974 and reached a peak in landings of 52,000 t in 1982. The fishery was relatively small in relation to other North Sea sandeel fisheries and in contrast to most other industrial fisheries operated at a number of small (0.5 - 10 km^2; Gauld unpubl. data; Figure 4.1) inshore grounds (< 10 km from the coast) throughout the Shetland Isles. For assessment purposes sandeels from these grounds were considered as belonging to a single stock. This distinction was based on the relatively slow growth rates of Shetland sandeels and the geographical discreteness of Shetland grounds in relation to other fished grounds. Landings declined following 1982 as a result of low recruitment and the fishery was closed in June 1990. The decision to close the fishery was based on the small size of spawning stock and the continued low recruitment.

4.2.3 Changes in seabird populations and breeding performance

Seabirds appear to be a major predator of sandeels in the vicinity of Shetland. Furness (1990) estimated that seabirds consumed 49,000 t yr^{-1} of sandeels between 1981 and 1983, similar to the amount taken by the fishery. Historical data on seabird numbers at Shetland are limited, and it is, therefore, not possible confidently to assess changes in numbers of most species in this area before 1969. During the 1970s, numbers of most species increased (Okill, 1989; Heubeck, 1989; Furness, 1990; Heubeck *et al.*, 1991), possibly in part due to immigration (Bourne and Saunders, 1992), although changes were largely in line with national trends.

The species of seabirds whose breeding success was most affected by the decline in sandeels were those that fed predominantly on young of the year (O-group), close (<0.5m) to the sea surface. These species included Arctic terns (Monaghan *et al.*, 1989), kittiwakes (Heubeck and Ellis, 1986), great skua *Catharacta skua* (Hamer *et al.*, 1991). Arctic skuas which are kleptoparasites of the surface feeding seabirds were also affected (Heubeck, 1989). Of these, the Arctic terns suffered the lowest breeding success, with almost complete breeding failure throughout Shetland between 1984 and 1990 (Heubeck and Ellis, 1986). The puffin, a small diving species, also suffered breeding failures in some areas of Shetland (Martin, 1989a). On the basis of census data collected in the early and mid-1980s (Joint Nature Conservancy Committee/Seabird Group,'seabird colony register', Lloyd *et al.*, 1991), there were approximately 160,000 pairs of guillemots, 100,000 pairs of puffins, 50,000 pairs of kittiwakes and 30,000 pairs of Arctic terns. By 1990, there appear to have been some notable declines in numbers of several species. For example, while numbers of Arctic terns in Shetland appear to have remained fairly constant between 1969 and 1980 (representing around 40% of the British and Irish population) (Bullock and Gomersall, 1981), a survey in 1989 indicated that numbers subsequently declined by 50% or more (Avery *et al.*, 1991). In addition, significant declines also occurred in kittiwake (Heubeck, 1989) and guillemot colonies (Heubeck *et al.*, 1991). Numbers of Arctic terns dramatically increased again in 1991, just prior to the appearance of the large 1991 sandeel year class.

Studies of seabirds at Foula, begun in the 1970s, showed a decrease in feeding on sandeels by great skuas (68%-95% of food regurgitates from chicks in 1974-83 but only 5% and 14% of regurgitates in 1988 and 1989), and a concomitant drop in chick survival and growth. Furthermore, adults worked harder to try to rear chicks and their mortality increased (Hamer *et al.*, 1991). This led to a slight fall in breeding numbers but this was buffered by an increased rate of recruitment of immature great skuas (Klomp and Furness, 1992). Thus, although great skuas showed only a small initial decline in breeding numbers in response to sandeel shortage (in contrast to the Arctic terns which chose not to breed when food availability was low), the recovery of sandeels in 1991-1993 allowed Arctic tern numbers to recover also immediately, but saw more rapid declines in great skua numbers as the pool of prebreeders matured. It is evident from this that seabird responses differ between species, and in this case Arctic terns showed a more successful response than the skuas by refraining from breeding when costs of foraging were elevated.

Seabird studies carried out at Sumburgh and Fair Isle showed that there were very marked changes in the breeding and foraging success of both surface feeding and diving seabirds between 1990 and 1992. In 1990, Arctic terns and kittiwakes suffered a total breeding failure. Guillemots and shags also experienced difficulties in provisioning chicks in 1990 (Monaghan *et al.*, 1992).

4.2.4 Changes in sandeel availability

Wright and Bailey (1993) investigated sandeel availability to Shetland seabirds between 1990 and 1992. They found that changes in seabird breeding performance and foraging success were associated with marked changes in sandeel abundance and distribution. Sandeels were scarce and restricted to within 5 km of colonies in 1990, widely distributed with the largest concentrations occurring offshore in 1991, and intermediate between the two years in 1992, with the highest concentrations occurring inshore (Figure 4.2). Age composition analysis indicated that these changes in abundance were due to changes in O-group abundance; a large year-class in 1991 giving rise to a large number of 1+ sandeels in 1992. O-group abundance was very low in both 1990 and 1992 in south Shetland. These changes in O-group abundance were not associated with any marked changes in the size of the potential spawning stock. The restricted sandeel range in 1990 appeared to mark the end of a period of stock contraction. The expansion of sandeel distribution in 1991 and 1992 was associated with the appearance of sandeels in many areas of unsuitable habitat.

Variability in year-class strength was not the only factor that affected prey availability to seabirds. In 1990, densities of O-group sandeels were markedly lower during the kittiwake chick period than in late July, owing to the late appearance of appreciable numbers of O-group sandeels into south Shetland waters. This observation demonstrates the importance of O-group sandeel movements to seabird foraging success. Inter-annual differences in the size and energetic value of O-group sandeels during the 1990-1992 study were also evident from both sampling and seabird diets. For example, it was estimated that O-group sandeels found in kittiwake regurgitates in 1990 would have had approximately 5-10% of the energetic value of O-group sandeels taken in 1991.

The problem of low sandeel availability to seabirds in 1990 may have also been exacerbated by the patchiness of shoal distribution and its effect on encounter rate, since sandeel patchiness was found to covary with abundance. Kittiwakes spent a longer time foraging and searched over a greater range (>40 km from colony) in 1990 than in later years. Radiotracking studies on guillemots and shags from Sumburgh colonies indicated that the distance these birds foraged from the colony decreased from 1990-1992, although tagged birds foraged within 10 km of their colony in all years (Monaghan *et al.*, 1992). Comparisons between the areas and frequency at which shags and guillemots returned to a feeding site and sandeel distribution and sediment data indicated that these diving species were able to select areas of suitable sandeel habitat.

4.2.5 Causes of varying sandeel year-class strength

Investigations into the early life-history of sandeels around Shetland seabird colonies found evidence for changes in the factors likely to affect O-group abundance. The poor year classes in 1990 and 1992 were associated with relatively early larval hatch dates and consequent low growth rates. Evidence was also found for immigration of O-group sandeels from outside the Shetland assessment area from a review of historic survey data and dedicated surveys of larval abundance. Temporal trends in recruitment, spawning stock and offshore densities of O-group sandeels indicated that high offshore densities of O-group sandeels coincided with years of relatively high recruitment per spawning stock biomass. Larval surveys indicated that by far the most important region of larval production in the Shetland-Orkney region was to the north and west of Orkney (Figure 4.3). Densities of late larvae were also found to be significantly higher in this region than in the inshore waters around Shetland. Thus it was postulated that spawning in Orkney gave rise to the high offshore densities of O-group sandeels seen in 1991 and other years of high recruitment and that these schools eventually immigrated into the Shetland grounds.

While the results of the Shetland sandeel research programme did not prove that the fishery had no deleterious effect on sandeel 'stocks' around Shetland, it was evident from the fluctuations in sandeel abundance observed following the closure of the fishery, that such an effect need not be invoked. The study highlights the variability in year-class strength and the importance of understanding prey population structure, given the possibility that there may be immigration of sandeels from other areas.

4.3 Faroe Islands

Nearly 2 million pairs of seabirds breed on the Faroe Islands (Table 4.1). During the breeding period all these birds and a great portion of the immatures feed close to the islands. Outside this period the situation is more complicated. Some of the local populations, e.g., that of the common guillemots migrate to other areas while a portion of the Scottish guillemot population spends the winter around the Faroe Islands.

Due to the relative isolation of the Faroes and their fish stocks, seabird/fish interactions may be less complicated than in other ICES areas. Furthermore the most important seabird food during the chick rearing period, the sandeel, is not locally exploited. The seabirds therefore have only to compete with larger fish and grey seals for the sandeels. Because the sandeels are not exploited, we know very little about their populations. Recent O-group cod surveys, however, give an index of sandeel recruitment (Figure 4.4).

Sustained harvests of seabirds and their eggs give an impression of great natural year-to-year variations in the production of seabirds as well as long-term fluctuation in the seabird populations (Reinert, 1976; Norrevang, 1977; Olsen, 1991). Reinert (1976) showed a close correlation between these fluctuations and the occurrence of spawning herring in the Faroes and in Norway. The export of feathers between 1710-1910 suggest a periodicity of 100 years (Figure 4.5), with the guillemot population reaching a third maximum in the 1950s.

In the late 1980s, the production of young guillemots and puffins almost completely failed. The situation is now improving. This improvement may be as much a positive response to an improvement in the environment of the prey species, as a result of the reduced competition by the groundfish stocks which also collapsed.

Common guillemots

Censuses indicate that the breeding population of common guillemots is now only 5-10% of the numbers breeding in the 1950s. Since 1973 a guillemot study plot has been censused (Figure 4.6). Following a decline until 1990, including a 25% crash between 1989-1990, they have increased over three consecutive years.

Puffins

The puffin population has been rather stable, but in 1989 and 1990, many dead young were found in the colonies. The same happened in 1991, when an experiment with supplementary feeding of the young showed that they were starving.

The survival of young during the last three years has improved from less than 50% in 1991 to about 70% and 98% in 1992 and 1993, respectively. The food brought to the young has also changed. The normal food is sandeels, but in 1991 and 1992, Norway pout and capelin dominated in periods. In 1993, sandeels were again the most common food, supplemented with Norway pout. The size of individual sandeels increased during these years.

Arctic terns

In 1984-1992 no Arctic tern chicks fledged, but in 1993 young were fledged in almost all the colonies.

Using these three species of seabirds as indicators for the availability of sandeels and other prey of forage fish during the last decades, they indicate a period with relatively low production of forge fish reaching a minimum around 1990. Since then there has been an improvement, and 1993 was the most productive for seabirds in the last 10 years.

The increase in sandeel availability for seabirds may also have been the result of reduced competition by groundfish stocks, which are at their lowest level for several decades. The groundfish stocks, however, have been low for many years and it has been suggested that the recruitment of food for both birds and fishes was low in the late 1980s (Olsen, 1991). The recruitment of cod and haddock has been low for many years and the mean weight of individual fishes in each year class has been decreasing, but in 1993 the recruitment of cod, sandeels and Norway pout was fairly good (J. Reinert, pers. comm.).

4.4 Norway

There have been recent and severe changes in stocks of two of the preferred prey species of Norwegian seabirds, the Norwegian spring-spawning herring and the Barents Sea capelin. Attributed to these changes are massive declines in the Røst population of the puffin and the Barents Sea population of the common guillemot respectively. However, the mechanisms behind the declines in the respective species to the changes in prey availability are very different. Norwegian spring-spawning herring and Barents Sea capelin represent two of the largest fish stocks in the North Atlantic. Both are pelagic and migratory, and their migrations are key factors in their availability to avian predators.

The main difference between the two fish species is that only the smallest/youngest stages of the herring are suitable as prey to most seabirds. Capelin, on the other hand, are rarely too large for seabirds to handle and some even seem to select for the large, gravid and hence energy-rich females (Furness and Barrett, 1985; Erikstad and Vader, 1989).

4.4.1 Puffins/herring

The Norwegian spring-spawning stock of the Atlanto-Scandian herring spawn off southwestern Norway in February-April and, after hatching ca. 2-3 weeks later, the larvae rise into the upper water layers (0-50 m) and are transported northwards, mainly by the Norwegian coastal current. The autumn distribution of the 0-group fish is widespread from the fjords of North Norway to offshore water in the Norwegian and Barents Seas (Dragesund *et al.*, 1980; Loeng, 1989). By then they have reached a length of 10-13 cm (Toresen, 1990).

On their way northwards, some pass the puffin colonies off the Nordland coast where 50-60 mm long juvenile herring constitute a major part of the puffin chick diet (Myrberget, 1962; Anker-Nilssen, 1992). Anker-Nilssen (1992) recently estimated that the puffin population at Røst, Lofoten Islands was > 1 million pairs at the end of the 1970s and is thus one of the most important concentrations of seabirds in the North Atlantic.

After the collapse in the herring spawning stock from > 11 million tonnes in 1957 to 20,000 tonnes in 1971, there was virtually no production of 0-group herring in the coastal waters (Figure 4.7). However, in the warm period of 1983-1985, three relatively strong year classes were produced, and after a slight increase in the spawning stock in 1988, a number of good year classes have been recorded in the Barents Sea annually.

These recent years of high herring year-class strength corresponded with years of good puffin chick production on Røst. Based on 16 seasons since 1975, Anker-Nilssen (1992) demonstrated a strong positive correlation between fledging estimates and corresponding herring 0-group abundance indices. Furthermore, he showed that herring abundance accounted for 67% of the observed variance in fledging success from a logistic model of the two data sets.

The years of repeated breeding failure combined with a relatively high rate of adult nest-site fidelity (Harris, 1976) are considered to be the direct cause of puffin breeding population declines on Røst (Anker-Nilssen and Røstad, 1993). Between 1979-1989, there was a 64% decrease, averaging 14% per annum in 1983-1987, in numbers of occupied burrows in the colony (Anker-Nilssen and Røstad, 1993). Although the decline now seems to have ceased through the recruitment of chicks produced in 1983-1985 (Anker-Nilssen and Barrett, 1991), the long-term recovery of the population will depend on repeated recruitment in the herring stocks.

The lack of food in the Røst area also affected the common guillemots. Although less well documented, much of the near 95% decrease between 1960 and 1988 in the common guillemot population on Røst may also be attributed to a production of few and underweight young and subsequent recruitment failure (Bakken, 1989). However, some of the decline may also be partly due to drowning in fishing nets and/or adverse feeding conditions outside the breeding season in the Barents Sea, where many of the adults spend the winter (Strann *et al.*, 1990; Vader *et al.*, 1990a).

4.4.2 Guillemots/capelin

Since the collapse in the herring stocks, capelin have become the dominant pelagic schooling fish in the Barents Sea and, together with sandeels, the main food source of most of seabirds in the region (Furness and Barrett, 1985; Erikstad and Vader, 1989; Barrett and Furness, 1990). Its distribution is restricted to the Barents Sea. Spawning occurs along the coast of Troms, Finnmark and Murmansk, with a more westerly spawning during cold years (Loeng, 1989) mainly in March and April, but also as late as June and July. The larvae drift northeastwards and the maturing individuals feed in the northern Barents Sea.

Between 1972 and 1975, the stocks of two-year-old and older capelin increased to ca. 7 million tonnes. However, after 1975 there was a steady decline in the stock until 1986/1987 when it decreased to 20,000 tonnes. However, capelin have a much shorter generation time (at present 2-3 years) than herring (5-7 years) and, following a brief moratorium on the capelin fishery, the stock has rapidly recovered. By 1991, it had reached approximately 4 million tonnes (Anon., 1993).

The effects of this rapid collapse in the capelin stock were twofold. During the decline in 1980-1983, capelin was a major part of the diet of many species on Hornøy (Tables 4.2-4.4) and the breeding success of kittiwakes, puffins, common guillemots and shags was high. Chick growth was rapid and guillemot chicks were heavier than average when leaving the cliffs (Furness and Barrett, 1985). In all respects, the Hornøy seabirds seemed to have had an exceptionally rich food supply in the early 1980s (Furness and Barrett, 1985).

In 1986 and 1987, the situation was very different. Both breeding seasons were very poor all along the south coast of the Barents Sea with several species producing no young at all (Vader *et al.*, 1987). In 1986, the kittiwakes all but gave up breeding on Syltefjord, the largest colony in Norway (ca. 140,000 pairs), and the common guillemots on Hjelmsøy in West Finnmark had a very poor season (Vader *et al.*, 1987). Kittiwakes also laid smaller than normal clutches and hence produced fewer than normal young.

By 1989, when capelin stocks were still very low (200,000 tonnes), all species were again breeding successfully and there was no evidence of food shortage (Barrett and Furness, 1990). Furthermore, the birds' diet contained more capelin in 1989 than in 1983, and Barrett and Furness (1990) suggested that they may have included an unidentified local fjordic stock of capelin that is distinct from the Barents Sea stock. The existence of such a stock has still to be validated.

The second, and most dramatic effect was on the breeding populations of guillemots. Until 1985/1986, the numbers of common guillemots breeding in East Finnmark and along the Murmansk coast were relatively stable (Syltefjord) or increasing (Hornøy, Bolshoi Kharlov). In 1987, a massive decline in the numbers of guillemots breeding on Hjelmsøy, Hornøy, Bolshoi Kharlov and Bear Island was registered. Counts made in 1987 revealed ca. 80% and 33-63% declines in the breeding populations of common guillemots and Brünnich's guillemots, respectively, since 1985/86 (Table 4.5; Vader *et al.*, 1990a,b; Barrett and Krasnov, unpubl. data). At the same time, numbers of both species dropped at their traditional wintering area in the Barents Sea (Vader *et al.*, 1990b), and thousands of emaciated common guillemots were washed ashore along the coast of Finnmark during the winter 1986/87 (Vader *et al.*, 1987).

The decline in numbers and the breeding failures in 1986/1987 coincided with the collapse in the capelin stock and have been attributed to both winter starvation by adults and problems in finding enough food for chicks during the summer. Since 1989, the capelin stocks have risen further and parallel to this numbers of common guillemots on Hornøy and Bolshoi Kharlov have started to recover.

While the effect of the near demise of the herring stocks on the puffin population is a clear demonstration of the effects of repeated recruitment failure, the effect of the collapse of the capelin stocks on guillemots also demonstrates the consequences of changes in adult mortality on long-lived birds with low reproductive potentials. Both cases show how large changes in the abundance of a key prey species can have serious implications for seabird populations.

A further response by seabirds to changing prey availability is the recent appearance of herring in the diet of several species breeding on Hornøy and Bolshoi Kharlov. As the herring stocks increase, more and more of the youngest year classes are entering the Barents Sea and are being preyed on by the seabirds. Since 1990, herring has made up a substantial amount of the diet of seabirds breeding on Hornoy (Tables 4.2-4.4). It is possible that the situation is reverting to that of the 1930-1940s when Belopol'skii (1957) recorded herring as an important constituent of the summer diet of many species breeding in the region.

5 COMPARISON OF SANDEEL AND SPRAT EXPLOITATION BY SEABIRDS AND INDUSTRIAL FISHING IN THE NORTH SEA

5.1 Sandeels

The lesser sandeel *Ammodytes marinus* predominates both in the diet of seabirds (see Section 2) and in the landings of industrial fisheries in the North Sea (Anon., 1992). In comparison to consumption by fish predators and fisheries landings (see Appendix 1), overall sandeel consumption by seabirds in the North Sea is relatively low (< 8 % of total annual consumption of sandeels by predators and fisheries.). However, regional comparisons of sandeel consumption indicate that most seabird predation is concentrated in the western North Sea, in ICES Division IVa (west) and to a lesser extent in Division IVb (west) (Table. 5.1). In contrast, fishery catch data indicates that most sandeels are caught in other areas of the North Sea. For example, the largest sandeel catches were from Division IVb (central) in the early 1980s and Division IVa (east) in the late 1980s. This suggests that there is relatively little overlap in the main areas of sandeel exploitation by fisheries and seabirds. This latter finding is not unexpected given that, while the largest seabird colonies are concentrated around the northern UK coast, the most productive areas for fishing occur at offshore banks beyond the normal foraging range of most breeding seabirds (see Giglason and Helgason, 1985). Major fishing grounds include the western part of Dogger bank, the Jutland Reef, the Inner Shoal, the western edge of the Norwegian Deep to Viking Bank.

The impact of seabird predation on sandeels in Division IVa (west) is difficult to assess owing to differences in the regional classifications of stocks and the lack of data on sandeel concentrations in this region. Industrial fisheries assessments divide the North Sea into three assessment divisions; Northern, Southern and Shetland, although the Shetland sandeel fishery was closed in 1990. ICES Division IVa (west) includes both the Shetland assessment area and part of the northern assessment area. Furness (1990) estimated that annual consumption of sandeels by seabirds at Shetland accounted for 27% (49,000 t yr^{-1}) of Shetland sandeel stock production between 1981 and 1983, which was similar to that taken by the local fishery. In addition to the sandeel grounds which form the Shetland assessment division, research surveys of adult and larval distribution have identified the presence of many sandeel concentrations around Orkney and the Scottish mainland coast (Figure 5.1). Little is known about long-term changes in sandeel abundance in these areas, since they are rarely fished. The degree to which these inshore sandeel concentrations inter-mix with the major offshore concentrations is also unknown, although investigations of larval and juvenile distributions suggest that inter-mixing between inshore and offshore sandeel concentrations in Division IVb (east) is unlikely (Langham, 1971; Wright and Bailey, 1993).

Based on these comparisons of seabird and fishery exploitation patterns and the possible differences in stocks exploited by seabirds and major industrial fishing fleets it would seem unlikely that changes in sandeel stocks reported for the two large industrial fish assessment divisions are particularly relevant to most seabird populations in the North Sea. However, it is feasible that any increases in fishing pressure within Division IVa (west) and other inshore grounds may result in competition between seabirds and fisheries.

5.2 Sprats

Sprat occur throughout the shallow southern North Sea and in the Moray Firth, Firth of Forth and over the Fladen Grounds east of Orkney. Sprat distribution varies seasonally as a result of migrations (Feldman, 1986). Traditional sprat fisheries are largely dependent on sprats moving close inshore to overwinter. Seabirds also take advantage of these overwintering concentrations, and so the factors influencing these sprat migrations may affect sprat availability to seabirds, in addition to overall stock levels.

As with sandeels, estimates of consumption suggest that seabird predation on sprats is relatively small in relation to piscivorous fish (see Table 5.1; Appendix 1). However, it should be noted that seabird consumption estimates were based on dietary data collected in the 1980s. Sprat fishery landings declined as a result of a reduction in the size of the spawning stock and the ratio of spawning and 1-year-old sprats between 1974 and 1984. By 1985, annual catches were approximately only double that taken by seabirds (Table 5.1). If seabird consumption data are representative of 1985, there would appear to be a spatial difference in seabird and fishery exploitation, with most seabird consumption of sprat being in Division IVb (west), while most sprat landings were from IVb (east) and the Skagerrak.

The 1970s decline in sprat stocks has been indicated as a possible cause of seabird mortality (Harris and Bailey, 1992). Overfishing, at least during the period of the stock decline, has been implicated in the decline of sprat stocks (Anon., 1986; Burd and Johnson, 1983), although its relative importance has been questioned. Burd and Johnson (1983) concluded that recruitment overfishing was a major contributor to the decline of the sprat stock. In contrast, fishery scientists from the 1986 ICES Sprat Working Group believed that stock fluctuations were largely related to long-term environmental changes, since the decrease in sprat abundance occurred almost instantaneously over a very wide area (Anon., 1986) . The nature of such environmental influences are unknown, but Corten (1986) and others have discussed the possibility that changes in Atlantic water inflow into the North Sea may have been important.

6 CONCLUSIONS AND RECOMMENDATIONS

6.1 Conclusions

1. Seabirds in the North Sea are estimated to consume 600,000 t of food per annum. This estimate is based on data obtained over the last decade, when seabird numbers were at a historically high level, and excludes consumption by seaducks and waders. Seabird consumption can be partitioned approximately as 200,000 t of sandeel, 30,000 t of sprats and small herring (predominately sprats), 22,000 t of live, small gadids and 13,000 t each of large herring and mackerel. Seabirds consumed an additional 109,000 t of discards and 71,000 t of offal with the remainder of their prey partitioned between zooplankton, intertidal and terrestrial foods. This harvest of prey species is different from that assumed for seabirds in the MSVPA, particularly in the case of sandeels. This is because seabirds are selective foragers and concentrate their foraging on a relatively small number of fish species.

2. Northern fulmars and common guillemots account for 54% of total seabird energy demand. The diet of guillemots is quite well known, even for the winter period. In contrast, little is known about the diet of fulmars, especially in winter. There is considerable spatial variation in the amount of dietary data available for all seabird species. Most data originate from studies made in Shetland or east Scotland, where seabird consumption is concentrated.

3. There is spatial and temporal variation in the consumption of sandeels by seabirds in the North Sea. Sandeels comprise nearly 50% of food consumption in the second quarter of the year, and remain the most important prey item in the third quarter. In winter, when sandeels become less available, they represent about 20% of the total seabird diet, and a large proportion of the population of the primary seabird consumer, common guillemot, emigrates from the North Sea. In winter, the importance and total consumption of other fish species increases considerably.

4. Discards and offal represent 30% of total food consumed by seabirds in the North Sea, and over half of the food taken in winter. Northern fulmars

take the largest portion of these foods.

5. Seabird consumption of prey is unevenly distributed across the North Sea. The highest proportion of total consumption is in Area IVa (west), where breeding colonies of seabirds are concentrated. In the breeding season (April-July), the foraging of breeding seabirds is restricted to within tens of km of their breeding sites. Therefore, much of their prey during this season is from coastal waters.

6. There is relatively little spatial overlap in sandeel harvest by seabirds and sandeel fisheries.

7. Although there is considerable information available on the length distributions of fish taken by seabirds, studies to date have rarely assigned fish to age classes. Considerable work is required to provide information on the age classes of fish consumed by seabirds.

8. For useful linkage of seabird prey consumption to fisheries management models, it is essential that temporal and spatial scales used in the two types of analyses correspond. Populations of many species of seabirds are concentrated at sea in relatively few areas.

9. Seabirds are characterised by having high rates of adult survival and low annual reproductive potential (1-3 young). Because adults can shift between prey species or foraging grounds, moderate variations in prey populations are unlikely to have severe effects on the survival of adult seabirds. However, because breeding birds are tied to insular and coastal colonies, and because many species depend on one or a few prey species to feed chicks, local fluctuations in fish recruitment can have major effects on seabird reproduction. Surface - and nearshore - foraging seabirds generally experience greater inter-annual variability in reproductive performance than do pursuit-diving and offshore-foraging seabirds.

10. The consumption of shellfish by seaducks in the North Sea is concentrated in the German Bight and the Wadden Sea. There, annual consumption is estimated to be 100,000 t of bivalves. Data on the consumption of shellfish by waders on the coasts of the North Sea and for seaducks in areas other than the German Bight remain to be assessed.

6.2 Recommendations

1. Despite considerable research into seabird breeding ecology at many sites around the North Sea, data from these sites have not been drawn together to examine interannual variability, the spatial scale over which such variation correlates among colonies, and the biological and physical oceanographic factors that may force seabird responses. It is therefore recommended that the Study Group on Seabird-Fish Interactions convene an interdisciplinary workshop that will include not only seabird ecologists, but also fishery biologists and oceanographers. Their goal should be to synthesize appropriate data sets on seabirds, prey populations and physical oceanographic phenomena that could elucidate spatial and temporal variability in the North Sea ecosystem.

2. The Study Group on Seabird-Fish Interactions should review the evidence for the potential effects of fisheries on the local abundance of prey species in the context of the spatial and temporal scales relevant to seabirds. This review should focus primarily on the North Sea, but should include information from other regions where relevant.

3. The Study Group on Seabird-Fish Interactions should assess the consumption of shellfish by seaducks and shorebirds, as well as the possible interactions with shellfish fisheries within the ICES area.

4. In view of the identified deficiencies in information on the diets of seabirds, it is recommended that data be sought on the diets of the major consumers in seasons and areas presently undersampled. Future sampling of seabird foods should include data on age of fish, as well as length, when possible. Additional analysis of fish consumption by age class using available data should be done.

7 REFERENCES

Abrams, R.W. 1985. Energy and food requirements of pelagic aerial seabirds in different regions of the African sector of the southern Ocean. Pp. 466-472 In: W.R. Siegfried, P.R. Condy & R.M. Laws (eds.) Antarctic nutrient cycles and food webs. Springer-Verlag, Berlin.

Adams, N.J. & Brown, C.R. 1984. Metabolic rates of sub-Antarctic Procellariiformes: a comparative study. Comp. Biochem. Physiol. 77A: 169-173.

Adams, N.J., Brown, C.R. & Nagy, K.A. 1986. Energy expenditure of free-ranging wandering albatrosses *Diomedea exulans*. Physiol. Zool. 59: 583-591.

Adams, N.J., Abrams, R.W., Siegfried, W.R., Nagy, K.A. & Kaplan, I.R. 199x. Energy expenditure and food consumption by breeding Cape gannets *Morus capensis*. Mar. Ecol. Prog. Ser.

Aebischer, N.J., and Wanless, S. 1992. Relationships between colony size, adult non-breeding and environmental conditions for shags *Phalacrocorax aristotelis* on the Isle of May, Scotland. Bird Study 39: 43-52.

Almkvist, B., Å. Andersson, A. Jögi, M.K. Pirkola, M. Soikkeli, & J. Virtanen 1974: The number of adult eiders in the Baltic Sea. Wildfowl 25: 89-94

Anderson, D.W., Gress, F., and Mais K.F. 1982. Brown pelicans: influence of food on reproduction. Oikos 39: 23-31.

Anderson, D.W., and Gress, F. 1984. Brown pelicans and the anchovy fishery off southern California. pp. 128-135 in D.N. Nettleship, G.A. Sander, and P.F. Springer, (Eds.). Marine birds, their feeding ecology and commercial fisheries relationships. Canadian Wildlife Service. Ottawa, Canada.

Anker-Nielsen, T. 1987. The breeding performance of puffins *Fratercula arctica* on Røst, northern Norway in 1979-1985. Fauna norv. Ser. C, Cinclus 10: 21-38.

Anker-Nielsen, T., and Lorentsen, S.H. 1990. Distribution of puffins *Fratercula arctica* feeding off Røst, northern Norway, during the breeding season, in relation to chick growth, prey and oceanographic parameters. Polar Res. 8: 67-76.

Anker-Nilssen, T. & Barrett, R.T. 1991. Status of seabirds in northern Norway. Brit. Birds 84: 329-341.

Anker-Nilssen, T. 1992. Food supply as a determinant of reproduction and population development in Norwegian puffins. Dr. Scient. thesis, Univ. Trondheim, 150 pp.

Anker-Nilssen, T. & Røstad, O.W. 1993. Census and monitoring of puffins *Fratercula arctica* on Røst, N. Norway, 1979-1988. Ornis Scand. 24: 1-9.

Anon. 1986. Report of the Sprat Biology Workshop. ICES, Doc. C.M.1988/H:4

Anon. 1991. Report of the Multispecies Assessment Working Group. ICES, Doc. C.M.1991/Assess:7.

Anon 1992. Report of the Multispecies Assessment Working Group, Copenhagen, 16-25 June 1992. ICES, Doc. CM 1992/Assess:16

Anon 1992. Report of the Industrial Fisheries Working Group, Copenhagen, 18-25 March 1992. ICES, Doc. C.M. 1992/Assess:9.

Anon. (1992a). Report of the Industrial Fisheries Working Group. ICES CM 1992/Assess: 14.N. ICES CM 1992/Assess:15.

Anon. 1992b. Preliminary report of the international 0-group fish survey in the Barents Sea and adjacent waters in August-September 1992. ICES, Doc. C.M.1992/G:82: 32 pp.

Anon. 1992. Report of the Study Group on Seabird-Fish Interactions. ICES, Doc. C.M.1992/L:8.

Anon. 1993. Ressursoversikt for 1993. Fisken og Havet, 1993. Særnr. 1, 68 pp.

Ashmole, N.P. 1971. Seabird ecology and the marine environment. Avian biology (Ed. by Farner, D.S. and King, J.B.), pp. 223-286. Academic Press, London, New York.

Bailey, R.S. 1986. Food consumption by seabirds in the North Sea in relation to the natural mortality of exploited fish stocks. ICES, Doc. C.M.1986/G:5.

Bailey, R.S. 1989. Interactions between fisheries, fish stocks and seabirds. Mar. Pollut. Bull., 20, 427-430.

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

Bailey, R.S. 1991. The interaction between sandeel and seabirds - a case history at Shetlands. ICES, Doc. C.M.1991/L:41.

Bakken, V. 1989. The population development of common guillemot *Uria aalge* on Vedoy, Røst. Fauna norv. Ser. C, Cinclus 12: 41-46.

Barrett, R.T., Anker-Nilssen, T., Rikardsen, F., Valde, K., Røv, N., and Wader, W. 1987. The food growth and fledging success of Norwegian puffin chicks *Fratercula arctica* in 1980-1983. Ornis, Scand. 18: 73-83 [1].

Barrett, R.T., Rov, N., Loen, J. & Montevecchi, W.A. 1990. Diets of shags *Phalacrocorax aristotelis* and cormorants *P. carbo* in Norway and implications for gadoid stock recruitment. Mar. Ecol. Prog. Ser. 66: 205-218.

Barrett, R.T. & Furness, R.W. 1990. The prey and diving depths of seabirds on Hornoy, north Norway after a decrease in Barents Sea capelin stocks. Ornis Scand., 21, 179-186.

Beaman, M.A.S. 1978. The feeding and population ecology of the great black-backed gull in northern Scotland. Ibis 120: 126-127.

Becker, P.H., Frank, D., and Walter, U. 1987. Geographische und jährliche Variation der Ernährung der Flußseeschwalbe (*Sterna hirundo*) an der Nordseeküste. J. Orn. 128: 457-475. [2].

Becker, P.H. 1992: Seevogelmonitoring: Brutbestände, Reproduktion, Schadstoffe. Vogelwelt 113: 262-272

Becker, P.H. 1993. Seevögel als Bioindikatoren. Whilhelmshavener Tage 4: 79-93. Brune-Druck, Wilhelmshaven.

Belopol'skiii, L.O. 1957. Ecology of sea colony birds of the Barents Sea. Israel Progr. Sci. Transl. 1961: 346 pp.

Bennett, P.M. & Harvey, P.H. 1987. Active and resting metabolism in birds: allometry, phylogeny and ecology. J. Zool. Lond. 213: 327-363.

Berruti, A. 1985. The use of seabirds as indicators of pelagic fish stocks in the southern Benguela Current. pp. 267-279. Ed. Bunning, L.J. in Proc. Sympos. Birds Man. Johannesburg, Witwatersrand Bird Club.

Beukema, J.J. 1989. Long-term changes in macrozoobenthic abundance on the tidal flats of the western part of the Dutch Wadden Sea. Helgol. Meeresunters. 43: 405-415

Bezzel, E. 1985. Kompendium ver Vögel Mitteleuropas. Non passeriformes. Aula Wiesbaden.

Birt, V.L., Birt, T.P., Goulet, D., Cairns, D.K. & Montevecchi, W.A. 1987. Ashmole's halo: direct evidence for prey depletion by a seabird. Mar. Ecol. Prog. Ser. 40, 205-208.

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: 357-367.

Blake, B.F. 1983. A comparative study of the diet of Auks killed during an oil incident in the Skagerrak in January 1981. J.Zool. Lond. 201: 1-12.

Blake, B.F. 1984. Diet and fish stock availability a possible factors in the mass death of auks in the North Sea. J. Exp. Mar. Biol. Ecol. 76: 89-103.

Blake, B.F., Dixon, T.J. Jones, P.H., and Tasker, M.L. 1985. Seasonal changes in the feeding ecology of guillemots (*Uria aalge*) off north and east Scotland. Est. Coast. Shelf. Sci. 20: 559-568.

Boecker, M. 1967. Vergleichende Untersuchungen zur Nahrungs- und Nistökologie der Flußseeschwalbe (*Sterna hirundo* L.) und er Küstenseeschwalbe (*Sterna paradisaea* Pont). Bonn. Zool. Beitr., 18: 15-126. [3].

Bourne, W.P., and Saunders, 1992. Operation Seafarer: Arctic terns at Shetland. Scott. Birds 16: 205-210.

Bradstreet, M.S.W., Brown, R.G.B. 1985. Feeding ecology of the Atlantic Alcidae. In: Nettleship, D.N. and Birhead, T.R.: The Atlantic Alcidae. Academic Press, London: 264-318.

Braune, B.M., and Gaskin, D.E. 1982. Feeding methods and diving rates of migrating larids off Deer Island, New Brunswick. Can. J. Zool. 60: 2190-2197.

Briggs, K.T., and Chu, E.W. 1987. Trophic relationships and food requirements of California seabirds: updating models of trophic impact. Pp. 279-304 in J.P. Croxall (ed.) Seabirds: feeding ecology and role in marine ecosystems. Cambridge Univ. Press, Cambridge.

Brown, C.R. & Adams, N.J. 1984. Basal metabolic rate and energy cost of incubation in the wandering albatross (*Diomedea exulans*). Condor 86: 182-186.

Brown, C.R. 1984. Resting metabolic rate and energetic cost of incubation in macaroni penguins (*Eudyptes chrysolophus*) and rockhopper penguins (*E. chrysocome*). Comp. Biochem. Physiol. 77A: 345-350.

Brown, C.R., and Adams, N.J. 1984. Basal metabolic rate and energy cost of incubation in the wandering albatross (*Diomedea exulans*). Condor 86: 182-186.

Brown, C.R. 1985. Energetic cost of moult in macaroni penguins (*Eudyptes chrysolophus*) and rockhopper penguins (E. chrysocome). J. Comp. Physiol. 155B: 515-520.

Brown, C.R. 1987. Energy requirements for growth and maintenance in macaroni and rockhopper penguins. Polar Biol. 8: 95-102.

Brown, C.R. 1989. Energy requirements and food consumption of *Eudyptes penguins* at the Prince Edward Islands. Antarct. Sci. 1: 15-21.

Bryant, D.M. & Furness, R.W. submitted. Basal metabolic rates of North Atlantic seabirds. Ibis

Bullock, I.D., and Gomersall, C.H. 1981. The breeding populations of terns in Orkney and Shetland in 1980. Bird Study 28: 187-200.

Burd, A.C., and Johnson, P.O. 1983. The assessment of the North Sea sprat stock. ICES Doc. CM 1983/H:32: 1-8.

Burger, A.E. 1981. Time budgets, energy needs and kleptoparasitism in breeding lesser sheathbills, *Chionis minor*. Condor 83: 106-112.

Burger, A. & Piatt, J. 1990. Flexible time budgets in breeding common murres: buffers against variable prey abundance. Studies in Avian Biol., 14, 71-83.

Burger, A.F., and Cooper, J. 1984. The effects of fisheries on seabirds in South Africa and Namibia. pp.155-160 in D.N. Nettleship, G.A. Sanger and P.F. Springer (Eds.) Marine Birds: Their fishing ecology and commercial fisheries interactions. Canadian Wildlife Service, Ottawa.

Butler, P.J. & Woakes, A.J. 1984. Heart rate and aerobic metabolism in Humboldt penguins, *Spheniscus humboldti,* during voluntary dives. J. Exp. Biol. 108: 419-428.

Cairns D.K., Montevecchi, W.A. & Birt, V.L. 1986. Energetics and prey consumption by seabirds breeding in Newfoundland. Pacific Seabird Group Bull., 13, 102.

Cairns, D.K. 1987. Seabirds as indicators of marine food supplies. Biol Oceanogr. 5:261-271.

Cairns, D.K., Montevecchi, W.A., Birt-Friesen, V.L. & Macko, S.A. 1990. Energy expenditures, activity budgets and prey harvest of breeding common murres. Studies in Avian Biol. 14: 84-92.

Cairns, D.K., Chapdelaine, G. & Montevecchi, W.A. 1991. Prey exploitation by seabirds in the Gulf of St. Lawrence. Pp. 277-291 in J.-C. Therriault (ed.) The Gulf of St. Lawrence: small ocean or big estuary? Can. Spec. Publ. Fish. Aquat. Sci. 113.

Cairns, D.K. 1992a. Bridging the gap between ornithology and fisheries science: use of seabird data in stock assessment models. Condor 94:811-824.

Cairns, D.K. 1992b. Population regulation of seabird colonies. Curr. Ornithol. 9: 37-61.

Camphuysen, K. 1990. Diet, age and sex of guillemots in the Dutch sector of the North Sea in spring. Sula 4: 41-54.

Camphuysen, C.J., Ensor, K., Furness, R.W., Garthe, S., Huppop, O., Leaper, G., Offringa, H. & Tasker, M.L. 1993. Seabirds feeding on discards in winter in the North Sea. NIOZ Rapport 1993-8. Neth. Inst. Sea Res., Texel.

Cantin, M., J. Bédard, & H. Milne 1974. The food and feeding of common eiders in the St. Lawrence estuary in summer. Can. J. Zool. 52: 319-334.

Carrne, D.K., and Schneider, D. Hot-spots in cold water: feeding habitat selection by thick-billed murres. Avion Biol. 14: 52-60.

Corten, A. 1986. On the causes of the recruitment failure of herring in the central and northern North Sea in years 1972-1978. J. Cons. int. Explor. Mer. 42: 281-294.

Costa, D.P., Daan, P. & Disher, W. 1986. Energy requirements of free-ranging little penguin, *Eudyptula minor.* Comp. Biochem. Physiol. 85A: 135-138.

Costa, D.P. & Prince, P.A. 1987. Foraging energetics of grey- headed albatrosses Diomedea chrysostoma at Bird Island, South Georgia. Ibis 129: 190-196.

Coulson, J.C., and Thomas, C.S. 1985. Changes in the biology of the kittiwake *Rissa tridactyla:* a 31-year study of a breeding colony. J. Anim. Ecol. 54: 9-26.

Coulson, J.C., and Butterfield, J. 1986. Studies on colony of colour-ringed herring gulls *Larus argentatus*: II colony occupation and feeding outside the breeding season. Bird Study 33: 55-59.

Crawford, R.J.M., Cruickshank, R.A., Shelton, P.A., and Kruger, I. 1985. Partitioning a goby resource among four arian predators and evidence for altered trophic flow in the pelagic community of an intense perenial upwelling system. Afr. J. Mar. Sci 3: 215-228

Crawford, R.J.M., Ryan, P.G. & Williams, A.J. 1991. Seabird consumption and production in the Benguela and western Agulhas ecosystems. S. Afr. J. mar. Sci. 11: 357-375.

Croll, D.A., Gaston, A.J. & Noble, D.G. 1991. Adaptive loss of mass in thick-billed murres. Condor 93: 496-502.

Croxall, J.P. & Prince, P.A. 1982. A preliminary assessment of the impact of seabirds on marine resources at South Georgia. Com. Nat. Franc. Recherch. Antarct. 51: 501-509.

Croxall, J.P. 1982. Energy costs of incubation and moult in petrels and penguins. J. Anim. Ecol. 51: 177-194.

Croxall, J.P., Ricketts, C. & Prince, P.A. 1984. Impact of seabirds on marine resources, especially krill, of South Georgia waters. pp. 285-317 in Seabird energetics. G.C. Whittow & H. Rahn (eds.) Plenum, New York.

Croxall, J.P. and Prince, P.A. 1987. Seabirds as predators on marine resources, especially krill, at South Georgia. in J.P. Croxall (ed.) Seabirds: Feeding ecology and role in marine ecosystems. Cambridge Univ. Press, Cambridge.

Croxall, J. ed. 1987. Seabirds: feeding ecology and role in marine ecosystems. Cambridge Univ. Press, Cambridge.

Croxall, J.P. 1989. Use of indices of predator status and performance in CCAMLR fishery management. Sci. Comm. Conserv. Antarc. Mar. Liv. Resources, pp. 353-365.

Croxall, J.P. & Briggs, D.R. 1991. Foraging economics and performance of polar and sub-polar Atlantic seabirds. Pp. 561-578 In Sakshaug, E., Hopkins, C.C.E. & Oritsland, N.A. (eds.) Proceedings of the Pro Mare symposium on Polar Marine Ecology, Trondheim, 12-16 May 1990. Polar Res. 10: 561-578.

Croxall, J.P., Ricketts, C. & Wood, A.G. 1991. Food consumption by predators in a CCAMLR integrated study region. Sci. Comm. Cons. Antarct. Mar. Living Resources Select. Sci. Paps. 1990: 489-519.

Daan, S., Masman, D. & Groenewold, A. 1990. Avian basal metabolic rates: their association with body composition and energy expenditure in nature. Am. J. Physiol. 259R: 333-340.

Dahl, K. 1992: Mussel fishery in the Danish Wadden Sea. In: Probleme der Muschelfischerei im Wattenmeer. Schriftenr. Schutzgemeinschaft Deutsche Nordsee 1: 71

Davis, R.W., Kooyman, G.L. & Croxall, J.P. 1983. Water flux and estimated metabolism of free-ranging gentoo and macaroni penguins at South Georgia. Polar Biol. 2: 41-46.

Davis, R.W., Croxall, J.P. & O'Connell, M.J. 1989. The reproductive energetics of gentoo (Pygoscelis papua) and macaroni (*Eudyptes chrysolophus*) penguins at South Georgia. J. Anim. Ecol. 58: 59-74.

Davydov, A.F. 1972. Seasonal variations in the energy metabolism in the black-headed gull. Sov. J. Ecol. 2: 436-439.

Dernedde, T. 1992. Untersuchungen zur Ernährung der Möwen im Königshafen auf Sylt. Diplomarbeit Universität zu Kiel.

Dekker, R. 1989: The macrozoobenthos of the subtidal western Dutch Wadden Sea. 1. Biomass and species richness. Neth. J. Sea Res. 23: 57-68

Diamond, A.W., Gaston, A.J. & Brown, R.G.B. 1993. Studies of high-latitude seabirds. 3. A model of the energy demands of the seabirds of eastern and Arctic Canada. Can. Wildl. Serv. Occ. Pap. No. 77: 1-39.

Dobben, W.H. van 1952. The food of the cormorant in the Netherlands. Ardea 40: 1-63.

Dragesund, O., Hamre, J. & Ulltang, Ø. 1980. Biology and population dynamics of the Norwegian spring-spawning herring. Rapp. P.-v. Réun. Cons. int. Explor. Mer. 177: 43-71.

Drent, R.H. & Daan, S. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea, 68, 225-252.

Drinkwaard, B. 1987: Development in the shellfish industry in recent years. Proc. 18th Ann. Conf. Shellfish Ass. Great Britain, London: 51-71

Duffy, D.C., and Jackson, S. 1986. Diet Studies of Seabirds: A review of methods. Colonial Waterbirds, 9: 1-17.

Duffy, D.C., Siegfried, W.R. & Jackson, S. 1987. Seabirds as consumers in the southern Benguela region. S. Afr. J. mar. Sci. 5: 771-790.

Duffy, D.C. and Siegfried, W.R. 1987. Historical variations in food consumption by breeding seabirds of the Humboldt and Benguela upwelling regions. pp. 327-346 in J. Croxall (ed.) Seabirds: Feeding ecology and role in marine ecosystems. J. Croxall, ed. Cambridge Univ. Press, Cambridge.

Duffy, D.C. and Schneider, D. Seabird-fishery interactions. Wildlife, 2001.

Duncan, N., Taylor, K., Wanless, S., and Wood, V. 1982. The birds of Boveray, St. Kilda. Seabird Report 6: 18-25.

Dunn, E.K. 1972. Studies on terns with particular reference to feeding ecology. Thesis University of Durham. [4]4.

Dunnet, G.M., R.W. Furness, M.L. Tasker, & P.H. Becker 1990. Seabird ecology in the North Sea. Neth. J. Sea Res. 26: 387-425

Durinck, J., Skov, H., and Danielsen, F. 1991. Winter food of guillemots *Uria aalge* in the Skagerrak. Dansk Orn. Foren. Tidsskr. 85: 145-150.

Durinck, J., Christensen, K.D. Skov, Danielsen, H.F. *et al.* in press.: Diet of Common Scoter Melanitta nigra and Velvet Scoter Melanitta fusca wintering in the North Sea. Ornis Fennica.

Ellis, H.I. 1984. Energetics of free-ranging seabirds. Seabird Energetics, Pp.203-234. G.C. Whittow and H. Rahn (Eds.). Plenum Press, New York.

Erikstad, K.E. & Vader, W. 1989. Capelin selection by common and Brünnich's guillemots during the prelaying season. Ornis Scand. 20: 151-155.

Ewins, P.J. 1985. Growth, diet and mortality of arctic tern *Sterna paradisaea* chicks in Shetland. Seabird, 8: 59-68.

Ewins, P.J. 1986. The ecology of black guillemots *Cepphus grylle* in Shetland. D. Phil. Thesis, Oxford University.

Ewins, P.J. 1990. The diet of black guillemots *Cepphus grylle* in Scotland. Holarctic Ecol. 13: 90-97.

Feldman, V.N. 1986. Queleques traits particuliers de la repartition de la biologie du sprat de la Mer du Nord en fonction de sa differenciation a l'interiur de la population. ICES Doc. CM 1986 (H:32): 1-15.

Fisher, J. 1952. The Fulmar. Collins, London.

Flint, E.N. & Nagy, K.A. 1984. Flight energetics of free-living sooty terns. Auk. 101: 288-294.

Fowler, J.A., and Dye, A.P. 1987. Sandeels *Ammodytes marinus* in the diet of the fulmar *Fulmarus glacialis* in Shetland, Scotland. Seabird 10: 71-74.

Franeker, J.A. van 1992. Top predators as indicators for ecosystem events in the confluence zone and marginal ice zone of the Weddell and Scotia Seas, Antarctica, November 1988 to January 1989 (EPOS Leg 2). Polar Biol. 12: 93-102.

Franz, M. 1992: Entwicklung einer naturverträglichen Miesmuschelfischerei im schleswig-holsteinischen Wattenmeer. In: Probleme der Muschelfischerei im Wattenmeer. Schritenr. Schutzgemeinschaft Deutsche Nordseeküste 1: 60-62

Frick, S. 1993. Nahrungsökologische Unterschiede von Fluß- und Küstenseeschwalbe (*Sterna hirundo* und *Sterna paradisaea*) im Wattenmeer. Diplomarbeit Universität zu Köln.

Franck, D. 1992. The influence of feeding conditions on food provisioning of chicks in common terns *Sterna hirundo* nesting in the German Wadden Sea. Ardea, 80: 45-55 [5].

Furness, R.W. 1978. Energy requirements of seabird communities: a bioenergetics model. J. Anim. Ecol. 47: 39-53.

Furness, R.W., and Hislop, J.R.G. 1981. Diets and feeding ecology of great skuas *Catharacta skua* during the breeding season in Shetland. J. Zool. Lond. 195: 1-23.

Furness, R.W. & Cooper, J. 1982. Interactions between breeding seabird and pelagic fish populations in the southern Benguela region. Mar. Ecol. Prog. Ser. 8: 243-250.

Furness, R.W. 1982. Competition between fisheries and seabird communities. Advan. Marine Biol. 20: 225-307.

Furness, R.W. 1983. The Birds of Foula. Ambleside: Brathay Hall Trust.

Furness, R.W. & Ainley, D.G. 1984. Threats to seabird populations presented by commercial fisheries. ICBP Tech. Publ. No. 2: 701-708. ICBP, Cambridge.

Furness, R.W., and Todd, C.M. 1984. Diets and feeding of fulmars *Fulmarus glacialis* during the breeding season: a comparison between St. Kilda and Shetland colonies. Ibis 126, 3: 279-387.

Furness, R.W. 1984. Seabird biomass and food consumption in the North Sea. Mar. Pollut. Bull. 15: 244-248.

Furness, R.W. & Barrett, R.T. 1985. The food requirements and ecological relationships of a seabird community in North Norway. Ornis Scand. 16: 305-313.

Furness, R.W. and Monaghan, P. 1987. Seabird ecology. Blackie, London.

Furness, R.W. 1987a. The Skuas. Poyser, Calton: 1-363.

Furness, R.W. 1987b. The impact of fisheries on seabird populations in the North Sea. The Status of North Sea Environment; reasons for concern (ed.) Peet, G.. Pp. 179-192). Werkgroep Noordzee, Amsterdam.

Furness, R.W., Hudson, A.V. and Ensor, K. 1988. Interactions between scavenging seabirds and commercial fisheries around the British Isles. pp. 232-268 in J. Burger (Ed.) Seabirds and other marine vertebrates. J. Burger, ed. Columbia Univ. Press, New York.

Furness, R.W. 1989. Changes in diet and feeding ecology of seabirds on Foula, 1971-1988. In: Heubeck, M. (Ed.) Seabirds and sandeels: 22-26. Lerwick. Shetland Bird Club.

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., and Barrett, R.T. 1991. Seabirds and fish declines. Nat. Ocogr. Res. and Explor. 7: 82-95.

Furness, R.W., Ensor, K. & Hudson, A.V. 1992. The use of fishery waste by gull populations around the British Isles. Ardea 80: 105-113.

Furness, R.W. 1992. Implications of changes in net mesh size, fishing effort and minimum landing size regulations in the North Sea for seabird populations. JNCC Report No. 133.

Gabrielsen, G.W., Mehlum, F. & Nagy, K.A. 1987. Daily energy expenditure and energy utilization of free-ranging black- legged kittiwakes. Condor 89: 126-132.

Gabrielsen, G.W., Mehlum, F. & Karlsen, H.E. 1988. Thermoregulation in four species of arctic seabirds. J. Comp. Physiol. 157: 703-708.

Gabrielsen, G.W., Taylor, J.R.E., Konarzewski, M. & Mehlum, F. 1991. Field and laboratory metabolism and thermoregulation in Dovkies (*Alle alle*). Auk 108: 71-78.

Gabrielsen, G.W., Mehlum, F. & Flint, E. 1993. Resting metabolic rate of six species of seabirds studied at St. Paul, Alaska. Auk (in press).

Galbraith, H. 1983. The diet and feeding ecology of breeding kittiwakes *Rissa tridactyla*. Bird Study 30: 109-120

Gales, R.P. & Green, B. 1990. The annual energetics cycle of little penguins (*Eudyptula minor*). Ecology 71: 2297-2312.

Garthe, S. 1993. Quantifizierung von Abfall und Beifang der Fischerei in der südöstlichen Nordsse und deren Nutzung durch Seevögel. Hamburger avifaun. Beitr. 25: 125-237.

Garthe, S., and Hüppop, O. 1993. Gulls and fulmars following ships and feeding on discards at night. Ornis Svecica 3: in press.

Garthe, S., and Hüppop, O. Distribution of ship-following seabirds and their utilization of discards in the North Sea in summer. Mar. Ecol. Progr. Ser.

Gaston, A.J. 1985. Energy invested in reproduction by thick- billed murres (*Uria lomvia*). Auk 102: 447-458.

Gavrilov, V.M. 1985. Seasonal and circadian changes of thermoregulation in passerine and non-passerine birds; which is more important? Acta XVIII Congressus Int. Ornithol. 2: 1254-1277.

Giglason, H. and Helgason, T. 1985. Species interaction in assessment of fish stocks with special application to the North Sea. Dana 5: 1-44.

Goethe, F. 1980. Herring gull (*Larus argentatus* Pontoppidau). In: C.J. Smit & W.J. Wolff (eds.): Birds of the Wadden Sea. Report 6, Wadden Sea Working Group, Leiden: 238-250

Gorke, M. 1990. Die Lackmöwe in Wattenmeer und Binnenland. Seevögel 11: Sonderheft 3.

Gorke, M., Hartwig, E., and Schrey, E. 1988. Feeding ecology of black-headed gull *Larus ridibundus* in German coastal areas - a review. In: Tasker, M.-L. (Ed.) Seabird Food and Feeding Ecology: Proc. 3rd Int. Conf. Seabird Group, p. 21 (abstract).

Goudie, R.I., and Ankney, D. 1988. [Seaduck diets/Newfoundland] Ornia Scand.

Grant, G.S. and Whittow, G.C. 1983. Metabolic cost of incubation in the Laysan albatross and Bonin petrel. Comp. Biochem. Physiol. 74A: 77-82.

Green, B. and Gales, R.P. 1990. Water, sodium and energy turnover in free-living penguins: a review. Pp. 245-268 in L. David and J. Darby (Eds.) Penguin biology. Academic Press, London.

Hamer, K.C., Furness, R.W. & Caldow, R.W.G. 1991. The effects of changes in food availability on the breeding ecology of great skuas *Catharacta skua* in Shetland. J. Zool. Lond. 223: 175-188.

Harris, M.P. 1984. The Puffin. Poyser, Calton. [7].

Harris, M.P. 1976. Inter-colony movements of Farne Islands Puffins. Trans. nat. Hist. Soc. Northumb. 42: 115-118

Harris, M.P. and Hislop, J.R.G. 1978. The food of young puffins (*Fratercula arctica*). J. Zool., Lond. 185: 213-236.

Harris, M.P. and Wanless, S. 1985. Fish fed to young guillemots, *Uria aalge*, and used in display on the Isle of May, Scotland. J. Zool. Long. 207: 441-458.

Harris, M.P., and Wanless, S. 1986. The food of young razorbills on the Isle of May and a comparison with that of young guillemots and puffins. Ornis Scand. 17: 41-46.

Harris, M.P., and Wanless, S. 1988. Measurements and seasonal changes in weight of guillemots *Uria aalge* at a breeding colony. Ring & Migr. 9: 32-36. [10].

Harris, M.P., and Riddiford, N.J. 1989. The food of some young seabirds on Fair Isle in 1986-1988. Scottish Birds, 15: 119-125. [2].

Harris, M.P. and Wanless, S. 1989. The breeding biology of razorbills *Alca torda* on the Isle of May. Bird Study 36: 105-114.

Harris, M.P., Towll, J.H., Russell, A.F., and Wanless, S. 1990. Maximum dive depths attained by auks feeding young on the Isle of May, Scotland. Scott. Birds 16: 25-28.

Harris, M.P., and Wanless, S. 1991. Population studies and conservation of puffins *Fratercula arctica*. Bird population studies: relevance to conservation and management (Ed.) Perrins, C.M., Lebreton, J.-D., and Hirons, G.J.M), pp. 230-248. Oxford University Press, New York. [9].

Harris, M.P., and Wanless, S. 1991. The important of the lesser sandeel *Ammodytes marinus* in the diet of the shag *Phalacrocorax aristotelis*. Ornis Scand. 22: 375-382. [11].

Harris, M.P. & Bailey, R.S. 1992. Mortality rates of puffin *Fratecula arctica* and guillemot *Uria aalge* and fish abundance in the North Sea. Biol. Conserv. 60: 39-46.

Harris, M.P. 1992. Sandeels and herring in the diet of the shag. Proc. Seabird Group Conf. 1992, 16 (abstract).

Harris, M.P., and Wanless, S. 1993. The diet of shags *Phalacrocoax aristotelis* during the chick-rearing period assessed by three methods. Bird Study 40: 135-139.

Hatch, S.A., and Sanger, G.A. 1992. Puffins as predators on juvenile pollack and other forage fish in the Gulf of Alaska. Mar. Ecol.-Prog. Ser. 80: 1-14.

Hennemann, W.W. 1983. Environmental influences on the energetics and behavior of anhingas and double-crested cormorants. Physiol. Zool. 56: 201-216.

Heubeck, M., and Ellis, P.M. 1986. Shetland Seabirds 1985. BTO News 143:10.

Heubeck, M. 1989. Seabirds and sandeels. Lerwick, Shetland Bird Club.

Heubeck, M. 1989. Breeding success of Shetland's seabirds: Arctic skua, kittiwake, guillemot, razorbill and puffin in Heubeck, M. (Ed.) Seabirds and Sandeels: Proceedings of a seminar held in Lerwick, Shetland, 15-16 October 1988. Shetland Bird Club 11-18.

Heubeck, M., Harvey, P.W. and Okill, D. 1991. Changes in the Shetland guillemot *Uria aalge* population and the pattern of recoveries of ringed birds, 1959-1989. Seabird 13: 3-21.

Hilden, M. 1988. Errors of perception in stock and recruitment studies due to wrong choices of natural mortality rate in Virtual Population Analysis. J. Cons. Int. Explor. Mer. 44: 123-134.

Hislop, J.R.G. 1978. The food of young puffins (*Fratercula arctica*). J. Zool. Lond. 185: 213-236.

Hislop, J.R.G. & Harris, M.P. 1985. Recent changes in the food of young puffins *Fratercula arctica* on the Isle of May in relation to fish stocks. Ibis 127: 234-239.

Hislop, J.R.G., and MacDonald, W.S. 1989. Damage to fish by seabirds in the Moray Firth. Scott. Birds 15: 151-155.

Hislop, J.R.G., Harris, M.P. and 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.

Hobson, K.A., and Montevecchi, W.A. 1991. Stable isotopic determinations of trophic

Howes, L.A., and Montevecchi, W.A. 1993. Population interactions of gulls and terns in Gros Morne National Park, Newfoundland. Canadian Journal of Zoology: in press.

Hudson, A.V. 1986. The biology of seabirds utilising fishery waste in Shetland. PhD thesis, University of Glasgow

Hudson, A.V. and Furness, R.W. 1988. Utilization of discarded fish by scavenging seabirds behind whitefish trawlers in Shetland. J. Zool Lond. 215: 151-166.

Hudson, A.V. & Furness, R.W. 1989. The behaviour of seabirds foraging at fishing boats around Shetland. Ibis 131: 225- 237.

Hüppop, O., and Garthe, S. 1993. Seabirds and fisheries in the southeastern North Sea. Sula, 7: 9-14.

Hunt, G.L., Piatt, J.F. and Erikstad, K.E. 1991. How do foraging seabirds sample their environment? Proc. XX Int. Ornithol. Congr.: pp. 2272-2279.

Jackson, S. 1986. Assimilation efficiencies of white-chinned petrels (*Procellaria aequinoctialis*) fed different prey. Comp. Biochem. Physiol. 85A: 301-303.

Johnson, S.R. & West, G.C. 1975. Growth and development of heat regulation in nestlings and metabolism in adult common murre and thick-billed murre. Ornis Scand. 6: 109-115.

Johnstone, I.G., Harris, M.P., Wanless, S., and Growes, J.A. 1990. The usefulness of pellets for assessing the diet of adult shags *Phalacrocorax aristotelis*. Bird Study 37: 5-11.

Kelle, W. 1976. Sterblichkeit untermaßiger Plattfische im Beifang der Garnelenfischerei. Meeresforsch. 25: 77-89.

Ketzenberg, C. 1991. Nahrungsökologie der Eiderente (Somateria mollissima, L. 1758) im Königshafen bei List/Sylt. Diplomarbeit Universität Kiel.

Klaassen, M., Bech, C. & Slagsvold, G. 1989. Basal metabolic rate and thermal conductance in growing Arctic tern chicks (*Sterna paradisaea*). Physiol. Zool.

Klaassen, M., Becker, P.H. & Wagener, M. 1992. Transmitter loads do not affect the daily energy expenditure of nesting common terns. J. Field Ornithol. 63: 181-185.

Klages, N.T.W., Willis, A.B., and Ross, G.B. 1991. Variability in the diet of the cape gannet at Bird Island, Algoa Bay, South Africa. In: Brink, A.L.L., Mann, K.H, Hilborn, R. (Eds.). Benguela trophic functioning. S. Afr. J. Mar. Sci. 12: 761-771.

Klomp, N.I. & Furness, R.W. 1992. Non-breeders as a buffer against environmental stress: declines in numbers of great skuas on Foula, Shetland, and prediction of future recruitment. J. Appl. Ecol. 29: 341-348.

Kooyman, G.L., Davis, R.W., Croxall, J.P. & Costa, D.P. 1982. Diving depths and energy requirements of king penguin. Science 217: 726-729.

Kooyman, G.L., Cherel, Y., Le Maho, Y., Croxall, J.P., Thorson, P.H., Ridoux, V. & Kooyman, C.A. 1992. Diving behavior and energetics during foraging cycles in king penguins. Ecol. Monogr. 62: 143-163.

Koteja, P. 1991. On the relation between basal and field metabolic rates in birds and mammals. Funct. Ecol. 5: 56-64.

Kunzlik, P.A. 1989. Small fish around Shetland. M. Heubeck (Ed.) in Seabirds and Sandeels: Proceedings of a seminar held in Lerwick, Shetland, 15-16 October 1988. Shetland Bird Club: 38-49.

Langham, L.P.E. 1971. The distribution and abundance of larval sand-eels (Ammodytidae) in Scottish waters. J. mar. biol. Ass. U.K. 51: 697-707.

Laursen, K., & J. Frikke 1987a. Preliminary study of eiders in relation to mussel fishery in the Danish Wadden Sea. Rapport nr. 11 Vildtbiologisk Station KalŸ

Laursen, K., & J. Frikke 1987b. Winter counts of seabirds off the southwest coast of Denmark. Dansk Orn. Foren, Tidsskr. 81: 167-172

Lemmetyinen, R. 1973. Feeding ecology of *Sterna paradisaea* Pontopp. and *S. hirundo* L. in the archipelago of southwestern Finland. Ann. Zool. Fennici, 10: 507-525.

Leopold, M.F., Wolf, P.A., Hüppop, O. 1992. Food of young colony-attendance of adult guillemots *Uria aalge* on Helgoland. Helgoländer Meeresunters., 46: 237-249. [13].

Lily, G.R. 1991. Interannual variability in predation by cod (*Gadus morhua*) on capelin (*Mallotus villosus*) and other prey off southern Labrador and northeastern Newfoundland. ICES, Mar. Sci. Symp. 193: 133-146.

Lloyd, C.S., Tasker, M.L. & Partridge, K. 1991. The Status of Seabirds in Britain and Ireland. T & AD Poyser, London.

Loeng, H. 1989. Ecological features of the Barents Sea. Proc. 6th Conf. Comité Arctique Intern.: 327-365.

Lustick, S., Battersby, B. & Kelty, M. 1978. Behavioral thermoregulation: orientation toward the sun in herring gulls. Science 200: 81-83.

Madsen, F.J., and Spärck, R. 1950. On the feeding habits of the southern cormorant (*Phalacrocorax carbo sinensis* Shaw). Dan. Rev. Game Biol. 1: 45-73.

Madsen, F.J. 1957. On the food habits of some fish-eaing birds in Denmark. Dan. Rev. Game Biol. 3: 19-83.

Martin, A.R. 1989a. The diet of Atlantic Puffin (*Fratercula artica*) and Northern Gannet (*Sula bassana*) chicks at Shetland colony during a period of changing prey availability. Bird Study 36: 170-180.

Martin, A.R. 1989b. Feeding strategies of feeding seabirds and recent changes in diet. in Heubeck, M. (Ed.) Seabirds and Sandeels: Proceedings of a seminar held in Lerwick, Shetland, 15-16 October 1988. Shetland Bird Club: 30-37.

Massias, A., and Becker, P.H. 1990. Nutritive value of food and growth in common tern (*Sterna hirundo*) chicks. Ornis Scand. 21: 187-194.

Meixner, R. 1992: Erkenntnisse der Fischereiforschung. in: Probleme der Muschelfischerei im Wattenmeer. Schriftenr. Schutzgemeinschaft Deutsche Nordsee 1: 47-49

Michaelis, H. 1992. Veränderungen des Miesmuschelbestandes im niedersächsischen Wattenmeer. in: Probleme der Muschelfischerei im Wattenmeer. Schriftenr. Schutzgemeinschaft Deutsche Nordsee 1: 16-25

Mills, D. 1969. The food of the cormorant at two breeding colonies on the east coast of Scotland. Scott. Birds 5: 268-276.

Milne, H., & G.M. Dunnet 1972. Standing crops, productivity and trophic relations of the fauna of Ythan estuary, Aberdeenshire. in: The estuarine environment. R.S.K. R. Barnes, and J. Green (Eds.) Appl. Science Publ. London: 86-106

Monaghan, P., Uttley, J.D., Burns, M.D., Thaine, C. and 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., Uttley, J.D., and Okill, J. 1989. Terns and sandeels: seabirds as indicators of changes in marine fish populations. J. Fish. Biol. 35A: 339-340.

Monaghan, P., Wright, P.J., Bailey, M.C., Uttley, J.D., & Walton, P. 1992. The influence of changes in food abundance on diving and surface feeding seabirds. In: Montevecchi, W.A. (ed.) Studies of high latitude seabirds 4, Trophic relationships of marine birds and mammals. Canadian Wildlife Service Occ. Paper.

Monaghan, P. 1992. Seabirds and sandeels: The conflict between exploitation and conservation in the northern North Sea. Biodiversity and Conserv., 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.

Montevecchi, W.A., and Piatt, J. 1984: Composition and energy contents of mature inshore spawning capelin (*Mallotus villosus*): implications for seabird predators. Comp. Biochem. Physiol. 78A: 15-20.

Montevecchi, W.A., and Barrett, R.T. 1987. Prey selection by gannets at breeding colonies in Norway. Ornis Scand. 18: 313-322.

Montevecchi, W.A., Birt, V.L. and Cairns, D.K. 1988. Dietary changes of seabirds associated with local fisheries failures. Biol. Oceangr. 5: 153-161.

Montevecchi, W.A., and Berruti, A. 1991. Avian bio-indication of pelagic fishery conditions in the southeast and northwest Atlantic. Acta XX Cong. Internat. Orinithol., 2246-2256.

Montevecchi, W.A. and Myers, R.A. 1992. Monitoring fluctuations in pelagic fish availability with seabirds. Can. Atlantic Fisheries Sc, Advisory Council Res. Doc. 1992/94.

Montevecchi, W.A., Birt-Friesen, V.L. & Cairns, D.K. 1992. Reproductive energetics and prey harvest of Leach's storm- petrels in the northwest Atlantic. Ecology 73: 823-832.

Montevecchi, W.A. 1993. Avian indicators of marine fish conditions. pp. 217-266 in: R.W. Furness and J.J.D. Greenwood (Eds.) Birds as environmental monitors. Chapman, London.

Montevecchi, W.A. 1993. Seabirds as monitors of fish stocks. Pp. xx-xx in R.W. Furness and J.J. D. Greenwood (Eds.) Birds as Monitors of Environmental Change. Chapman and Hall, London.

Myrberget, S. 1962. Undersokelser over forplantningsbiologien til lunde (Fratercula arctica (L.)). Medd. St. Viltunders. 2 (11): 1-51.

Nagy, K.A. 1980. CO2 production in animals: analysis of potential errors in the doubly labeled water method. Am. J. Physiol. 238R: 466-473.

Nagy, K.A., Siegfried, W.R. & Wilson, R.P. 1984. Energy utilization by free-ranging jackass penguins, *Spheniscus demersus*. Ecology 65: 1648-1655.

Nagy, K.A. 1987. Field metabolic rate and food requirement scaling in mammals and birds. Ecol. Monogr. 57: 111-128.

Nauka, Moscow. Grant, G.S. and Whittow, G.C. 1983. Metabolic cost of incubation in the Laysan albatross and Bonin petrel. Comp. Biochem. Physiol. 74A: 77-82.

Nehls, G., & M. Thiel (in press). Large-scale distribution patterns of the mussel Mytilus edulis in the Wadden Sea of Schleswig-Holstein do storms structure the ecosystem? Neth. J. Sea Res.

Nehls, G., S. Bräger, J. Meissner, M. Thiel 1988. Zum Bestand der Eiderente (*Somateria mollissima*) an der deutschen Nordseeküste. Corax 13: 41-58

Nehls, G. 1989. Occurence and food consumption of the common eider, *Somateria mollissima*, in the Wadden Sea of Schleswig-Holstein. Helgol. Meeresunters. 43: 385-393

Nehls, G. 1991. Bestand, Jahresrhythmus und Nahrungsökologie der Eiderente, *Somateria mollissima*, L. 1758, im Schleswig-Holsteinischen Wattenmeers. Corax 14: 146-209

Nelson, J.B. 1978. The Sulidae - gannets and boobies. Oxford University Press [14].

Nettleship, D.N., Sanger, G.A. and Springer, P. F. (Eds.) 1984. Marine birds: their feeding ecology and commercial fisheries relationships. Can. Wildife Service. Ottawa.

Noordhuis, R., and Spaans, A.L. 1992. Interspecific competition for food between herring *Larus argentatus* and lesser black-backed gulls *L. fuscus* in the Dutch Wadden Sea area. Ardea, 80: 115-132. [15].

Norrevang, A. 1977. Fuglefangsten pa Faeroerne. Rhodos. 276 pp.

Obst, B.S., Nagy, K.A. & Ricklefs, R.E. 1987. Energy utilization in Wilson's storm-petrel (*Oceanites oceanicus*). Physiol. Zool. 60: 200-210.

Offringa, H. 1991: Verspreiding en voedselconsumptie van de zwarte zeeëend (*Melanitta nigra*) voor de Nederlandse kust. - NIOZ-Rapport 1991-13 (50 pp).

Okill, D. 1989. Breeding success of Shetland's seabirds: Red-throated diver, fulmar, gannet, cormorant and shag in: Heubeck, M. (Ed.) Seabirds and Sandeels: Proceedings of a seminar held in Lerwick, Shetland, 15-16 October 1988. Shetland Bird Club: 6-11.

Okill, J.D., Fowler, J.A., Ellis, P.M., and Petrie, G.W. 1992. The diet of cormorant *Phalacrocorax carbo* chicks in Shetland in 1989. Seabird 14: 21-26. [16].

Olsen, B. 1991. Census of guillemots on Hovdin Skuvoy 1973-93 (In faroese). Fiskirannsoknir nr. 7. p 6-15.

Pearson, T.H. 1968. The feeding biology of seabird species breeding on the Farne Islands, Northumberland. J. Anim. Ecol. 37: 521-552. [17].

Pehrsson, O. 1984. Diving duck populations in relation to their food supplies in: P.R. Evans, J.D. Goss-Custard, and W.G. Hall (Eds.) Coastal waders and wildfowl in winter. Univ. Press, Cambridge: 101-116

Pennycuick, C.J. 1987. Flight of auks (Alcidae) and other northern seabirds compared with southern Procellariiformes: ornithodolite observations. J. Exp. Biol. 128: 335-347.

Pennycuick, C.J. 1989. Bird flight performance. A practical calculation manual. Oxford University Press, Oxford.

Pettit, T.N., Nagy, K.A., Ellis, H.I. & Whittow, G.C. 1988. Incubation energetics of the laysan albatross. Oecologia 74: 546-550.

Piatt, J.J., and Nettleship, D.N. 1985. Diving depths of four alcids. Auk 102: 293-297.

Pihl, S., Laursen, P., Hounisen, J.P. & Frikke, J. 1992. Landsdakkende optalling af vandfugle fra flyvemaskine,januar/februar 1991 og januar/marts 1992. - DMU rapport 44. Miljoministeriet 1992.

Pitcher, T.J., and Wyche, C.J. 1983. Predator avoidance behaviour of sandeel schools: why schools seldom switch. In: D.L. G. Noakes. Predators and prey in fishes. W. Junk, The Hague: 193-204.

Porter, J.M., and Sealey, S.G. 1981. Dynamics of seabird multi-species feeding flocks: chronology of flocking in Barkley Sound, British Columbia, in 1979. Colonial Waterbirds 4: 104-113.

Porter, J.M., and Sealey, S.G. 1982. Dynamics of seabird multi-species feeding flocks: age related feeding behaviour. Behaviour 81: 91-109.

Prüter, J. 1988. The food of gulls at Helgoland (German Bight): an indication of ecological changes in the marine environment. In: Tasker, M.L. (Ed.) Seabird Food and Feeding Ecology; Proc. 3rd Int. Conf. Seabird Group, p. 43 (abstract).

Rae, B.B. 1969. The food of cormorants and shags in Scottish estuaries and coastal waters. DAFS Mar. Res. 1969 (1): 1-16.

Reinert, A. 1976. The guillemot (In faroese). 6 articles in the newsletter Dimmalatting nr. 97-120.

Rice, J.C. 1992. Multispecies interactions in marine ecosystems: current approaches and implications for study of seabird ppulations in: Wildlife 2001: Populations.

Ricklefs, R.E., Roby, D.D. & Williams, J.B. 1986. Daily energy expenditure of adult Leach's storm-petrels during the nesting cycle. Physiol. Zool. 59: 649-660.

Roby, D.D. & Ricklefs, R.E. 1986. Energy expenditure in adult least auklets and diving petrels during the chick-rearing period. Physiol. Zool. 59: 661-678.

Roseneau, D.G., Lloyd, D.S., McRoy, C.P. & Murphy, E.C. 1986. Seabird responses to fluctuating prey availability in the eastern Bering Sea. Mar. Ecol. Prog. Ser. 32: 1-12.

Ruth, M. 1992. Miesmuschelfischerei im schleswig-holsteinischen Wattenmeer. Ein Beispiel für die Problematik einer Fischerei im Nationalpark. In: Probleme der Muschelfischerei im Wattenmeer. Schriftenr. Schutzgemeinschaft Deutsche Nordsee 1: 26-46.

Schaefer, M.B. 1970. Men, birds and anchovies in the Peru Current-dynamic interactions. Trans. Amer. Fisheries Soc. 99: 461-467.

Schneider, D.C. and Hunt, G.L. 1982. Carbon flux to seabirds in waters with different mixing regimes in the southeastern Bering Sea. Mar. Biol. 67: 337-344.

Schneider, D.C., Hunt, G.L. & Harrison, N.M. 1986. Mass and energy transfer to seabirds in the southeastern Bering Sea. Continental Shelf Res. 5: 241-257.

Schneider, D.C., Hunt, G.L. & Powers, K.D. 1987. Energy flux to pelagic birds: a comparison of Bristol Bay (Bering Sea) and Georges Bank (Northwest Atlantic). Pp. 259-277 in Croxall, J.P. (Ed.). Seabirds: feeding ecology and role in marine ecosystems. Cambridge Univ. Press, Cambridge.

Sherman, K., Jones, C., Sullivan, L., Smith, W., Berrien, P. & Ejsymont, L. 1981. Congruent shifts in sand eel abundance in western and eastern North Atlantic ecosystems. Nature 291: 486-489. Springer, A.M.,

Sibly, R.M., and McCleery, R.H. 1983. The distribution between feeding sites of herring gulls breeding at Walney Island, UK. J. Anim. Ecol. 52: 51-68.

Smit, C.J. and Wolff, W.J. 1980. Birds of the Wadden Sea. Report 6, Wadden Sea Working Group, Leiden.

Spaans, A. L. 1971. On the feeding ecology of the herring gull *Larus argentatus* Pont. in the northern part of the Netherlands. Ardea, 59: 73-188.

Springer, A.M., Roseneau, D.G., Lloyd, D.S., McRoy, C.P. and Murphy, E.C. 1986. Seabird responses to fluctuating prey availability in the eastern Bering Sea. Mar. Ecol. Prog. Ser. 32: 1-12.

Stienen, E.W.M., and Tienen, P.G.M. 1991. Prooi- en energieconsumptie door kuikens van noordse stern (*Sterna paradisaea*) en visdief (*S. hirundo*) in relatie tot enkele abiotische factoren. Rijkinstituut voor Natuurbeheer Arnhem, Intern rapport 91/32: 1-37. [18].

Stjernberg, T. 1982. The size of the breeding Eider population of the Baltic in the early 1980s. Orn. Fenn. 59: 135-140

Strann, K.-B., Vader, W. and Barrett, R.T. 1991. Auk mortality in fishing nets in north Norway. Seabird 13: 22-29.

Swennen, C. 1976. Populatie-stuctuur en Voedsel van Eidereend *Somateria m. mollissima* in de Nederlandse Waddenzee. Ardea 64: 311-371

Swennen, C., and Duiven, P. 1977. Sizes of food objects of three fish-eating seabird species *Uria aalge, Alca torda* and *Fratercula arctica*. Neth. J. Sea Res. 11: 92-98.

Swennen, C., G. Nehls, K. Laursen 1989. Numbers and distribution of eiders *Somateria mollissima* in the Wadden Sea. Neth. J. Sea Res. 24: 83-92

Swennen, C. 1991. Ecology and population dynamics of the Common Eider in the Dutch Wadden Sea. PhD Thesis, Univ. Groningen

Tasker, M.L., Hope-Jones, P., Dixon, T. and Blake, B.F. 1984. Counting seabirds at sea from ships: a review of methods employed and a suggestion for a standardized approach. Auk 101: 567-577.

Tasker, M.L., Jones, P.H., Blake, B.F., and Dixon, T.J. 1985. The marine distribution of the gannet *Sula bassana* in the North Sea. Bird Study 32: 82-90.

Tasker, M.L., Jones, P.H., Blake, B.F., and Dixon, T.J. 1985. Distribution and feeding habits of the great skua *Chatharacta skua* in the North Sea. Seabird 8: 34-44.

Tasker, M.L., Webb., A., Hall, A.J. Pienkowski, M.W. and Langslow, D.R. 1987. Seabirds in the North Sea. Nature Conservancy Council, Peterborough.

Taylor, I.R. 1979. Prey selection during courtship feeding in common tern. Ornis Scand. 10: 142-144.

Taylor, K. 1985. Great black-backed gull *Larus marinus* predation of seabird chicks on three Scottish islands. Seabird 8: 45-52.

Thorson, G. 1979: Havbundens dyreliv: infaunaen, den javne havbunds dyresamfund. - In: Norrevang & Lundo (Eds.): Danmarks Natur. Vol. 3., pp. 112-122. Politiken, Copenhagen.

Toresen, R. 1990. Long-term changes in growth of Norwegian spring-spawning herring. J. Cons. int. Explor. Mer. 47: 48-56.

Uttley, J., Monaghan, P., and White, S. 1989. Differential effects of reduced sandeel availability on two sympathically breeding species of tern. Ornis Scand. 20: 273-277.

Uttley, J. 1991. The influence of food supply on the parental investment of arctic terns *Sterna paradisaea*. PhD. Thesis University of Glasgow.

Vader, W., Barrett, R.T. & Strann, K.-B. 1987. Sjøfuglhekking i Nord-Norge 1987, et svartår. Vår Fuglefauna 10: 144-147.

Vader, W., Barrett, R.T., Erikstad, K.E. and Strann, K.-B. 1990a. Differential responses of common and thick-billed murres to a crash in the capelin stock in the southern Barents Sea. Stud. Avian Biol. 14: 175-180.

Vader, W., Anker-Nilssen, T., Bakken, V., Barrett, R. and Strann, K.-B. 1990b. Regional and temporal differences in breeding success and population development of fisheating seabirds in Norway after collapses of herring and capelin stocks. Trans. 19th IUGB Congr. (Trondheim) 1989: 143-150.

Veen, J. 1977. Functional and causal aspects of nest distributions in colonies of the sandwich tern (*Sterna s. sandivensis* Lath.). Behaviour Suppl. 20: 1-193. [19].

Veer, H.W. van der 1989. Eutrophication and mussel culture in the Western Dutch Wadden Sea: impact on the benthic ecosystem; a hypothesis. Helgol. Meeresunters. 43: 517-527

Wahl, T.R. and Heinemann, D. 1979. Seabirds and fishing vessels: co-occurrence and attraction. Condor 81: 390-396.

Wanless, S. 1984. The growth and food of young gannets *Sula bassana* on Aitsa Craig. Seabird 7: 62-70.

Wanless, S., and Harris, M.P. 1989. Kittiwake attendance patterns during chick-rearing on the Isle of May. Scott. Birds 15: 156-161

Wanless, S. & Harris, M.P. 1992. Activity budgets, diet and breeding success of kittiwakes *Rissa tridactyla* on the Isle of May. Bird Study 39: 145-154.

Wanless, S. 1992. Factors influencing food load sizes of shags. Proc. Seabird Group Conf. 1992, 20 (abstract).

Wanless, S., Harris, M.P., and Russell, A.F. 1993. Factors influencing food load sizes brought in by shags *Phalacrocorax aristotelis* during chick-rearing. Ibis 135 (in press).

Weins, J.A. and Scott, J.M. 1975. Model estimation of energy flow in Oregon coastal seabird populations. Condor 77: 439-452.

Woehler, E.J. & Green, K. 1992. Consumption of marine resources by seabirds and seals at Heard Island and the McDonald Islands. Polar Biol. 12: 659-665.

Wright, P.J. 1992. What determines sandeel availability to seabirds? Proc. Seabird Group Conf. 1992, 22 (abstract).

Wright, P.J., and Bailey, M.C. 1993. Biology of sandeels in the vicinity of seabird colonies at Shetland. Fisheries Research Services Report 14/93. Marine Laboratory Aberdeen.

Table 1.1 Community energetics models of fish harvests by seabirds.

Location	Estimated % pelagic fish production consumed	Major consumers	Sources
Oregon coast	22	Shearwaters, Storm-petrel, Cormorant, Guillemot	Wiens & Scott, 1975
Foula	29	Fulmar, Guillemot, Shag, Puffin	Furness, 1978
North Sea	5-8	Fulmar, Gulls, Terns, Guillemot, Puffin	Bailey, 1986; Bailey *et al.*, 1991
North Sea	5-10	Fulmar, Gannet, Shag, Gulls, Kittiwake, Terns, Razorbill, Guillemot, Puffin	Tasker *et al.*, 1989
Saldanha Bay	29	Penguin, Gannet, Cormorant	Furness & Cooper, 1982
Benguela region	6	Gannet, Cormorant	Duffy *et al.*, 1987

Table 1.2 Correspondence between collapses of fish stocks and breeding failures or population declines of seabirds.

Fish	Years	Location	Bird	Source
Herring	1964-1989	Norway	Atlantic puffin	Barrett *et al.*, 1987; Anker-Nilssen, 1987,1992
Capelin	1985-1987	Barents Sea	Guillemot	Vader *et al.*, 1990a,b
Sandeel, herring	1986-1990	Shetland	Shag, great skua, kittiwake, Arctic and common terns, guillemot	Monaghan *et al.*, 1989; Uttley *et al.*, 1989; Furness, 1990; Bailey *et al.*, 1991; Hammer *et al.*, 1991; Klomp and Furness, 1992
Capelin	1981	NW Atlantic	Atlantic puffin	Brown and Nettleship, 1984
Anchovy	1969-1980	S. California Bight	Brown pelican	Anderson *et al.*, 1982
Anchoveta	1950s-1970s	Humbolt Current	Perivian brown pelican, Guanay cormorant, Peruvian booby	Duffy, 1983
Pilchard	1956-1980	Benguela	Jackass penguin, Cape gannet	Burger and Cooper, 1984; Crawford *et al.*, 1985

Table 2.1 Feeding methods employed by seabirds in the North Sea. From Dunnet *et al.*, 1990.

Species	Wing propelled underwater swimming	Foot propelled underwater swimming	Plunge diving	Surface settled feeding	Flying near-surface feeding	Kleptoparasitism
Diver species	*	***				
Fulmar	*	*	**	***		
Sooty shearwater	*		**	***		
Manx shearwater	**		**	**		
Storm petrel					***	
Leach's petrel				*	***	
Gannet	*		***	*		
Cormorant		***				
Shag		***				
Seaduck species	*	***				
Pomarine skua				*	*	**
Arctic skua					*	***
Great skua			*	*	*	***
Little gull					***	
Black-headed gull			*	*	**	
Common gull			*	*	**	*
Lesser black-backed gull			*	**	**	**
Herring gull			*	**	*	*
Iceland gull			**	**	*	
Glacous gull			*	***		
Greater black-backed gull			*	**	*	**
Kittiwake			*	*	***	*
Arctic tern			***		*	
Common tern			***		**	*
Roseate tern			***		*	**
Sandwich tern			***			
Little tern			***		*	
Guillemot	***					
Razorbill	***					
Black guillemot	***					
Little auk	***					
Puffin	***					

*rarely used feeding method; **common feeding method; ***main and predominant feeding method.

Table 2.2 Regular food of seabirds in the North Sea (References: Bezzel, 1985; Bradstreet and Brown, 1985; Garthe, 1993; Harris and Wanless, 1986; Hudson and Furness, 1988; Smit and Wolff, 1980)

Species	Invertebrates			Vertebrates			Anthropogenic sources		
	cepha./moll.	crustaceans	others	fish	birds	mammals	discards	offal	garbage
Diver species	*	*		**					
Fulmar	*	*	*	*			*	*	*
Sooty shearwater	*	*		*				*	
Manx shearwater	*	*		*				*	
Storm petrel	*	*		*				*	
Leach's petrel		*		*				*	
Gannet				**			*		
Cormorant				**					
Shag	*	*	*	**					
Seaduck species	*	*	*						
Pomarine skua			*	*	*	*		*	
Arctic skua				*	*	*	*		
Great skua				*	*	*	*	*	*
Little gull		*	*	*					
Black-headed gull	*	*	*	*	*(eggs)	*	*	*	*
Common gull	*	*	*	*	*(eggs)	*	*	*	*
Lesser black-backed gull	*	*	*	**			*	*	
Herring gull	*	*	*	*	*		*	*	*
Iceland gull	*	*		*				*	*
Glacous gull		*		*	*		*	*	*
Greater black-backed gull				*	*	*	*	*	*
Kittiwake	*	*		**			*	*	
Arctic tern		*		*			*		
Common tern		*		**					
Roseate tern				**					
Sandwich tern				**					
Little tern		*	*	*					
Guillemot		*		**					
Razorbill		*	*	**					
Black guillemot	*	*	*	*					
Little auk		*		*					
Puffin		*	*	**					

**if fish is the predominant food.

Table 2.3 Most important fish families and species consumed by fish eating seabirds in the North Sea.

	Ammodytidae sandeels	Clupeidae clupeids (Herring, Sprat)	Gadidae gadoids (Cod, Haddock, Saithe, Whiting)	Gobiidae	Osmeridae (Smelt)	Scombridae (Mackerel)	Pleuron-ectiformes flatfish	Others	Source
Gannet	☐	☐	☐			☐			14
Cormorant	☐		☐				☐	Cottidae	16,17
Shag	☐	☐	☐	☐			☐	Cottidae	11,12,17
Lesser black-backed gull	☐	☐	☐					Gasterosteidae	15,17
Herring gull		☐	☐		☐		☐	Triglidae, Carangidae	6,15
Kittiwake	☐	☐	☐						17
Arctic tern	☐	☐	☐					Gasterosteidae	3,4,17,18,20,21
Common tern	☐	☐	☐		☐			Gasterosteidae	2-5,17,18,20
Sandwich tern	☐	☐							4,19
Guillemot	☐	☐	☐						10,13,17
Razorbill	☐	☐							9,12
Puffin	☐	☐	☐						1,7,8,17

Sources: 1. Barret *et al.*, 1987; 2. Becker *et al.*, 1987; 3. Boecker, 1987; 4. Dunn, 1972; 5. Frank, 1992; 6. Goethe, 1980; 7. Harris, 1984; 8. Harris and Hislop, 1978; 9. Harris and Wanless, 1991a; 10. Harris and Wanless, 1988; 11. Harris and Wanless, 1991b; 12. Harris and Riddiford, 1989; 13. Leopold *et al.*, 1992; 14) Nelson, 1978; 15. Nordhuis and Spaans, 1992; 16. Okill *et al.*, 1992; 17. Pearson, 1968; 18. Stienen and Tienen, 1991; 19. Veen, 1977; 20. Frick, 1993; 21. Uttley, 1991.

Table 2.4 Mean length (and range, mm) of fish collected at Welsh colonies over five seasons (Harris, 1984).

	Sandeel	Sprat
Puffin	61 (36-90)	46 (25-86)
Razorbill	73 (55-158)	54 (30-105)
Guillemot	122 (115-130)	102 (73-130)

Table 2.5 Average length (cm) of some fish species swallowed by seabirds during experimental discarding from fishery vessels in Shetland (area I, summer 1985) and in the North Sea (area II, spring and summer 1992). From Hudson and Furness (1988) and Garthe (1993).

	Area	Whiting	Haddock	Herring	Sandeel
Offered	I	29	28	-	-
	II	23	21	26	19
Fulmar	I	24	23	-	-
	II	22	20	24	20
Gannet	I	31	29	-	-
	II	24	24	27	20
G. black-backed gull	I	29	28	-	-
	II	22	-	27	-
Herring gull	I	26	26	-	-
	II	23	22	27	17
L. black backed gull	I	27	25	-	-
	II	24	23	22	19
Great skua	I	27	26	-	-
	II	21	-	26	-
Kittiwake	II	19	14	16	19

Table 2.6 Geographic variation in the food of the herring gull in the Shetlands 1983-1985, Forth 1979-1981 (Furness, *et al.*, 1992) and in the Wadden Sea in summer 1987 (Noordhuis and Spaans, 1992) or in fall 1991 (Schleswig-Holstein, November: Dernedde, 1992). Shetland, Forth: Each pellet is assigned to the prey type of which it was predominantly or entirely composed; Wadden Sea: Occurence of prey items in % of pellets.

Diet	Shetland	Forth	Texel	Vlieland	Terschelling	Schiermonnikoog	Schleswig -Holstein
Marine invertebrates	91	27	77	85	76	72	>80
Terrestrial invertebrates		7	1		12	12	
Marine fish		1	12	1	8	4	5
Terrestrial fish			8	10	5	4	
Fish not specified			1		4		
Birds, Mammals	1			2	5	3	
Discards	6	52					
Garbage	1	12	3	2	7	4	7

Table 2.7 Geographic variation in the food of the common tern on the Farne Islands (PEARSON 1968), Mousa (Uttley, *et al.*, 1989) and in the Wadden Sea (a) Stienen and van Tienen, 1991; (b) Frank, 1992).

		Percent food							
Colony	Year	n	Clupeoids	Sandeels	Gadids	Sticklebacks	Flatfish	Other and unidenti-fish	Crusta-ceans
Farne Islands	1961-1963	519	44	38	11	2		5	
Mousa, Shetlands	1988	110		20				80[c]	
Wadden Sea									
Griend[a]	1989-1990	?	52				7	9	32
Oldeoog[b]	1986	638	60	19		1		18	
Augustgroden[b]	1986	1,457	31	3		55	2	4	1

[c] mainly saithe

Table 2.8 Geographic and annual variation in the food of guillemot chicks on the Fair Isle (Harris and Riddiford, 1989), the Isle of May (1981-1986, Harris and Wanless, 1988), the Farne Islands (Pearson, 1968) and on Helgoland (Leopold, *et al.*, 1992, Grunsky, unpubl. data). On the Isle of May fed clupeids consisted only of sprats.

	% of chick diet		
	Sandeels	Clupeids	Others
Fair Isle			
1986	96	4	0
1987	100	0	0
1988	99	0	1
Isle of May			
1981	58	41	1
1982	89	8	3
1983	75	24	1
1984	86	14	0
1985	80	20	0
1986	94	6	0
Farne Islands			
1961-1963	49	42	4
Helgoland			
1990	5	95	0
1991	69	31	0
1992	22	78	0
1993	49	51	0

Table 2.9 Geographic and annual variation in the food of puffin chicks (% by weight) on Runde (Barret, *et al.*, 1987), Fair Isle and Isle of May (Harris and Hislop, 1978) and on the Farne Islands (Pearson, 1968).

	Sandeels	Clupeids		Gadids				Others
		Herring	Sprat	Saithe	Cod	Haddock	Rockling	
Runde								
1980	17	29		22	4	6	18	
1981	59	4				30		
1982	48			15		25		
Fair Isle								
1974	81						3	
1975	94		4					
1976	96			4				
Isle of May								
1972	55		18	1			26	
1973	90		7				3	
1974	48		51	1				
1975	14		86					
1976	38		53	9				
Farne Islands								
1961-1963	80		13					7

Table 2.10 Papers giving details of diets of seabirds in the North Sea and adjacent areas, and used in the compilation of diet summaries for use in this study.

a) Papers dealing with diets of several seabird species:

Bailey, 1986; Bailey *et al.*, 1991; Barrett and Furness, 1990; Camphuysen *et al.*, 1993; Dunnet *et al.*, 1990; Furness, 1983, 1989, 1990, 1992; Furness and Barrett, 1985, 1991; Furness *et al.*, 1992; Garthe, 1993; Harris and Riddiford, 1989; Heubeck, 1989; Hislop *et al.*, 1991; Hudson and Furness, 1988, 1989; Huppop and Garthe, 1993; Madsen, 1957; Pearson, 1968; plus handbooks (e.g., Bezzel, 1985; Cramp and Simmons, 1977).

b) Fulmar: Fisher, 1952; Fowler and Dye, 1987; Furness and Todd, 1984.

c) Gannet: Martin, 1989; Montevecchi and Barrett, 1987; Nelson, 1978; Tasker *et al.*, 1984; Wanless, 1984.

d) Cormorant: Barrett *et al.*, 1990; Dobben, 1952; Madsen and Spärck, 1950; Mills, 1969; Okill *et al.*, 1992; Rae, 1969.

e) Shag: Aebischer and Wanless, 1992; Barrett *et al.*, 1990; Harris, 1992; Harris and Wanless, 1991, 1993; Johnstone *et al.*, 1990; Rae, 1969; Wanless, 1992; Wanless *et al.*, 1993.

f) Great skua: Furness, 1987; Furness and Hislop, 1981; Hamer *et al.*, 1991; Tasker *et al.*, 1985.

g) Black-headed gull: Gorke *et al.*, 1988; Gorke, 1990.

h) Lesser black-backed gull: Noordhius and Spaans, 1992.

i) Herring gull: Beaman, 1978; Coulson and Butterfield, 1986; Dernedde 1992; Goethe, 1980; Noordhuis and Spaans, 1992; Prüter, 1988; Sibly and McCleery, 1983; Spaans, 1971.

j) Great black-backed gull: Taylor, 1985.

k) Kittiwake: Coulson and Thomas, 1985; Galbraith, 1983; Wanless and Harris, 1989, 1992.

l) Arctic tern: Boecker, 1967; Dunn, 1972; Ewins, 1985; Frick, 1993; Lemmetyinen, 1973; Monaghan *et al.*, 1989; Stienen and Tienen, 1991; Uttley, 1991; Uttley *et al.*, 1989.

m) Common tern: Becker *et al.*, 1987; Boecker, 1967; Dunn, 1972; Frank, 1992; Frick 1993; Lemmetyinen, 1973; Massias and Becker, 1990; Stienen and Tienen, 1991; Uttley *et al.* 1989.

n) Sandwich tern: Dunn, 1972; Veen, 1977.

o) Guillemot: Blake, 1983, 1984; Bradstreet and Brown, 1985; Camphuysen, 1990; Durinck *et al.*, 1991; Harris and Wanless, 1985, 1986; Harris *et al.*, 1990; Hislop and MacDonald, 1989; Leopold *et al.*, 1992; Swennen and Duiven, 1977.

p) Razorbill: Blake, 1983, 1984; Bradstreet and Brown, 1985; Harris and Wanless, 1986, 1989; Harris *et al.*, 1990; Swennen and Duiven, 1977.

q) Black guillemot: Ewins, 1986, 1990.

r) Puffin: Anker-Nilssen, 1992; Anker-Nilssen and Lorentsen, 1990; Blake, 1983, 1984; Barrett *et al.*, 1987; Bradstreet and Brown, 1985; Harris, 1984; Harris and Hislop, 1978; Harris and Wanless, 1986; Harris *et al.*, 1990; Martin, 1989; Swennen and Duiven, 1977.

Table 2.11 Diets of seabirds in North Sea and adjacent areas and summary of diet used in the model.

Species	Area	Years	Months sampled	Diet	Reference
Fulmar	Shetland	1978-1982	6-8	72% sandeel, 14% offal	Furness and Todd, 1984
	Shetland	1984-1985	6-8	Sandeels 95% of fish (4-10 cm)	Fowler and Dye, 1987
		1991-1993	6-8	20% sandeel, 30% discard gadoids, 30% offal, 20% zooplankton	Furness, unpubl. data
	Fair Isle	1986-1988	7-8	3-29% sandeel, 65-96% offal and discard gadoids	Harris and Riddiford, 1989
	For model assume		May-Aug Sep-Apr	30% sandeel (4-10 cm), 30% offal, 30% discards, 10% zooplankton 0% sandeel, 50% offal, 25% discards, 25% zooplankton	
Herring gull	For model assume		All year	30% discard gadoids, 30% invertebrates, 30% terrestrial foods, 10% offal	
Guillemot	Shetland	1975-1983	5-7	100% sandeel (10-14 cm)	Bailey *et al.*, 1991
		1988	5-7	95% sandeel	Bailey *et al.*, 1991
	E. Scotland	1983	3-8	95% sandeel (10-16 cm)	Blake *et al.*, 1985
			9-2	30% sandeel, 30% sprat, 30% gadoids	Blake *et al.*, 1985
	Shetland	1985	1	50% sandeel	Tasker *et al.*, 1987
		1989	5-7	100% sandeel	Furness and Barrett, 1991
	Fair Isle	1986-1988	6-7	98% sandeel (10-14 cm)	Harris and Riddiford, 1989
	Skagerrak	1988	1-2	49% herring (5 cm), 21% sprat (11 cm), 3% sandeel (8 cm)	Durinck *et al.*, 1991
	East Anglia	1983	2	30% sprat (1-group), 15% sandeel (1-group), 9% gadoids	Blake, 1984
	Newcastle	1983	2	39% sandeel, 15% sprat, 7% gadoids	
	Moray Firth	1983	2	22% sprat, 18% sandeel, 34% gadoids (12 cm)	
	Isle of May	1981-1984	5-7	82% sandeel (13-16 cm), 17% sprat, 1% herring	Harris and Wanless, 1985
			10-5	89% sandeel, 10% sprat	
	Helgoland	1990-1993	6-7	5-61% sandeel, 31-95% clupeids	Leopold *et al.*, 1992 Grunsky unpubl.
	Farnes	1961-1963	4-8	49% sandeel (10-13 cm), 42% sprat	Pearson, 1968
	Skagerrak	1981	1	70% gadoids, 15% clupeids, 15% gadoids	Blake, 1983
	For model assume areas IVa (West)		Mar-Aug Sep-Feb	100% sandeel (10-14 cm) 33% sandeel (10-14 cm), 33% sprat (10 cm), 33% gadoids (12 cm)	
	For model assume areas IVa (East), IVb, IVc		Mar-Aug Sep-Feb	80% sandeel (10-14 cm), 20% sprat (10 cm) 40% sandeel (1014 cm), 30% sprat (10 cm); 30% gadoids (12 cm)	
Shag	Shetland	1975-1983	4-8	100% sandeel (12 cm)	Furness, 1990
		1988	4-8	99% sandeel (12 cm)	Furness and Barrett, 1991

cont'd

Table 2.11 (continued)

Species	Area	Years	Months sampled	Diet	Reference
		1989	4-8	99% sandeel	Furness and Barrett, 1991
		1990	1	90% sandeel	Furness, unpubl.
	Fair Isle	1986-1988	6-7	98% sandeel (12 cm)	Harris and Riddiford, 1989
	Isle of May	1991	7	99% sandeel (5-15 cm)	Harris and Wanless, 1993
	Isle of May	1985-1990	5-8	99% sandeel	Harris and Wanless, 1993
			10-2	93% sandeel, 6% rockling	Harris and Wanless, 1993
			3-4	90% sandeel, 8% rockling	Harris and Wanless, 1993
	Farnes	1961-1963	11-12	90% sandeel, 10% gadoids	Pearson, 1968
	For model assume		All year	100% sandeel (5-15 cm)	
Great Black-bached Gull	For model assume		Apr-Aug	60% gadoid discards, 20% sandeels (12 cm), 20% other prey	
			Sep-Mar	70% gadoid discards, 30% other prey	
Kittiwake	N shields	1968	2-4	75% clupeids, 13% sandeels	Coulson and Thomas, 1985
		1973		10% gadoids	Coulson and Thomas, 1985
			6-7	66% sandeels, 20% clupeids, 12% gadoids	
	Faroe Islands	1961	6-7	56% sandeels (7 cm), 22% clupeids	Pearson, 1968
		1973		21% gadoids	
	Isle of May	1982	6-7	94% sandeels (133 mm), 5% clupeidss	Galbraith, 1983
		1989	6-7	95% sandeels (15 cm)	Wanless and Harris, 1992
		1990	6-7	86% sandeels	
	Fair Isle	1986-1988	6-7	98% sandeels (8 cm)	Harris and Riddiford, 1989
	Foula	1975-1983	5-7	100% sandeels	Bailey *et al.*, 1991
		1988	6-7	65% sandeels (9 cm)	Furness, 1990
	Foula	1989	6-7	92% sandeels	Furness and Barrett, 1991
	For model assume IVa(west)		May-Aug Sep-Apr	100% sandeels (6-14 cm) 25% sprat (8 cm), 25% zooplankton, 25% offal, 25% discards	
	For model assume IVb, IVc, IVa(east)		May-Aug Sep-Apr	60% sandeels (6-14 cm), 20% sprat (8 cm), 20% zooplankton 25% sprat (8 cm), 25% zooplankton, 25% offal, 25% discards	
Gannet	Foula	1975-1989	5-8	50% sandeels	Furness, 1990

cont'd.

Table 2.11 (continued)

Species	Area	Years	Months sampled	Diet	Reference
	Hermaness	1981-1988	6-7	1981: 90% sandeels, 5% mackerel, 0% herring, 5% gadoids 1983: 60% sandeels, 22% mackerel, 3% herring, 9% gadoids 1984: 39% sandeels, 31% mackerel, 8% herring, 21% gadoids 1986: 15% sandeels, 24% mackerel, 41% herring, 13% gadoids 1987: 16% sandeels, 25% mackerel, 47% herring, 13% gadoids 1988: 6% sandeels, 22% mackerel, 51% herring, 19% gadoids	Martin, 1989
	Bass Rock			Herring, mackerel, sandeel, gadoids	Nelson, 1978
	For model assume			30% sandeels, 30% herring, 30% mackerel, 10% discards (sandeeels: 0-1 group)	
Puffin	Shetland	1973	6-7	90% sandeel (0-group)	Martin, 1989
		1974	6-7	79% sandeel, 14% haddock	
		1976	6-7	81% sandeel, 16% rockling	
		1978	6-7	87% sandeel	
		1979	6-7	90% sandeel	
		1981	6-7	99% sandeel	
		1983	6-7	98% sandeel	
		1984	6-7	90% sandeel	
		1986	6-7	100% sandeel	
		1987	6-7	19% sandeel, 31% rockling, 26% sprat	
		1988	6-7	36% sandeel, 42% rockling, 21% saithe	
	Fair Isle	1974-1987	6-7	75%-100% sandeel (4-8 cm)	Harris and Riddiford, 1989
		1988	6-7	42% sandeel, 51% whiting, 5% sprat	
	Farne Islands	1961-1963	6-7	80% sandeel, 13% sprat	Pearson, 1988
	E. Anglia	1983	2	60% sandeel, 38% clupeid	Blake, 1984
	Shetland	1975-1983	5-8	100% sandeel (8-12 cm)	Furness, 1990
		1988	6-7	39% sandeel	Furness and Barrett, 1991
		1989	6-7	91% sandeel	Furness and Barrett, 1991
	Isle of May	1972	6-7	45% sandeel, 4% sprat, 50% whiting	Harris and Hislop, 1978
		1973	6-7	93% sandeel, 3% sprat	
		1974	6-7	69% sandeel, 28% sprat	
		1975	6-7	21% sandeel, 74% sprat	
		1976	6-7	55% sandeel, 29% sprat, 14% saithe (Sandeels 7 cm, sprat 7 cm)	
	For model assume IVa (West)		May-Aug	90% sandeel (0-group), 10% rockling	
			Sep-Apr	30% sandeel, 30% gadoids, 30% sprat, 10% zooplankton	
	For model assume IVa (East), IVb, IVc		All year	50% sandeel, 30% sprat, 20% gadoids (all 0-group)	
Razorbill	Fair Isle	1989	6-7	100% sandeel	Harvey *et al.*, 1989

cont'd

Table 2.11 (continued)

Species	Area	Years	Months sampled	Diet	Reference
	Canna	1989	6-7	100% sandeel	Swann, 1989
	East Anglia	1983	2	51% sandeel, 49% clupeid	Blake, 1984
	Moray Firth	1983	2	50% sandeel, 45% clupeid, 5% gadid	Blake, 1984
	Newcastle	1983	2	87% sandeel, 8% gobies, 5% clupeid	Blake, 1984
	Isle of May	1982-1987	6-7	70% sandeel (1015 cm), 20% sprat, 10% herring	Harris and Wanless, 1989
	Foula	1971-1982	6-7	100% sandeel (6-8 cm)	Furness and Barrett, 1991
	Fair Isle	1986 1987	6-7 6-7	100% sandeel 97% sandeel, 3% sprat	Harris and Riddiford, 1989
	For model assume IVa (west)		Mar-Aug Sep-Feb	100% sandeel (6-10 cm) 60% sandeel, 40% sprat	
	For model assume Iva (east), IVb, IVc		Mar-Aug Sep-Feb	70% sandeel, 30% sprat 60% sandeel, 40% sprat	

Table 2.12 Diets of seabirds in Shetland 1975-1983. Total annual energy demands of populations and sandeel consumption (tonnes). Species are ranked by estimated annual consumption of sandeels. Furness (1990).

Species	Percentage (by mass) of sandeels in diet	Modal sandeel length taken in June-July (mm)	Annual energy needs of population (kJ × 10^9)	Sandeels consumed (tonnes)
Guillemot	100% May-Aug[1]; >90% Mar-Aug[2]; 50% Jan[3]	140-170	96·0	14,400
Fulmar	70% Jun-Aug[4]; >50% Jun[5]	60-120	145·3	13,700
Puffin	100% May-Aug[1]; 97% Jun-Jul[6]	80-120	41·1	6,300
Gannet	80% Jun-Jul[6]; >50% May-Aug[1]	no data	46·1	5,300
Shag	100% Apr-Aug[1]	100-150	18·5	2,500
Kittiwake	100% May-Jul[1]	80-100	14·6	2,100
Razorbill	100% Jun-Jul[1]	60-80	5·4	600
Great Black-backed Gull	40% May-Jul[1]; 80% Apr-Jun; 50% Jul-Aug[7]	80-140	9·4	600
Great Skua	30% Mar, 50% Apr; 80% May-Jun; 50% Jul[1,8]	100-140	3·5	400
Black Guillemot	60% May-Aug[1]	100-180	3·8	300
Arctic Tern	100% Jun-Jul[1,10]	30-80	1·4	300
Herring Gull	20% May-Aug[9]	80-140	4·4	100
Arctic Skua	100% May-Jul[1]	60-140	0·3	50
All other seabirds				*ca.* 200
All seabirds				*ca.* 47,000

References: 1 = Furness (1983, 1989), 2 = Blake *et al.* (1985), 3 = Tasker *et al.* (1987), 4 = Furness & Todd (1984), 5 = Fowler & Dye (1987), 6 = Martin (1989), 7 = Beaman (1978), 8 = Furness & Hislop (1981), 9 = Hudson (1986), 10 = Ewins (1985a).

Table 2.13 Percentage of seabird diet consisting of sandeels, Foula. Furness and Barrett (1991).

		MEAN PERCENTAGE OF SANDEELS					
		1971–1982		1988		1989	
SPECIES	CATEGORY	%	*n*	%	*n*	%	*n*
NORTHERN FULMAR	adult or chick regurgitates	72	(177)	3	(28)	0	(50)
GREAT BLACK-BACKED GULL	nonbreeder pellets	40	(700)	0	(100)	0	(100)
BLACK GUILLEMOT	in bill	60	(375)	6	(31)	0	(5)
GREAT SKUA	nonbreeder pellets	50	(1000)	0	(300)	4	(247)
GREAT SKUA	chick regurgitates	82	(579)	5	(22)	14	(21)
RED-THROATED LOON	in bill	97	(62)	17	(41)	61	(23)
ARCTIC TERN	in bill	100	(1850)	19	(42)	97	(27)
ATLANTIC PUFFIN	in bill	96	(477)	39	(121)	91	(56)
KITTIWAKE	adult or chick regurgitates	100	(106)	67	(6)	92	(13)
RAZORBILL	in bill	100	(30)	43	(7)	100	(2)
COMMON MURRE	in bill	100	(74)	97	(91)	100	(26)
SHAG	chick regurgitates	100	(214)	100	(35)	100	(3)
SHAG	adult pellets	—	(0)	98	(10)	98	(150)
PARASITIC JAEGER	chick regurgitates	100	(156)	100	(20)	100	(7)

Breeding seasons only. Species are approximately ranked by decreasing extent of reduction in the amount of sandeel in their diet.

Table 2.14 The percentages of different items in food regurgitated by great skua chicks on Foula between 1 and 15 July, for every year from 1974 to 1989. Hamer *et al.* (1991).

Year	*n*	Sandeel (%)	Whitefish (%)	Birdmeat (%)
1974	90	91	9	0
1975	90	70	28	2
1976	95	86	14	0
1977	56	86	14	0
1978	45	71	24	4
1979	49	73	24	2
1980	69	68	28	4
1981	64	88	6	6
1982	21	95	5	0
1983	41	95	2	2
1984	36	61	33	6
1985	58	62	33	5
1986	61	66	30	5
1987	36	56	42	3
1988	22	5	77	18
1989	21	14	76	10

For every year, *n* is the number of regurgitates and the number of chicks producing them, since every chick produced a single regurgitate. The percentages refer to the proportions of regurgitates containing each food item. Deviations of the summed values from 100% are due to rounding errors

Table 2.15 Food items in pellets produced by non-breeding great skuas on Foula between 1 and 15 July, for every year from 1973 to 1989 except 1985, and by breeding adults in 1989. hamer *et al.* (1991).

Year	*n*	Sandeel (%)	Whitefish (%)	Bird (%)	Other (%)
1973	100	71	27	2	0
1974	100	24	71	5	0
1975	100	21	69	6	4
1976	100	72	26	2	0
1977	100	59	35	4	2
1978	100	64	35	1	0
1979	100	41	54	3	2
1980	100	17	74	6	3
1981	100	18	77	4	1
1982	100	13	80	3	4
1983	305	9	70	17	4
1984	100	0	74	23	3
1986	200	0	82	14	5
1987	98	9	77	10	4
1988	200	0	73	24	4
1989	247	4	62	30	4
1989 (B)	549	1	69	29	2

For every year, *n* is the number of pellets analysed. The number of birds producing these pellets is similar to the number of pellets in the case of non-breeders, while the sample for breeding birds was collected from 50 territories. The percentages refer to the proportions of pellets containing each item. 'Other' items were invertebrates, rabbits, mice, fulmar *Fulmarus glacialis* eggs or great skua eggs. 1989 (B) refers to breeding adults

Table 2.16 Composition of regurgitated from nestling Kittiwakes. Galbraith (1993).

Prey species	*Number obtained*	*% of recognised items*	*% frequency*
Sandeels *Ammodytes marinus*	218	93.9	87.3
Sprats or Herring	10	4.5	6.8
Herring *Clupea harengus*	2	0.9	1.3
Squid	1	0.4	0.6
Nephrops norvegicus	1	0.4	0.6
Fish offal	—	—	3.4

Table 2.17 Food regurgitated by young or adult shags with young on the Isle of May in 1985-1990. Harris and Wanless (1991).

Year	Regurgitations n	Range of sampling dates	Total weight (g)	Sandeels		
				Presence in regurgitations %	By weight %	% 0-group[1]
1985	19	24 July–16 Aug	925	100	98	57
1986	38	13 July–14 Aug	1672	100	97	65
1987	22	26 May– 5 July	1074	100	100	18
1988	16	15 June–19 July	675	100	98	4
1989	26	29 May– 5 July	1027	100	100	93
1990	20	6 July–20 July	570	100	95	99
Total	141		5943	100	99	

[1] Distribution of lengths and sample sizes are shown in Fig. 1. All fish 10 cm or less long were assumed to be 0-group.

Table 2.18 Fish families (and positively identified genera and species) whose otoliths were recorded in pellets from shags on the Isle of May in 1985-1990. The numbers of otoliths are given in brackets after the species or genus. Pellets containing no otoliths are excluded. Harris and Wanless (1991).

	% Pellets containing (n = 1476)	% Otoliths (n = 185636)
Ammodytidae		
Sandeel, mainly *Ammodytes marinus* (179240)	93.4	96.7
Gadidae		
Rockling *Gaidropsarus/Ciliata* spp. (1502)	22.8	1.9
Cod *Gadus morhua* (351)		
Poor cod *Trisopterus minutus (20)*		
Norway pout T. esmarkii (6)		
Trisopterus sp. (229)		
Saithe *Pollachius virens* (73)		
Whiting *Merlangius merlangus* (60)		
Tadpole-fish *Raniceps raninus* (3)		
Gobiidae	7.6	0.8
Pleuronectidae		
Probably long rough dab *Hippoglossoides platessoides*	16.8	0.5
Cottidae	8.2	0.3
Clupeidae		
Herring *Clupea harengus* (12)	0.7	<0.1
Anarhichadidae		
Catfish *Anarhichas lupus* (9)	<0.1	<0.1
Zoarcidae		
Eel pout *Zoarces viviparus* (9)	<0.1	<0.1
Agonidae		
Hook-nose *Agonus cataphractus* (1)	<0.1	<0.1

Table 2.19 Body lengths (cm) of fish calculated from lengths of otoliths extracted from shag pellets on the Isle of May in 1988-1990. Harris and Wanless (1991).

Family		Body length (cm)	
		n	mean ± SE
Ammodytidae		1275	9.8 ± 0.08
Gadidae	– large	379	11.3 ± 0.24
	– small	422	5.1 ± 0.39
Cottidae		64	15.2 ± 0.5
Gobiidae		66	3.0 ± 0.2
Pleuronectidae		98	7.8 ± 0.4

Table 2.20 Seasonal variation in the percentage of shag pellets containing otoliths from five fish families on the Isle of May in 1985-1990. The percentage frequency of otoliths in each family is given in brackets. Harris and Wanless (1991).

	Pellets[1] n	Otoliths[2] n	% pellets where present (% frequency of otoliths)				
			Ammodytidae	Gadidae	Cottidae	Gobiidae	Pleuronectidae
Winter 1985-86	53	4842	96 (93)	51 (5)	2 (*)	13 (2)	2 (*)
Winter 1987-88	30	1748	97 (96)	20 (2)	7 (1)	3 (*)	3 (*)
Prebreeding 1988	78	12043	90 (99)	27 (1)	5 (*)	1 (*)	11 (*)
Breeding 1988	89	2286	87 (70)	20 (20)	5 (1)	3 (6)	9 (1)
Winter 1988-89	28	1142	93 (91)	28 (6)	7 (*)	0 (0)	3 (*)
Prebreeding 1989	60	10970	83 (98)	26 (1)	15 (*)	14 (1)	11 (*)
Breeding 1989	248	17220	91 (95)	25 (2)	11 (1)	10 (1)	13 (1)
Winter 1989-90	243	43311	93 (99)	26 (1)	7 (*)	16 (*)	14 (*)
Prebreeding 1990	132	24797	94 (98)	23 (1)	10 (*)	6 (*)	35 (*)
Breeding 1990	441	45462	97 (94)	16 (3)	8 (*)	10 (2)	22 (1)
Winter 1990-91	74	20777	97 (99)	15 (*)	7 (*)	9 (*)	8 (*)
Total	1476	185636	93 (97)	22 (2)	8 (*)	7 (*)	17 (*)

[1] Pellets with no otoliths excluded. [2] Unidentified otoliths included. *Less than 0.5%.

Table 2.21 Seasonal variation in the numerical predominance of five fish families in pellets from shags on the Isle of May in 1985-1990. Percent contributions are given in brackets. Harris and Wanless (1991).

Season	Total	Ammodytidae	Gadidae	Cottidae	Gobiidae	Pleuronectidae
Winter 1985-86	53	47 (88.7)	6 (11.3)	0 (0)	0 (0)	0 (0)
Winter 1987-88	30	28 (93.3)	2 (6.7)	0 (0)	0 (0)	0 (0)
Prebreeding 1988	78	67 (87.0)	9 (11.7)	1 (1.3)	0 (0)	0 (0)
Breeding 1988	89	84 (98.4)	8 (7.2)	2 (1.8)	1 (0.9)	0 (0)
Winter 1988-89	28	26 (92.8)	2 (7.1)	0 (0)	0 (0)	0 (0)
Prebreeding 1989	60	52 (85.2)	3 (4.9)	5 (7.2)	0 (1.6)	0 (0)
Breeding 1989	248	218 (87.9)	19 (7.7)	5 (2.0)	3 (1.2)	3 (1.2)
Winter 1989-90	243	219 (91.2)	16 (6.7)	4 (1.7)	0 (0)	1 (0.4)
Prebreeding 1990	132	120 (92.3)	6 (4.6)	4 (3.1)	0 (0)	0 (0)
Breeding 1990	441	417 (94.8)	15 (3.4)	2 (0.4)	3 (0.7)	3 (0.7)
Winter 1990-91	74	73 (98.6)	1 (1.4)	0 (0)	0 (0)	0 (0)
Total	1476[a]	1351 (91.5)	87 (5.8)	23 (1.5)	8 (0.5)	7 (0.5)

[a] Eighty-two pellets where there was no predominant item are excluded.

Table 2.22 Percentages by number, mass and caloric value of fish brought back by puffins feeding young. Harris and Hislop (1978)

		Total			Sandeels			Sprats			Rockling			Whiting			Saithe			Haddock			Other species		
Colony	Year	Number	Weight, g	Calorific value kJ	% (No.)	% (Wt.)	% (Cal. val.)	% (No.)	% (Wt.)	% (Cal. val.)	% (No.)	% (Wt.)	% (Cal. val.)	% (No.)	% (Wt.)	% (Cal. val.)	% (No.)	% (Wt.)	% (Cal. val.)	% (No.)	% (Wt.)	% (Cal. val.)	% (No.)	% (Wt.)	% (Cal. val.)
St Kilda	1971	363	96	595	34·4	25·8	20·8				60·0	61·2	70·3	4·7	11·3	7·4							0·8	1·7	1·5
	1973	359	240	1290	32·0	13·9	13·0	0·8	14·0	27·7	27·0	8·5	11·2	32·3	62·4	47·0							7·8	1·2	1·2
	1974	820	580	2895	58·8	27·4	33·0	16·6	14·5	17·2	5·6	2·8	3·9	18·3	52·0	42·2				0·7	3·3	3·6			
	1975	992	731	5442	9·2	10·3	11·0	75·8	83·8	84·0	12·4	4·2	4·0	2·0	1·4	0·7				0·2	0·2	0·2	0·4	0·1	0·1
	1976	2143	808	4860	37·5	26·8	26·5	40·6	57·9	56·2	20·8	13·8	16·3	0·7	1·0	0·7							0·5	0·4	0·4
Isle of May	1972	104	68	416	45·2	54·6	45·0	3·8	18·4	23·9	50·0	26·0	30·2				1·0	1·0	0·9						
	1973	350	551	3794	92·6	90·2	89·1	2·9	6·9	8·3	3·1	1·4	1·5				0·6	0·4	0·3				0·9	1·1	0·8
	1974	588	947	7291	69·2	47·6	42·4	27·6	50·6	56·6	0·9	0·2	0·2				1·2	1·1	0·8				1·2	0·4	0·2
	1975	476	1096	8495	21·0	13·5	12·0	73·5	85·6	87·3	4·0	0·4	0·4				1·3	0·3	0·2				0·2	0·1	0·1
	1976	735	1175	8428	55·1	38·1	34·8	29·4	52·6	58·5	0·3	+	+				14·2	9·1	6·5				1·1	0·2	0·1
Fair Isle	1974	47	223	1540	74·5	81·0	89·0							25·5	19·0	11·0									
	1975	117	231	1605	76·1	93·7	94·1	10·3	3·8	3·3	13·7	2·5	2·6												
	1976	212	368	2477	93·9	95·6	96·6				2·8	0·4	0·4				3·3	4·0	3·0						
Hermaness	1973	138	145	974	68·1	90·0	90·0				31·2	8·6	9·1	0·7	1·4	0·8									
	1974	110	247	1770	43·6	79·2	83·0	0·9	0·7	0·7	38·2	4·2	4·2	0·9	0·4	0·3				9·1	13·8	10·6	7·3	1·6	1·2
	1976	431	399	2699	47·8	81·2	81·1	5·1	1·9	1·5	43·9	15·6	16·4										3·2	1·2	1·0
Shiant Islands	1973	509	425	2343	58·3	42·5	49·1	0·6	4·6	7·8	4·9	1·4	1·8	27·5	38·5	28·3				3·1	6·6	6·6	5·5	6·4	6·4
	1975	31	39	219	71·0	46·2	52·5	3·2	10·8	16·3				25·8	43·1	31·1									
	1976	205	262	1811	10·2	5·2	4·7	53·2	62·5	76·2	1·5	0·2	0·2	34·6	32·0	18·7	0·5	0·1	0·1						
Faraid Head	1973	4	30	225	25·0	12·5	12·0	25·0	41·4	59·7				25·0	20·5	11·0	25·0	25·6	17·3						
	1975	98	225	1847	75·5	93·8	94·7	4·1	3·4	3·5	7·1	0·5	0·5	13·3	2·2	1·3									
Flannan Islands	1975	633	719	4934	68·1	80·8	78·7	25·6	17·7	19·9	5·1	1·1	1·1	1·3	0·5	0·3									
Foula	1974	43	174	1273	100·0	100·0	100·0																		
North Rona	1972	61	40	265	49·2	72·0	70·0				50·8	28·0	30·0												
	1976	411	264	1903	32·6	72·7	73·3				66·7	27·0	26·6	0·7	0·3	0·2									
Sule Skerry	1975	31	44	266	12·9	17·6	20·8	74·2	59·5	64·0				12·9	22·9	15·2									
Co. Kerry	1973	78	69	433	19·2	18·2	18·6	76·9	76·3	76·6													3·8	5·5	4·8

cont'd.

Table 2.22 (continued)

		Total			Sandeels			Sprats			Rockling			Whiting			Saithe			Haddock			Other species		
Colony	Year	Number	Weight, g	Calorific value kJ	% (No.)	% (Wt.)	% (Cal. val.)	% (No.)	% (Wt.)	% (Cal. val.	% (No.)	% (Wt.)	% (Cal. val.)	% (No.)	% (Wt.)	% (Cal. val.)	% (No.)	% (Wt.)	% (Cal. val.)	% (No.)	% (Wt.)	% (Cal. val.)	% (No.)	% (Wt.)	% (Cal. val.)
St Kilda	1971	363	96	595	34·4	25·8	20·8				60·0	61·2	70·3	4·7	11·3	7·4							0·8	1·7	1·5
	1973	359	240	1290	32·0	13·9	13·0	0·8	14·0	27·7	27·0	8·5	11·2	32·3	62·4	47·0							7·8	1·2	1·2
	1974	820	580	2895	58·8	27·4	33·0	16·6	14·5	17·2	5·6	2·8	3·9	18·3	52·0	42·2				0·7	3·3	3·6			
	1975	992	731	5442	9·2	10·3	11·0	75·8	83·8	84·0	12·4	4·2	4·0	2·0	1·4	0·7				0·2	0·2	0·2	0·4	0·1	0·1
	1976	2143	808	4860	37·5	26·8	26·5	40·6	57·9	56·2	20·8	13·8	16·3	0·7	1·0	0·7							0·5	0·4	0·4
Isle of May	1972	104	68	416	45·2	54·6	45·0	3·8	18·4	23·9	50·0	26·0	30·2				1·0	1·0	0·9						
	1973	350	551	3794	92·6	90·2	89·1	2·9	6·9	8·3	3·1	1·4	1·5				0·6	0·4	0·3				0·9	1·1	0·8
	1974	588	947	7291	69·2	47·6	42·4	27·6	50·6	56·6	0·9	0·2	0·2				1·2	1·1	0·8				1·2	0·4	0·2
	1975	476	1096	8495	21·0	13·5	12·0	73·5	85·6	87·3	4·0	0·4	0·4				1·3	0·3	0·2				0·2	0·1	0·1
	1976	735	1175	8428	55·1	38·1	34·8	29·4	52·6	58·5	0·3	+	+				14·2	9·1	6·5				1·1	0·2	0·1
Fair Isle	1974	47	223	1540	74·5	81·0	89·0							25·5	19·0	11·0									
	1975	117	231	1605	76·1	93·7	94·1	10·3	3·8	3·3	13·7	2·5	2·6												
	1976	212	368	2477	93·9	95·6	96·6				2·8	0·4	0·4				3·3	4·0	3·0						
Hermaness	1973	138	145	974	68·1	90·0	90·0				31·2	8·6	9·1	0·7	1·4	0·8									
	1974	110	247	1770	43·6	79·2	83·0	0·9	0·7	0·7	38·2	4·2	4·2	0·9	0·4	0·3				9·1	13·8	10·6	7·3	1·6	1·2
	1976	431	399	2699	47·8	81·2	81·1	5·1	1·9	1·5	43·9	15·6	16·4										3·2	1·2	1·0
Shiant Islands	1973	509	425	2343	58·3	42·5	49·1	0·6	4·6	7·8	4·9	1·4	1·8	27·5	38·5	28·5				3·1	6·6	6·6	5·5	6·4	6·4
	1975	31	39	219	71·0	46·2	52·5	3·2	10·8	16·3				25·8	43·1	31·1									
	1976	205	262	1811	10·2	5·2	4·7	53·2	62·5	76·2	1·5	0·2	0·2	34·6	32·0	18·7	0·5	0·1	0·1						
Faraid Head	1973	4	30	225	25·0	12·5	12·0	25·0	41·4	59·7				25·0	20·5	11·0	25·0	25·6	17·3						
	1975	98	225	1847	75·5	93·8	94·7	4·1	3·4	3·5	7·1	0·5	0·5	13·3	2·2	1·3									
Flannan Islands	1975	633	719	4934	68·1	80·8	78·7	25·6	17·7	19·9	5·1	1·1	1·1	1·3	0·5	0·3									
Foula	1974	43	174	1273	100·0	100·0	100·0																		
North Rona	1972	61	40	265	49·2	72·0	70·0				50·8	28·0	30·0												
	1976	411	264	1903	32·6	72·7	73·3				66·7	27·0	26·6	0·7	0·3	0·2									
Sule Skerry	1975	31	44	266	12·9	17·6	20·8	74·2	59·5	64·0				12·9	22·9	15·2									
Co. Kerry	1973	78	69	433	19·2	18·2	18·6	76·9	76·3	76·6													3·8	5·5	4·8

Table 2.23 Characteristics of the puffin diet on Hermaness, by year. Martin (1989).

Year	*Load weight (g)*		*Fish per load*		*No. species*	*Dates*	*Sandeels by weight(%)*	*Sandeels by number ±2 s.e. (%)*	*Sandeel length (mm)*		*% Sandeel > 100 mm (at least 1 year old)*
	N	*x̄ ±2 s.e.*	*N*	*x̄ ±2 s.e.*					*N*	*x̄*	
1973			18	7.9±2.0	3	12/7–27/7	90	68±8	94	77.3	8
1974	13	11.6±3.1	31	3.3±1.5	5	8/7–14/7	79	53±10	58	97.4	57
1976	38	7.9±1.3	43	10.1±1.6	5	17/7–1/8	81	48±5	206	80.9	12
1978	43	6.8±1.1	43	7.8±1.4	7	28/6–30/6	87	54±7	176	79.8	3
						9/7–27/7					12
1979	28	6.8±1.8	29	7.6±2.3	4	8/7–10/7	90	23±6	53	105.4	68
1981	74	9.8±0.8	75	6.6±0.8	2	18/6–21/6	99	98±1	471	76.7	4
1983	74	8.1±0.8	74	11.4±1.2	3	12/6–21/6	96	94±2	601	64.3	3
1984	77	6.7±1.0	78	15.1±1.9	7	16/6–24/6	90	76±2	607	56.9	2
1986	9	3.4±1.0	9	13.2±7.1	1	14/6	100	100	177	43.8	< 1
1987	4	4.4±2.9	4	12.3±6.0	4	2/7	19	20±12	10	< 30	0
1988	74	3.3±0.5	74	18.0±1.9	6	24/6–1/7	36	49±1	692	37.3	0.2

Table 2.24 Composition of the diet of gannets on Hermaness, by fish species in each sampling year. The importance of the main prey species in each year is shown by the percentage of the weight of the total year's sample which comprised that species. Weights shown are the estimated total consumption of each fish species by the Hermaness gannet colony in the year assuming (a) a colony requirement of 4.4423 x 10^8 kcals per season, (b) that the sample is representative of the season as a whole, and (c) that adult and nestling gannets have the same diet. Martin (1989).

Year	*No. loads examined*	*Sandeel* (%)	(wt(t))	*Mackerel* (%)	(wt(t))	*Gadoids** (%)	wt(t))	*Herring* (%)	(wt(t))	*Other* (%)	(wt(t))	*Seasonal consumption* (t)
1981	61	90	2570	5	143	5	143	0	0	0	0	2855
1983	76	66	1727	22	576	9	234	3	79	0	0	2616
1984	99	39	1019	31	810	21	549	8	209	0	0	2587
1986	125	15	351	24	563	13	306	41	963	7	164	2347
1987	85	14	316	25	563	13	293	47	1059	1	23	2254
1988	111	6	140	22	514	19	444	51	1192	2	47	2337

*'Gadoids' includes Cod, Haddock, Saithe and Whiting.

Table 2.25 Foraging success index (experimentally discarded fish swallowed per bird of each species present, on average, over all fishing trips) for different seabirds feeding on fish discarded from trawling fishing boats in Shetland during summers of 1984 and 1985. Furness (1992).

Species	Mean number at boat	Total number of fish swallowed	Success index
Gannet	9	452	50
Great skua	12	347	29
Great black-backed gull	234	2753	12
Lesser black-backed gull	6	32	5.3
Herring gull	30	107	3.6
Fulmar	485	85	0.2
Kittiwake	3	0	0.0

Table 2.26 Seabird distribution at sea in the North Sea. Data collected between 1980 and 1993. Survey effort (km^2) covered in each month in each area and the number of ICES rectangles visited.

	Area											
Month	IVaW		IVaE		IVbW		IVbC		IVbE		IVc	
	km^2	rectangles	km^2	rectangles	km^2	rectangles	km^2	rectangles	km^2	rectangles	km^2	rectangles
Total in area	156,906	62	97,271	34	69,447	27	140,933	40	62,781	24	56,763	22
January	295	30	30	5	359	17	568	25	698	21	920	18
February	1,246	45	80	10	642	25	1,166	38	1,092	23	1,499	22
March	1,642	41	29	4	209	16	660	26	257	17	1,214	18
April	1,494	43	86	10	280	15	929	28	1,041	23	1,481	19
May	1,395	40	426	22	772	21	1,146	35	926	21	672	20
June	1,612	50	159	15	708	22	1,322	29	395	19	1,029	19
July	2,238	44	765	30	714	22	1,629	38	681	21	661	17
August	2,369	49	1,066	31	2,381	26	1,860	39	942	24	1,108	20
September	1,728	38	376	24	2,567	25	1,370	38	420	17	1,435	20
October	656	35	46	5	550	20	593	27	1,322	24	665	19
November	1,256	34	180	17	540	20	1,143	33	822	22	1,133	17
December	844	32	13	4	544	21	812	23	320	20	1,411	18
Total survey effort	16,775		3,253		10,266		13,198		8,916		13,228	

Table 2.27 Summary of at-sea densities (numbers per km^2) of bird species by month and by area.

ICES IVa (west)	January	February	March	April	May	June	July	August	September	October	November	December
Fulmar	2.43	4.23	5.76	5.39	15.01	1.89	6.38	2.26	6.78	7.36	6.54	1.29
Gannet	0.26	0.30	0.43	0.51	0.25	0.12	0.36	0.31	0.33	0.35	0.24	0.05
Great skua	0.00	0.00	0.00	0.05	0.14	0.11	0.19	0.13	0.18	0.04	0.00	0.00
Black-headed gull	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00
Common gull	0.02	0.01	0.01	0.00	0.02	0.00	0.04	0.02	0.00	0.01	0.01	0.03
Lesser black-backed gull	0.06	0.00	0.00	0.14	0.05	0.15	0.12	0.01	0.01	1.87	0.00	0.00
Herring gull	0.13	0.61	1.80	0.84	0.33	0.33	0.30	0.37	0.14	4.77	2.16	2.16
Great black-backed gull	0.59	0.68	0.90	1.46	0.22	0.11	0.11	0.10	0.49	1.10	0.45	0.42
Kittiwake	1.96	9.95	1.99	2.33	1.79	1.05	1.53	1.15	1.60	2.26	2.54	0.43
Guillemot	1.69	1.48	2.92	2.95	4.23	5.57	4.15	6.18	5.66	1.99	1.89	1.09
Razorbill	0.14	0.42	0.49	0.79	0.45	0.51	0.67	2.00	1.52	0.43	0.26	0.35
Puffin	0.13	2.14	0.25	0.93	0.68	1.17	1.18	1.33	0.20	0.01	0.15	0.09

ICES IVa (east)	January	February	March	April	May	June	July	August	September	October	November	December
Fulmar	0.80	1.78	3.17	0.78	1.87	2.32	1.35	8.70	21.08	2.47	3.20	0.17
Gannet	0.11	0.08	0.50	0.37	0.04	0.19	0.06	0.12	0.12	0.28	0.11	26.61
Great skua	0.00	0.01	0.12	0.04	0.01	0.05	0.02	0.11	0.02	0.00	0.04	0.00
Black-headed gull	0.00	0.03	0.00	0.04	0.03	0.00	0.01	0.00	0.00	0.00	0.04	0.00
Common gull	0.52	0.13	0.13	0.02	0.08	0.00	0.25	0.10	0.06	0.00	0.02	0.00
Lesser black-backed gull	0.00	0.09	0.12	0.05	0.06	0.11	0.15	0.22	0.16	0.04	0.00	0.00
Herring gull	0.72	0.63	0.04	0.05	0.44	0.00	0.07	0.06	0.55	0.48	0.25	0.41
Great black-backed gull	0.00	0.18	0.05	0.09	0.12	0.00	0.04	0.44	1.62	0.01	0.06	0.06
Kittiwake	4.81	0.66	0.02	0.01	0.33	0.10	0.03	0.12	0.91	0.03	0.54	0.54
Guillemot	0.86	5.21	0.62	0.43	2.65	0.06	1.94	0.88	1.42	0.43	5.92	1.54
Razorbill	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00
Puffin	0.00	1.12	0.17	0.07	0.02	0.05	0.10	0.08	0.00	0.00	0.02	0.00

cont'd.

ICES IVb (west)	January	February	March	April	May	June	July	August	September	October	November	December
Fulmar	2.38	1.09	0.29	0.55	0.30	0.62	1.53	4.33	5.15	3.88	0.67	0.22
Gannet	0.20	0.90	0.20	0.78	0.40	1.25	0.21	0.72	0.99	0.62	0.21	0.06
Great skua	0.00	0.00	0.00	0.01	0.00	0.00	0.02	0.09	0.15	0.08	0.01	0.02
Black-headed gull	0.00	0.08	0.00	0.00	0.00	0.07	0.12	0.08	0.03	0.08	0.00	0.00
Common gull	0.21	0.50	0.09	0.03	0.02	0.02	0.03	0.11	0.03	0.14	0.02	0.43
Lesser black-backed gull	0.00	0.00	0.00	0.24	0.02	0.15	0.02	2.48	0.07	0.16	0.03	0.00
Herring gull	8.96	8.13	0.77	0.61	0.17	0.78	0.23	1.86	0.30	0.48	0.44	0.94
Great black-backed gull	1.75	2.61	0.04	0.29	0.02	0.04	0.01	3.79	1.33	2.00	0.65	1.32
Kittiwake	1.04	1.51	1.38	2.09	1.41	1.95	2.10	9.14	3.09	3.02	1.03	0.78
Guillemot	1.59	3.59	1.89	1.74	2.40	7.22	11.42	8.91	9.33	5.99	6.23	2.41
Razorbill	0.14	0.14	0.35	0.06	0.20	0.62	1.45	2.15	1.57	2.01	1.87	0.20
Puffin	0.13	2.05	0.74	0.95	0.29	2.94	0.90	1.27	0.81	0.13	0.67	0.34

ICES IVb (central)	January	February	March	April	May	June	July	August	September	October	November	December
Fulmar	1.26	1.47	1.03	0.55	0.75	0.45	1.04	2.47	3.08	2.78	1.61	0.66
Gannet	0.09	0.30	0.26	0.04	0.03	0.08	0.11	0.16	0.30	0.90	0.20	0.07
Great skua	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.04	0.05	0.03	0.01	0.00
Black-headed gull	0.00	0.00	0.05	0.01	0.01	0.00	0.02	0.02	0.01	0.01	0.02	0.01
Common gull	0.20	0.06	0.04	0.10	0.01	0.07	0.06	0.02	0.01	0.03	0.05	0.03
Lesser black-backed gull	0.00	0.00	0.03	0.19	0.16	0.07	0.14	0.05	0.01	0.00	0.01	0.00
Herring gull	0.82	0.67	0.19	0.08	0.02	0.18	0.01	0.03	0.06	0.04	0.73	0.76
Great black-backed gull	0.81	0.38	0.24	0.06	0.01	0.01	0.01	0.04	0.32	2.03	1.03	2.62
Kittiwake	0.74	2.42	0.73	0.66	0.86	0.24	0.38	0.35	0.30	2.53	1.29	0.54
Guillemot	0.76	1.79	0.80	0.88	0.24	0.12	1.17	1.43	1.13	3.00	3.19	0.87
Razorbill	0.06	0.14	0.13	0.16	0.04	0.00	0.01	0.03	0.12	0.48	0.28	0.16
Puffin	0.25	0.83	0.15	0.11	0.24	0.04	0.01	0.04	0.03	0.08	0.15	0.24

Table 2.27 (continued)

ICES IVb (east)	January	February	March	April	May	June	July	August	September	October	November	December
Fulmar	0.53	0.55	0.32	0.38	0.47	1.31	1.17	2.58	2.87	2.52	1.29	0.12
Gannet	0.02	0.01	0.01	0.05	0.03	0.02	0.05	0.06	0.08	0.19	0.03	0.01
Great skua	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.04	0.01	0.01	0.00	0.00
Black-headed gull	0.01	0.01	0.05	0.23	0.07	0.02	0.14	0.02	0.08	0.15	0.06	1.26
Common gull	0.80	1.42	0.19	1.76	0.19	0.02	0.27	0.04	0.12	0.27	0.67	1.38
Lesser black-backed gull	0.00	0.00	0.25	0.68	0.21	0.26	0.46	0.37	0.29	0.06	0.01	0.00
Herring gull	1.86	0.81	0.53	1.97	0.33	0.39	0.91	0.27	1.23	0.92	1.27	1.81
Great black-backed gull	0.42	0.84	0.50	0.38	0.09	0.11	0.14	0.30	0.50	0.37	0.36	0.07
Kittiwake	0.78	0.80	2.35	0.18	0.11	0.15	0.11	0.16	0.16	0.41	1.03	0.64
Guillemot	1.78	1.14	0.94	0.47	0.07	0.60	0.24	0.80	0.37	1.52	2.85	0.44
Razorbill	0.30	0.59	0.20	0.00	0.00	0.00	0.00	0.02	0.01	0.25	0.49	0.04
Puffin	0.04	2.20	0.08	0.01	0.00	0.00	0.00	0.00	0.00	0.01	0.03	0.00

ICES IVc	January	February	March	April	May	June	July	August	September	October	November	December
Fulmar	0.29	0.23	0.42	0.29	0.32	0.22	0.30	0.38	0.61	0.12	0.12	0.26
Gannet	0.04	0.06	0.12	0.07	0.01	0.03	0.04	0.20	0.14	0.45	0.23	0.14
Great skua	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.02	0.02	0.04	0.00	0.01
Black-headed gull	18.90	0.18	0.16	0.15	0.02	0.20	0.06	0.06	0.06	0.72	0.74	1.17
Common gull	2.06	0.88	1.07	0.58	0.23	0.18	0.18	0.23	0.05	1.84	1.45	1.04
Lesser black-backed gull	0.07	0.03	0.30	0.17	0.86	0.24	0.44	0.17	0.70	0.66	0.45	0.10
Herring gull	6.67	3.27	1.27	4.03	0.32	10.07	0.20	2.18	0.42	52.81	2.02	3.60
Great black-backed gull	1.68	0.92	0.39	0.12	0.05	0.03	0.02	0.05	0.58	0.68	0.60	1.84
Kittiwake	1.28	1.42	0.46	0.43	0.38	0.10	0.15	0.21	0.12	0.88	0.71	1.39
Guillemot	1.00	0.73	0.80	0.24	0.22	0.01	0.14	0.17	1.98	1.10	0.74	0.93
Razorbill	0.11	0.14	0.30	0.04	0.03	0.00	0.00	0.00	0.32	0.28	0.11	0.15
Puffin	0.00	1.09	0.00	0.02	0.00	0.00	0.00	0.18	0.00	0.00	0.00	0.09

Table 2.28 Numbers of seabirds breeding on coasts of the five ICES areas considered.

Species	IVa (west)	IVa (east)	IVb (west)	IVb (east)	IVc	Census units
Fulmar	294128	0	12596	36	697	occupied sites
Gannet	21648	0	22130	0	0	pairs
Cormorant	1483	18	703	0	18	"
Shag	13486	1755	4563	0	0	"
Great skua	7299	4	0	0	0	"
Black-headed	3455	36854	15980	53781	19272	"
gull	15770	43240	80	6452	7790	"
Common gull	2583	25502	2180	15791	3255	"
Lesser black-backed	41827	34037	40445	96293	24512	"
gull	9924	14480	31	1	0	"
Kittiwake	206606	2991	199949	3310	2571	"
Arctic tern	55951	8634	5349	4712	83	"
Common tern	1157	39815	1730	14407	4378	"
Sandwich tern	1121	1502	5592	14687	7644	
Guillemot	507487	438	167609	4900	0	individual at ledges
Razorbill	54537	302	18260	16	0	"
Black guillemot	20847	2891	3	0	0	individuals in spring
Puffin	124289	21695	79973	0	0	individuals, or burrowsx2

Table 2.29 Factors used in converting seabird population colony census data to numbers of individuals at colonies in each month of the year. Proportion of census number that are present at colonies.

[illegible]ies	Month											
	Jan	Feb	Mar	Apr	May	June	July	August	Sept	October	Nov	Dec
Fulmar	0.75	1.00	1.00	1.00	0.75	1.00	0.50	0.25	0.10	0.00	0.20	0.50
Gannet	0.00	0.00	0.25	0.75	1.00	1.00	1.00	1.00	0.50	0.10	0.00	0.00
Cormorant	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.80
Shag	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
Great skua	0.00	0.00	0.00	0.50	1.00	1.00	1.00	0.50	0.10	0.00	0.00	0.00
Black h. gull	0.00	0.00	0.25	0.50	1.00	1.00	1.00	0.50	0.10	0.00	0.00	0.00
Common gull	0.00	0.00	0.25	0.50	1.00	1.00	1.00	0.50	0.10	0.00	0.00	0.00
Lesser bb gull	0.00	0.00	0.00	0.50	1.00	1.00	1.00	0.50	0.10	0.00	0.00	0.00
Herring gull	0.00	0.10	0.50	0.75	1.00	1.00	1.00	0.50	0.10	0.00	0.00	0.00
Great bb gull	0.00	0.10	0.50	0.75	1.00	1.00	1.00	0.50	0.10	0.00	0.00	0.00
Kittiwake	0.10	0.25	0.50	1.00	1.00	1.00	1.00	0.50	0.10	0.00	0.00	0.00
Arctic tern	0.00	0.00	0.00	0.00	1.00	1.00	1.00	0.20	0.00	0.00	0.00	0.00
Common tern	0.00	0.00	0.00	0.00	1.00	1.00	1.00	0.20	0.00	0.00	0.00	0.00
Sandwich tern	0.00	0.00	0.00	0.00	1.00	1.00	1.00	0.20	0.00	0.00	0.00	0.00
Guillemot	0.10	0.25	0.50	1.00	1.00	1.00	0.50	0.00	0.00	0.00	0.00	0.00
Razorbill	0.10	0.25	0.50	1.00	1.00	1.00	0.50	0.00	0.00	0.00	0.00	0.00
Black guillemot	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Puffin	0.00	0.00	0.00	0.25	1.00	1.00	1.00	0.25	0.00	0.00	0.00	0.00

Table 2.30 Factors used to estimate the number of nonbreeders at colonies in each month as a proportion of the colony census unit.

Species	Factors			
Fulmar	0.0	all months		
Gannet	0.2	(May,Jun,Jul)		
Cormorant	0.2	all months		
Shag	0.2	all months		
Great skua	0.2	(May,Jun)	0.1	(Jul)
Black h. gull	0.2	(May,Jun)	0.1	(Jul)
Common gull	0.2	(May,Jun)	0.1	(Jul)
Lesser -b. gull	0.2	(May,Jun)	0.1	(Jul)
Herring gull	0.2	(May,Jun)	0.1	(Jul)
Great -b. gull	0.2	(May,Jun)	0.1	(Jul)
Kittiwake	0.2	(May,Jun)		
Arctic tern	0.1	(May,Jun)		
Common tern	0.1	(May,Jun)		
Sandwich tern	0.1	(May,Jun)		
Guillemot	0.0	all months		
Razorbill	0.0	all months		
Black guillemot	0.0	all months		
Puffin	0.3	(May,Jun,Jul)		

Table 2.31 Field Metabolic Rates (FMRs) of seabirds (determined using labelled water) as multiples (using mass-specific values) of Basal Metabolic Rate (BMR).

Species	BMR Mass (g)	BMR (kj/d)	FMR Mass (g)	FMR (kj/d)	FMR/BMR	References
Reproducing birds						
Aptenodytes patagonicus	13000	2948	16200	9307	3.1	5
Pygoscelis papua	6290	1605	6100	3900	2.5	1
Pygoscelis adeliae	3868	1039	3868	4002	3.9	2
Eudyptes chrysolophus	3870	747	4250	3084	3.8	1
Diomedea exulans	8130	1756	8305	3288	1.8	1
Diomedea immutabilis	3103	637	3064	2072	3.3	1
Diomedea chrysostoma	3665	718	3665	1729	2.4	2
Macronectes giganteus	4044	976	4044	4443	4.6	2
Fulmarus glacialis	728	313	730	1005	3.2	3
Oceanites oceanicus	36	37	42	157	3.6	1
Oceanodroma leucorhoa	47	43	43	123	3.1	1
Oceanodroma leucorhoa	45	42	45	89	2.1	2
Puffinus pacificus	384	146	384	614	4.2	2
Pelecanoides georgicus	119	122	109	464	4.2	1
Pelecanoides urinatrix	132	126	136	557	4.3	1
Sula bassana	3030	701	3210	4865	6.6	1
Sula bassana	2574	1115	3244	5867	4.2	3
Sula capensis	2660	731	2580	3380	4.7	7
Stercorarius parasiticus	351	198	351	752	3.8	3
Rissa tridactyla	386	322	386	794	2.6	2
Sterna hirundo	125	93	128	356	3.8	8
Sterna fuscata	148	69	184	340	4.0	1
Anous stolidus	195	95	195	352	3.7	2
Aethia pusilla	83	115	84	358	3.1	1
Uria aalge	940	348	940	1789	5.1	2
Uria lomvia	834	525	834	1420	2.7	2
Alle alle	152	178	164	696	3.9	6

Mean FMR/BMR (all seabirds) n=27 studies 3.64
Mean FMR/BMR (excluding albatrosses) n=24 studies 3.78
Mean FMR/BMR (regular N. Sea species only) n=6 studies 4.25

Non-reproducing seabirds

Species	BMR Mass (g)	BMR (kj/d)	FMR Mass (g)	FMR (kj/d)	FMR/BMR	References
Eudyptula minor	900	384	1076	986	2.2	1

References: 1=Koteja, 1991 (review, Appendix), 2, Birt-Friesen et al., 1989 (Table 1 review), 3=Bryant and Furness unpubl., 4=Bennett and Harvey, 1987, 5=Kooyman et al., 1992, 6=Gabrielsen et al., 1991, 7=Adams et al., 199x, Klaassen et al., 1992.

Table 2.32 Estimated and measured BMRs of seabirds. Mean body mass taken from Cramp & Simmons (19xx), Furness (1983), Furness (1990). BMR in column 2 is from the allometric equation dervied by Bryant & Furness (submitted) for North Sea seabirds BMR=1.986W0.796

Species	Body mass (g)	BMR (kj/d) (Bryant & Furness)	Measured BMR, mass-specific BMR and reference	
Fulmar	810	410		0.506
			313, 728g (1)	0.430
			314, 651g (2)	0.482
Gannet	3000	1164		0.388
			1115,2574g (1)	0.433
			742,3210g (3)	0.231
Cormorant	2200	909		0.413
Shag	1810	778		0.430
			762,1619g (1)	0.471
Great skua	1400	634		0.453
			543,1159g (1)	0.469
B hdd gull	250	161		0.644
			188, 252g (7)	0.746
			177, 285g (8)	0.621
Common gull	380	225		0.592
			201, 428g (8)	0.470
LB-b gull	800	406		0.508
Herring gull	900	446		0.496
			433, 924g (1)	0.469
			415,1000g (4)	0.415
			349,1115g (9)	0.313
Gb-b gull	1600	705		0.441
Kittiwake	390	229		0.587
			233, 304g (1)	0.766
			289, 365g (2)	0.792
			322, 386g (3)	0.834
Arctic tern	100	78		0.780
			79, 85g (5)	0.929
Common tern	125	93		0.744
Sandwich tern	235	153		0.651
Guillemot	980	478		0.488
			386, 771g (1)	0.501
			588, 956g (6)	0.615
			348, 940g (3)	0.370
Razorbill	620	332		0.535
			307, 589g (1)	0.521
Black guillemot	410	239		0.583
			262, 342g (2)	0.766
Puffin	390	229		0.587
			218, 329g (1)	0.663

References: 1=Bryant & Furness (submitted), 2=Gabrielsen et al. (1988), 3=Birt-Friesen et al. (1989), 4=Bennett & Harvey (1988), 5=Klaassen et al. (1989), 6=Johnson & West (1975), 7=Davydov (1972), 8=Gavrilov (1985), 9=Lustick et al. 1978.

Table 2.33 Energy requirements (kJ x 10^9) of 18 seabird species in six sections of the North Sea.

ICES IVa (west)	January	February	March	April	May	June	July	August	September	October	November	December	Total
Fulmar	25.419	36.562	50.616	46.625	169.786	37.654	75.641	28.175	44.731	48.824	44.351	14.776	623.16
Gannet	4.889	5.101	8.808	11.167	12.119	8.095	15.524	13.028	7.260	6.781	4.291	0.936	98.00
Cormorant	0.306	0.276	0.306	0.296	0.477	0.461	0.477	0.306	0.296	0.306	0.296	0.306	4.11
Shag	2.379	2.149	2.379	2.302	3.712	3.592	3.712	2.379	2.302	2.379	2.302	2.379	31.97
Great skua	0.000	0.000	0.000	0.702	3.150	2.596	3.890	1.521	1.784	0.389	0.044	0.000	14.08
Black-headed gull	0.000	0.000	0.014	0.038	0.121	0.104	0.128	0.031	0.006	0.000	0.000	0.000	0.44
Common gull	0.071	0.033	0.145	0.189	0.793	0.673	0.853	0.252	0.045	0.039	0.030	0.094	3.22
Lesser black-backed gull	0.386	0.000	0.018	0.940	0.761	1.679	1.463	0.128	0.062	12.292	0.019	0.000	17.75
Herring gull	0.961	4.144	13.953	7.261	7.350	7.054	6.694	3.648	1.145	34.408	15.053	15.581	117.25
Great black-backed gull	6.702	7.073	10.660	16.609	5.263	3.185	3.142	1.511	5.523	12.592	4.932	4.824	82.02
Kittiwake	7.764	34.386	9.801	13.057	19.497	14.703	17.234	6.698	6.218	8.356	9.086	1.599	148.40
Arctic tern	0.000	0.000	0.000	0.000	0.772	0.747	0.450	0.090	0.000	0.000	0.000	0.000	2.06
Common tern	0.000	0.000	0.000	0.000	0.019	0.018	0.011	0.002	0.000	0.000	0.000	0.000	0.05
Sandwich tern	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.00
Guillemot	15.550	15.984	35.068	46.271	89.993	102.743	44.601	47.785	42.334	15.353	14.130	8.413	478.22
Razorbill	0.932	2.471	3.560	5.899	6.682	6.986	4.532	10.732	7.904	2.323	1.357	1.859	55.24
Black guillemot	0.514	0.464	0.514	0.497	0.801	0.775	0.801	0.514	0.497	0.514	0.497	0.514	6.90
Puffin	0.470	7.166	0.916	4.059	9.858	12.313	12.765	5.650	0.723	0.022	0.540	0.337	54.82

cont'd.

Table 2.33 (continued)

ICES IVa (east)	January	February	March	April	May	June	July	August	September	October	November	December	
Fulmar	3.289	6.609	13.031	3.103	11.992	14.398	8.657	55.791	83.859	10.154	12.730	0.699	224.31
Gannet	1.284	0.843	5.835	4.179	0.728	3.348	1.092	2.185	1.355	3.268	1.242	0.311	25.67
Cormorant	0.004	0.003	0.004	0.004	0.006	0.006	0.006	0.004	0.004	0.004	0.004	0.004	0.05
Shag	0.310	0.280	0.310	0.300	0.483	0.467	0.483	0.310	0.300	0.310	0.300	0.310	4.16
Great skua	0.000	0.057	0.763	0.246	0.100	0.480	0.199	0.699	0.123	0.000	0.246	0.000	2.91
Black-headed gull	0.000	0.044	0.153	0.358	1.214	1.108	1.077	0.306	0.059	0.000	0.062	0.000	4.38
Common gull	1.173	0.265	0.544	0.529	2.168	1.817	2.598	0.730	0.229	0.000	0.044	0.000	10.09
Lesser black-backed gull	0.000	0.331	0.488	0.713	2.348	2.609	2.794	1.440	0.736	0.173	0.000	0.000	11.63
Herring gull	3.220	2.686	0.961	1.352	6.004	2.835	3.139	1.054	2.542	2.133	1.082	1.833	28.84
Great black-backed gull	0.000	1.244	0.880	1.379	3.337	1.906	2.283	3.603	11.161	0.075	0.410	0.424	26.70
Kittiwake	2.210	1.385	0.081	0.091	1.314	0.475	0.229	0.311	2.029	0.069	1.200	1.240	10.63
Arctic tern	0.000	0.000	0.000	0.000	0.119	0.115	0.069	0.014	0.000	0.000	0.000	0.000	0.32
Common tern	0.000	0.000	0.000	0.000	0.655	0.634	0.382	0.076	0.000	0.000	0.000	0.000	1.75
Sandwich tern	0.000	0.000	0.000	0.000	0.041	0.039	0.037	0.005	0.000	0.000	0.000	0.000	0.12
Guillemot	4.102	22.570	2.999	2.019	19.871	0.473	9.307	4.223	6.568	2.065	27.438	7.366	109.00
Razorbill	0.001	0.002	0.005	0.010	0.016	0.016	0.072	0.000	0.000	0.000	0.000	0.000	0.12
Black guillemot	0.071	0.064	0.071	0.069	0.111	0.108	0.111	0.071	0.069	0.071	0.069	0.071	0.96
Puffin	0.000	2.325	0.397	0.283	1.107	1.188	1.383	0.302	0.000	0.000	0.043	0.000	7.03

cont'd.

Table 2.33 (continued)

ICES IVb (west)	January	February	March	April	May	June	July	August	September	October	November	December	
Fulmar	7.395	3.364	1.387	2.066	1.990	3.553	7.422	20.030	14.670	11.383	2.014	0.926	76.20
Gannet	1.676	6.803	2.325	8.211	10.145	20.510	7.731	13.444	9.245	5.435	1.705	0.480	87.71
Cormorant	0.145	0.131	0.145	0.140	0.226	0.219	0.226	0.145	0.140	0.145	0.140	0.145	1.95
Shag	0.805	0.727	0.805	0.779	1.256	1.215	1.256	0.805	0.779	0.805	0.779	0.805	10.82
Great skua	0.000	0.000	0.000	0.029	0.000	0.000	0.175	0.399	0.639	0.370	0.046	0.093	1.75
Black-headed gull	0.000	0.078	0.066	0.128	0.496	0.594	0.676	0.227	0.062	0.088	0.000	0.000	2.41
Common gull	0.332	0.732	0.149	0.050	0.054	0.053	0.081	0.184	0.041	0.226	0.032	0.685	2.62
Lesser black-backed gull	0.005	0.000	0.000	0.710	0.274	0.817	0.245	7.240	0.202	0.471	0.089	0.000	10.05
Herring gull	28.618	23.619	3.386	3.238	4.320	7.130	4.315	6.867	1.104	1.518	1.348	2.992	88.45
Great black-backed gull	8.851	11.894	0.181	1.395	0.124	0.295	0.095	19.127	6.516	10.095	3.175	6.648	68.40
Kittiwake	2.177	3.301	4.624	7.884	12.429	13.377	13.467	17.346	5.354	4.957	1.638	1.279	87.83
Arctic tern	0.000	0.000	0.000	0.000	0.074	0.071	0.043	0.009	0.000	0.000	0.000	0.000	0.20
Common tern	0.000	0.000	0.000	0.000	0.028	0.028	0.017	0.003	0.000	0.000	0.000	0.000	0.07
Sandwich tern	0.000	0.000	0.000	0.000	0.151	0.146	0.138	0.018	0.000	0.000	0.000	0.000	0.45
Guillemot	6.276	12.968	10.600	13.738	25.681	49.757	43.213	30.500	30.904	20.513	20.613	8.249	273.01
Razorbill	0.404	0.450	1.154	0.748	1.720	3.184	3.748	5.114	3.609	4.776	4.300	0.486	29.69
Black guillemot	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.00
Puffin	0.220	3.041	1.218	1.968	4.581	10.989	6.139	2.557	1.286	0.214	1.068	0.563	33.84

cont'd.

Table 2.33 (continued)

ICES IVb (central)	January	February	March	April	May	June	July	August	September	October	November	December	
Fulmar	7.478	7.890	6.145	3.193	6.954	4.050	9.684	22.984	17.762	16.551	9.288	3.947	115.92
Gannet	1.603	4.526	4.439	0.731	0.799	1.967	2.932	4.262	4.961	15.140	3.208	1.168	45.73
Cormorant	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.00
Shag	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.00
Great skua	0.037	0.018	0.000	0.013	0.017	0.021	0.291	0.383	0.481	0.276	0.049	0.000	1.58
Black-headed gull	0.000	0.010	0.115	0.034	0.035	0.001	0.088	0.045	0.030	0.018	0.047	0.016	0.44
Common gull	0.660	0.166	0.140	0.327	0.028	0.359	0.300	0.061	0.044	0.100	0.162	0.095	2.44
Lesser black-backed gull	0.000	0.000	0.186	1.079	1.489	0.622	1.249	0.284	0.074	0.000	0.078	0.000	5.06
Herring gull	5.314	3.921	1.239	0.486	0.243	1.759	0.082	0.167	0.352	0.273	4.582	4.916	23.33
Great black-backed gull	8.323	3.476	2.492	0.620	0.177	0.115	0.199	0.432	3.210	20.797	10.214	26.861	76.92
Kittiwake	2.455	7.286	2.435	2.110	4.471	1.192	1.957	1.162	0.967	8.423	4.167	1.811	38.43
Arctic tern	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.00
Common tern	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.00
Sandwich tern	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.00
Guillemot	5.304	11.245	5.568	5.882	2.632	1.207	8.159	9.946	7.595	20.818	21.410	6.017	105.78
Razorbill	0.301	0.601	0.604	0.751	0.323	0.021	0.067	0.133	0.548	2.303	1.299	0.748	7.70
Black guillemot	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.00
Puffin	0.832	2.502	0.491	0.340	1.246	0.200	0.034	0.140	0.088	0.257	0.480	0.797	7.41

cont'd.

Table 2.33 (continued)

ICES IVb (east)	January	February	March	April	May	June	July	August	September	October	November	December	
Fulmar	1.404	1.315	0.838	0.979	1.961	5.256	4.859	10.683	7.377	6.694	3.322	0.315	45.00
Gannet	0.143	0.056	0.050	0.349	0.297	0.214	0.569	0.710	0.613	1.431	0.233	0.063	4.73
Cormorant	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.00
Shag	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.00
Great skua	0.014	0.012	0.000	0.000	0.000	0.036	0.040	0.144	0.042	0.036	0.008	0.000	0.33
Black-headed gull	0.012	0.013	0.271	0.668	1.783	1.649	1.767	0.471	0.163	0.160	0.056	1.315	8.33
Common gull	1.164	1.874	0.318	2.555	0.708	0.315	0.867	0.132	0.183	0.393	0.947	2.005	11.46
Lesser black-backed gull	0.000	0.011	0.645	2.055	2.107	2.215	3.017	1.296	0.790	0.146	0.019	0.000	12.30
Herring gull	5.362	2.502	3.757	8.711	9.794	9.740	11.694	2.994	3.859	2.667	3.541	5.236	69.86
Great black-backed gull	1.914	3.473	2.263	1.687	0.637	0.737	1.000	1.387	2.210	1.692	1.570	0.335	18.91
Kittiwake	1.164	1.083	3.521	0.330	0.399	0.473	0.385	0.272	0.230	0.614	1.483	0.947	10.90
Arctic tern	0.000	0.000	0.000	0.000	0.065	0.063	0.038	0.008	0.000	0.000	0.000	0.000	0.17
Common tern	0.000	0.000	0.000	0.000	0.237	0.229	0.138	0.028	0.000	0.000	0.000	0.000	0.63
Sandwich tern	0.000	0.000	0.000	0.000	0.397	0.385	0.361	0.046	0.000	0.000	0.000	0.000	1.19
Guillemot	5.523	3.246	3.034	1.640	0.735	3.150	0.860	2.476	1.112	4.707	8.536	1.350	36.37
Razorbill	0.638	1.151	0.434	0.001	0.010	0.001	0.000	0.044	0.017	0.544	1.022	0.091	3.95
Black guillemot	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.00
Puffin	0.067	2.938	0.115	0.016	0.000	0.000	0.000	0.000	0.000	0.016	0.049	0.000	3.20

cont'd.

Table 2.33 (continued)

ICES IVc	January	February	March	April	May	June	July	August	September	October	November	December	
Fulmar	0.718	0.524	1.046	0.707	1.244	0.858	1.149	1.419	1.423	0.296	0.285	0.631	10.30
Gannet	0.286	0.371	0.813	0.447	0.149	0.343	0.414	2.122	0.914	3.073	1.500	0.948	11.38
Cormorant	0.004	0.003	0.004	0.004	0.006	0.006	0.006	0.004	0.004	0.004	0.004	0.004	0.05
Shag	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.00
Great skua	0.005	0.000	0.003	0.011	0.031	0.029	0.015	0.076	0.081	0.145	0.004	0.021	0.42
Black-headed gull	17.802	0.152	0.233	0.294	0.633	0.862	0.636	0.217	0.089	0.674	0.672	1.103	23.37
Common gull	2.718	1.050	1.451	0.822	0.804	0.693	0.689	0.389	0.077	2.423	1.852	1.374	14.34
Lesser black-backed gull	0.165	0.057	0.710	0.447	3.442	1.106	1.871	0.462	1.611	1.573	1.028	0.246	12.72
Herring gull	17.401	7.798	3.873	11.003	3.407	41.692	2.756	6.265	1.181	13.781	5.110	9.397	123.67
Great black-backed gull	6.949	3.420	1.603	0.480	0.303	0.208	0.097	0.197	2.299	2.825	2.384	7.588	28.35
Kittiwake	1.717	1.736	0.650	0.618	0.913	0.313	0.424	0.313	0.164	1.184	0.922	1.860	10.81
Arctic tern	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.00
Common tern	0.000	0.000	0.000	0.000	0.072	0.070	0.042	0.008	0.000	0.000	0.000	0.000	0.19
Sandwich tern	0.000	0.000	0.000	0.000	0.207	0.200	0.188	0.024	0.000	0.000	0.000	0.000	0.62
Guillemot	2.785	1.832	2.229	0.655	0.978	0.041	0.403	0.488	5.367	3.076	2.003	2.614	22.47
Razorbill	0.213	0.249	0.583	0.071	0.086	0.000	0.000	0.000	0.596	0.550	0.208	0.283	2.84
Black guillemot	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.00
Puffin	0.005	1.317	0.005	0.024	0.000	0.000	0.000	0.245	0.000	0.000	0.000	0.121	1.72

Table 2.34 Annual energy requirements (KJ x 10^9) of 18 species of seabirds in the North Sea.

Annual energy requirements	Total	% ages
Fulmar	1094.90	28.1
Gannet	273.22	7.0
Cormorant	6.15	0.2
Shag	46.94	1.2
Great skua	21.08	0.5
Black-headed gull	39.37	1.0
Common gull	44.18	1.1
Lesser black-backed gull	69.52	1.8
Herring gull	451.40	11.6
Great black-backed gull	301.29	7.7
Kittiwake	307.01	7.9
Arctic tern	2.75	0.1
Common tern	2.70	0.1
Sandwich tern	2.38	0.1
Guillemot	1024.86	26.3
Razorbill	99.54	2.6
Black guillemot	7.86	0.2
Puffin	108.02	2.8
	3903.17	

Table 2.35 7 types of food consumed by nine species of seabird by quarter in six areas of the North Sea.

SANDEEL CONSUMPTION

ICES IVa (west) sandeel	First	Second	Third	Fourth	Totals
Fulmar	0	11723	4790	0	16513
Gannet	867	1448	1652	554	4522
Shag	1062	1447	1291	1086	4917
Herring gull	0	0	0	0	0
Great black-backed gull	0	771	143	0	914
Kittiwake	0	5260	3681	0	8941
Guillemot	6994	36759	16358	1923	62034
Razorbill	862	3009	3077	511	7459
Puffin	395	3256	2582	41	6275
Total	10180	63704	33574	4116	111574

ICES IVa (east) sandeel	First	Second	Third	Fourth	Totals
Fulmar	0	1218	2974	0	4191
Gannet	367	381	214	222	1184
Shag	138	192	168	141	640
Herring gull	0	0	0	0	0
Great black-backed gull	0	204	181	0	385
Kittiwake	0	165	50	0	215
Guillemot	2010	2752	2069	2268	9098
Razorbill	1	4	8	0	13
Puffin	209	198	130	3	540
Total	2726	5114	5792	2635	16267

ICES IVb (west) sandeel	First	Second	Third	Fourth	Totals
Fulmar	0	256	1267	0	1522
Gannet	499	1793	1404	352	4047
Shag	359	500	437	367	1664
Herring gull	0	0	0	0	0
Great black-backed gull	0	56	591	0	647
Kittiwake	0	2381	2843	0	5225
Guillemot	2448	10972	10971	3037	27469
Razorbill	203	608	1287	882	2981
Puffin	344	1349	768	142	2603
Total	3894	17915	19567	4781	46157

Table 2.35 (Cont'd)

ICES IVb (centre) sandeel	First	Second	Third	Fourth	Totals
Fulmar	0	508	1507	0	2015
Gannet	488	161	561	900	2110
Shag	0	0	0	0	0
Herring gull	0	0	0	0	0
Great black-backed gull	0	28	19	0	47
Kittiwake	0	523	288	0	810
Guillemot	1703	1196	2695	2968	8562
Razorbill	148	118	72	401	740
Puffin	294	137	20	118	570
Total	2633	2671	5163	4388	14854

ICES IVb (east) sandeel	First	Second	Third	Fourth	Totals
Fulmar	0	333	717	0	1050
Gannet	12	40	87	80	218
Shag	0	0	0	0	0
Herring gull	0	0	0	0	0
Great black-backed gull	0	94	73	0	168
Kittiwake	0	81	61	0	141
Guillemot	913	680	479	898	2969
Razorbill	212	1	6	153	372
Puffin	240	1	0	5	246
Total	1376	1230	1424	1135	5165

ICES IVc sandeel	First	Second	Third	Fourth	Totals
Fulmar	0	97	118	0	215
Gannet	68	43	159	255	525
Shag	0	0	0	0	0
Herring gull	0	0	0	0	0
Great black-backed gull	0	30	9	0	40
Kittiwake	0	113	68	0	181
Guillemot	558	206	440	473	1677
Razorbill	105	17	55	96	273
Puffin	102	2	19	9	132
Total	834	509	868	833	3044

Table 2.35 (Cont'd)

SPRAT AND SMALL HERRING CONSUMPTION

ICES IVa (west) sprat	First	Second	Third	Fourth	Totals
Fulmar	0	0	0	0	0
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	0	0	0	0	0
Great black-backed gull	0	0	0	0	0
Kittiwake	1997	502	239	732	3471
Guillemot	1600	0	2149	1923	5673
Razorbill	209	0	486	341	1036
Puffin	395	187	33	41	657
Total	4202	689	2907	3038	10836

ICES IVa (east) sprat	First	Second	Third	Fourth	Totals
Fulmar	0	0	0	0	0
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	0	0	0	0	0
Great black-backed gull	0	0	0	0	0
Kittiwake	141	59	95	96	391
Guillemot	1323	688	719	1701	4431
Razorbill	0	2	3	0	6
Puffin	126	119	78	2	324
Total	1590	867	895	1800	5152

ICES IVb (west) sprat	First	Second	Third	Fourth	Totals
Fulmar	0	0	0	0	0
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	0	0	0	0	0
Great black-backed gull	0	0	0	0	0
Kittiwake	388	1097	1154	303	2942
Guillemot	1214	2743	3693	2278	9928
Razorbill	106	261	631	588	1586
Puffin	207	809	461	85	1562
Total	1915	4910	5398	3254	16017

Table 2.35 (Cont'd)

ICES IVb (centre) sprat	First	Second	Third	Fourth	Totals
Fulmar	0	0	0	0	0
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	0	0	0	0	0
Great black-backed gull	0	0	0	0	0
Kittiwake	468	255	133	554	1410
Guillemot	935	299	907	2226	4367
Razorbill	83	51	43	268	444
Puffin	176	82	12	71	342
Total	1663	687	1096	3118	6564

ICES IVb (east) sprat	First	Second	Third	Fourth	Totals
Fulmar	0	0	0	0	0
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	0	0	0	0	0
Great black-backed gull	0	0	0	0	0
Kittiwake	222	40	29	117	407
Guillemot	498	170	154	673	1495
Razorbill	130	1	3	102	236
Puffin	144	1	0	3	148
Total	994	211	186	895	2286

ICES IVc sprat	First	Second	Third	Fourth	Totals
Fulmar	0	0	0	0	0
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	0	0	0	0	0
Great black-backed gull	0	0	0	0	0
Kittiwake	158	61	29	152	401
Guillemot	282	52	275	355	963
Razorbill	55	7	37	64	163
Puffin	61	1	11	6	79
Total	556	121	352	577	1606

Table 2.35 (Cont'd)

LIVE GADID CONSUMPTION

ICES IVa (west) live gadids	First	Second	Third	Fourth	Totals
Fulmar	0	0	0	0	0
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	0	0	0	0	0
Great black-backed gull	0	0	0	0	0
Kittiwake	0	0	0	0	0
Guillemot	1600	0	2149	1923	5673
Razorbill	0	0	0	0	0
Puffin	395	403	317	41	1156
Total	1995	403	2465	1965	6829

ICES IVa (east) live gadids	First	Second	Third	Fourth	Totals
Fulmar	0	0	0	0	0
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	0	0	0	0	0
Great black-backed gull	0	0	0	0	0
Kittiwake	0	0	0	0	0
Guillemot	1231	0	303	1701	3235
Razorbill	0	0	0	0	0
Puffin	84	79	52	1	216
Total	1314	79	355	1702	3451

ICES IVb (west) live gadids	First	Second	Third	Fourth	Totals
Fulmar	0	0	0	0	0
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	0	0	0	0	0
Great black-backed gull	0	0	0	0	0
Kittiwake	0	0	0	0	0
Guillemot	888	0	1426	2278	4592
Razorbill	0	0	0	0	0
Puffin	138	539	307	57	1041
Total	1026	539	1733	2335	5633

Table 2.35 (Cont'd)

ICES IVb (centre) live gadids	First	Second	Third	Fourth	Totals
Fulmar	0	0	0	0	0
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	0	0	0	0	0
Great black-backed gull	0	0	0	0	0
Kittiwake	0	0	0	0	0
Guillemot	764	0	350	2226	3340
Razorbill	0	0	0	0	0
Puffin	118	55	8	47	228
Total	881	55	359	2273	3568

ICES IVb (east) live gadids	First	Second	Third	Fourth	Totals
Fulmar	0	0	0	0	0
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	0	0	0	0	0
Great black-backed gull	0	0	0	0	0
Kittiwake	0	0	0	0	0
Guillemot	405	0	51	673	1129
Razorbill	0	0	0	0	0
Puffin	96	0	0	2	98
Total	501	0	51	675	1228

ICES IVc live gadids	First	Second	Third	Fourth	Totals
Fulmar	0	0	0	0	0
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	0	0	0	0	0
Great black-backed gull	0	0	0	0	0
Kittiwake	0	0	0	0	0
Guillemot	213	0	248	355	816
Razorbill	0	0	0	0	0
Puffin	41	1	8	4	53
Total	254	1	255	359	868

Table 2.35 (Cont'd)

MACKEREL CONSUMPTION

	First	Second	Third	Fourth	Totals
Gannet (IVa west)	867	1448	1652	554	4522
Gannet (IVa east)	367	381	214	208	1170
Gannet (IVb west)	499	1793	1404	352	4047
Gannet (IVb centre)	488	161	561	900	2110
Gannet (IVb east)	12	40	87	80	218
Gannet (IVc)	68	43	159	255	525
Total	2300	3866	4077	2363	12592

LARGE HERRING CONSUMPTION

	First	Second	Third	Fourth	Totals
Gannet (IVa west)	867	1448	1652	554	4522
Gannet (IVa east)	367	381	214	208	1170
Gannet (IVb west)	499	1793	1404	352	4047
Gannet (IVb centre)	488	161	561	900	2110
Gannet (IVb east)	12	40	87	80	218
Gannet (IVc)	68	43	159	255	525
Total	2300	3866	4077	2349	12592

OFFAL CONSUMPTION

ICES IVa (west) offal	First	Second	Third	Fourth	Totals
Fulmar	8659	13157	8230	8302	38347
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	293	333	177	1000	1803
Great black-backed gull	0	0	0	0	0
Kittiwake	1997	502	239	732	3471
Guillemot	0	0	0	0	0
Razorbill	0	0	0	0	0
Puffin	0	0	0	0	0
Total	10949	13992	8646	10034	43621

Table 2.35 (Cont'd)

ICES IVa (east) offal	First	Second	Third	Fourth	Totals
Fulmar	1763	1456	9422	1813	14455
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	106	157	104	78	444
Great black-backed gull	0	0	0	0	0
Kittiwake	141	3	78	96	319
Guillemot	0	0	0	0	0
Razorbill	0	0	0	0	0
Puffin	0	0	0	0	0
Total	2010	1616	9604	1988	15218

ICES IVb (west) offal	First	Second	Third	Fourth	Totals
Fulmar	934	415	2395	1101	4845
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	855	226	189	90	1360
Great black-backed gull	0	0	0	0	0
Kittiwake	388	303	206	303	1200
Guillemot	0	0	0	0	0
Razorbill	0	0	0	0	0
Puffin	0	0	0	0	0
Total	2178	944	2790	1494	07405

ICES IVb (centre) offal	First	Second	Third	Fourth	Totals
Fulmar	1654	753	2873	2291	7571
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	161	38	9	150	359
Great black-backed gull	0	0	0	0	0
Kittiwake	468	81	37	554	1140
Guillemot	0	0	0	0	0
Razorbill	0	0	0	0	0
Puffin	0	0	0	0	0
Total	2284	873	2920	2995	9070

Table 2.35 (Cont'd)

ICES IVb (east) offal	First	Second	Third	Fourth	Totals
Fulmar	274	408	1284	794	2761
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	179	434	285	176	1074
Great black-backed gull	0	0	0	0	0
Kittiwake	222	13	9	117	360
Guillemot	0	0	0	0	0
Razorbill	0	0	0	0	0
Puffin	0	0	0	0	0
Total	674	855	1578	1088	4195

ICES IVc offal	First	Second	Third	Fourth	Totals
Fulmar	176	151	228	93	648
Gannet	0	0	0	0	0
Shag	0	0	0	0	0
Herring gull	447	863	157	435	1902
Great black-backed gull	0	0	0	0	0
Kittiwake	158	24	6	152	340
Guillemot	0	0	0	0	0
Razorbill	0	0	0	0	0
Puffin	0	0	0	0	0
Total	781	1038	391	681	2891

DISCARD FISH CONSUMPTION

ICES IVa (west) discards	First	Second	Third	Fourth	Totals
Fulmar	4329	11364	6510	4151	26354
Gannet	289	483	551	185	1507
Shag	0	0	0	0	0
Herring gull	879	1000	530	3001	5410
Great black-backed gull	2631	2312	1024	2406	8373
Kittiwake	1997	502	239	732	3471
Guillemot	0	0	0	0	0
Razorbill	0	0	0	0	0
Puffin	0	0	0	0	0
Total	10126	15661	8854	10475	45115

Table 2.35 (Cont'd)

ICES IVa (east) discards	First	Second	Third	Fourth	Totals
Fulmar	882	1337	6198	907	9323
Gannet	122	127	71	74	395
Shag	0	0	0	0	0
Herring gull	317	470	311	233	1331
Great black-backed gull	229	611	1745	98	2682
Kittiwake	141	3	78	96	319
Guillemot	0	0	0	0	0
Razorbill	0	0	0	0	0
Puffin	0	0	0	0	0
Total	1691	2549	8403	1408	14051

ICES IVb (west) discards	First	Second	Third	Fourth	Totals
Fulmar	467	335	1831	551	3184
Gannet	166	598	468	117	1349
Shag	0	0	0	0	0
Herring gull	2566	678	567	270	4081
Great black-backed gull	2253	167	2475	2144	7040
Kittiwake	388	303	206	303	1200
Guillemot	0	0	0	0	0
Razorbill	0	0	0	0	0
Puffin	0	0	0	0	0
Total	5841	2081	5547	3385	16854

ICES IVb (centre) discards	First	Second	Third	Fourth	Totals
Fulmar	827	630	2190	1145	4793
Gannet	163	54	187	300	703
Shag	0	0	0	0	0
Herring gull	483	115	28	451	1077
Great black-backed gull	1539	84	404	6231	8257
Kittiwake	468	81	37	554	1140
Guillemot	0	0	0	0	0
Razorbill	0	0	0	0	0
Puffin	0	0	0	0	0
Total	3480	964	2846	8681	15970

Table 2.35 (Cont'd)

ICES IVb (east) discards	First	Second	Third	Fourth	Totals
Fulmar	137	371	1001	397	1905
Gannet	4	13	29	27	73
Shag	0	0	0	0	0
Herring gull	536	1303	856	528	3223
Great black-backed gull	824	282	458	387	1952
Kittiwake	222	13	9	117	360
Guillemot	0	0	0	0	0
Razorbill	0	0	0	0	0
Puffin	0	0	0	0	0
Total	1722	1982	2353	1456	7513

ICES IVc discards	First	Second	Third	Fourth	Totals
Fulmar	88	124	173	47	432
Gannet	23	14	53	85	175
Shag	0	0	0	0	0
Herring gull	1341	2589	471	1305	5706
Great black-backed gull	1289	91	275	1378	3033
Kittiwake	158	24	6	152	340
Guillemot	0	0	0	0	0
Razorbill	0	0	0	0	0
Puffin	0	0	0	0	0
Total	2899	2842	978	2967	9686

Table 2.36 Annual consumption (tonnes) of main foods taken by seabirds per quarter in six areas of the North Sea. This excludes about one quarter of total food. Other food include zooplankton, terrestrial foods, cephalopods and other seabirds.

January to March	IVa (west)	IVa (east)	IVb (west)	IVb (centre)	IVb (east)	IVc	Totals	%ages
Sandeel	10180	2726	3894	2633	1376	834	21642	26
Sprat/small herring	0	1590	1915	1663	994	61	6223	7
Live gadid	1995	1314	1026	881	501	254	5971	7
Mackerel	867	367	499	488	12	68	2300	3
Large herring	867	367	499	488	12	68	2300	3
Offal	10949	2010	2178	2284	674	781	18876	23
Discards	10126	1691	5841	3480	1722	2899	25758	31
						Total	83069	

April to June	IVa (west)	IVa (east)	IVb (west)	IVb (centre)	IVb (east)	IVc		%ages
Sandeel	63704	5114	17915	2671	1230	509	91142	60
Sprat/small herring	0	867	4910	687	211	1	6676	4
Live gadid	403	79	539	55	0	1	1078	1
Mackerel	1448	381	1793	161	40	43	3866	3
Large herring	1448	381	1793	161	40	43	3866	3
Offal	13992	1616	944	873	855	1038	19318	13
Discards	15661	2549	2081	964	1982	2842	26079	17
						Total	152027	

July to September	IVa (west)	IVa (east)	IVb (west)	IVb (centre)	IVb (east)	IVc		%ages
Sandeel	33574	5792	19567	5163	1424	868	66388	46
Sprat/small herring	0	895	5938	1096	186	11	8126	6
Live gadid	2465	355	1733	359	51	255	5218	4
Mackerel	1652	214	1404	561	87	159	4077	3
Large herring	1652	208	1404	561	87	159	4071	3
Offal	8646	9604	2790	2920	1578	391	25928	18
Discards	8854	8403	5547	2846	2353	978	28980	20
						Total	142789	

October to December	IVa (west)	IVa (east)	IVb (west)	IVb (centre)	IVb (east)	IVc		%ages
Sandeel	4116	2635	4781	4388	1135	833	17888	24
Sprat/small herring	0	1800	3254	3118	895	6	9073	12
Live gadid	1965	1702	2335	2273	675	359	9309	12
Mackerel	554	222	352	900	80	255	2363	3
Large herring	554	208	352	900	80	255	2349	3
Offal	174	187	1494	2995	1088	681	6618	9
Discards	10475	1408	3385	8681	1456	2967	28372	37
						Total	75972	
						Overall	453857	

Table 2.37 Quarterly requirements (tonnes) of major marine foods by all seabirds in the North Sea.

	January to March	April to June	July to September	October to December	Total	%ages of main marine foods	%ages of overall food need
Sandeel	21642	91142	66388	17888	197060	43	33
Sprat/small herring	6223	6676	8126	9073	30098	7	5
Live gadid	5971	1078	5218	9309	21576	5	4
Mackerel	2300	3866	4077	2363	12606	3	2
Large herring	2300	3866	4071	2349	12587	3	2
Offal	18876	19318	25928	6618	70740	16	12
Discards	25758	26079	28980	28372	109189	24	18
Total	83069	152027	142789	75972	453857		76
				Overall food need	600000		

Table 2.38 Diet of the 5 MSVPA predator species in 1981 according to the MSVPA keyrun (Anon. 1987) and diet of North Sea seabirds as estimated in this study.

Prey	Tonnes x 10^3 taken by MSVPA fish predators	% of total mass of prey taken by MSVPA fish	Tonnes x 10^3 taken by seabirds	% of total mass of prey taken by seabirds
Mackerel	-	-	13	2.2
Cod	29	0.4	22	3.7
Whiting	117	1.8		
Haddock	233	3.5		
Norway Pout	812	12.3		
Herring	173	2.6	13	2.2
Sprat	190	2.9	30	5.0
Sandeel	624	9.4	197	32.8
Discards	-	-	109	18.2
Offal	-	-	71	11.8
Other food	4,443	67.1	146	24.3
Total	6,621	100.0	600*	100.1

*Note: This total is derived from estimated energy needs (3.9 x 10^{12}kJ per year) assuming an average calorific value of foods of 6.5 kJ/g.

Table 3.1: Changes in mid-winter numbers of eiders in the Wadden Sea between 1987 and to 1991

Area	Year 1987[a]	 1991
Netherlands	147 300	90 030[b]
Germany		
Niedersachsen	36 580	120 278[c]
Schleswig-Holstein	16 720	54 258[c]
Denmark	45 300	66 911[d]
total	245 900	331 447

[a] Swennen <u>et al.</u> (1989)

[b] Swennen (1991b)

[c] Nehls, unpubl. data

[d] Pihl <u>et al.</u> (1992) (41,907 in 1992)

Table 3.2: Mid-winter numbers (1,000s) of selected species of seaducks (excluding eiders) off the Wadden Sea and in the Baltic Sea * (Durinck <u>et al.</u>, 1993; Pihl <u>et al.</u>, 1992; Skov et al. unpubl. data).

Species	Off the Wadden Sea	Baltic*
Common scoter	200	1,000
Velvet scoter	3	600
Long-tailed duck	0	3,000

* includes Skagerrak and Kattegat

Table 3.3: Numbers of eiders on or near mussel cultures in January 1987 (Swennen et al. 1989), c.f. Fig. 3.1

Wadden Sea area		Total number	Number on or near cultivated mussels	Percentage of eiders near cultivated mussels
Denmark	A	45 300	1 000	2
Germany	B	15 500	6 000	40
Germany	C	6 200	0	0
Germany	D	31 600	14 000	34
Netherlands	E	14 400	0	0
Netherlands	F	132 900	69 900	52
	A-F	245 900	90 600	37

Table 3.4: Estimated average annual food consumption by eiders in the Wadden Sea (Swennen et al., 1989). AFDW = Ash free dry weight.

daily food demand	
AFDW	138 g
molluscs incl. shells	2.5 kg
average no. of eiders	180 000
total food consumption	
AFDW	9×10^6 kg
wet biomass including shell	164×10^6 kg
total consumption of bivalves (wet biomass including shells)	60×10^6 kg

Table 3.5: Estimations of eider food consumption per m^2 and total biomass in the Wadden Sea

average no. of Eiders	179 450	Swennen *et al.* (1989)
km^2	7 590	Swennen *et al.* (1989)
bird-days . km^{-2} x y^{-1}	8 630	Swennen *et al.* (1989)
food consumption (AFDW x y^{-1})		
total	9 x 10^6 kg	Swennen *et al.* (1989)
per m^2	1.19 g	Swennen *et al.* (1989)
average benthic biomass (AFDW x m^{-2})		
Dutch intertidal flats	38 g	Beukema (1989)
Dutch subtidal areas	43 g	Dekker (1989)
% of biomass taken by eiders		
total biomass	3-5 %	
mussels and cockles	12.5%	Nehls (1989)

Table 3.6: Mussel yield (in tonnes) in the German part of the Wadden Sea (means per ten years, Meixner, 1992)

	Schleswig-Holstein	Niedersachsen	total
1941-1950	3 900 t	950 t	4 850 t
1951-1960	6 050 t	1 650 t	7 700 t
1961-1970	4 700 t	3 500 t	8 200 t
1971-1980	7 000 t	4 700 t	11 700 t
1981-1990	17 700 t	8 500 t	26 200 t

Table 3.7: Annual mussel harvest (in 10^6 kg) in the Wadden Sea during the 1980s by the mussel fisheries

Netherlands	40-75	Drinkwaard (1987)
Germany	26	Meixner (1992)
Denmark	20	Dahl (1992)
total	**~ 100**	

Table 4.1 Approximate numbers of seabirds breeding on the Faroe Islands in the 1980s.

Species	**Number of pairs**
Fulmar	600,000
Puffin	550,000
Storm petrel	250,000
Kittiwake	230,000
Common guillemot	175,000
Shearwater	25,000
Others (13 species each < 10.000 pairs)	31,000
Total	1,861,000

Table 4.2 Composition (% by number) of fish brought to puffin chicks, Hornøy, North Norway. N = no. of loads observed.

Year	N	Capelin	Sandeel	Herring	Other
1980	72	76	21	0	0
1981	52	37	63	0	0
1982	49	74	26	0	0
1983	193	76	24	0	0
1989	15	72	1	0	26
1992		20	23	30	27

Table 4.3 Composition (% by number) of fish brought to common guillemot chicks, Hornøy and Syltefjord (1985), North Norway. N = no. of fish observed.

Year	N	Herring	Capelin	Sandeel	Other
1980	46	2	72	20	6
1981	22	0	54	46	0
1982	28	0	61	39	0
1983	1580	0	59	41	0
1985	21	5	33	43	19
1989	190	0	91	6	3
1990	481	8	45	44	0
1991	707	7	47	46	0
1992	149	51	24	26	0

Table 4.4 Composition (% by wet mass) of Kittiwake adult and chick regurgitates, Hornøy and Syltefjord, N. Norway. N = no. of regurgitates.

Year	N	Herring	Capelin	Sandeel	Crustacea	Other
1980	31	0	92	0	8	0
1981	32	0	54	4	41	0
1983	72	0	93	3	0	4
1985[a]	24	25	66	7	0	2
1988	17	0	82	0	7	11
1988[a]	63	0	84	0	3	13
1989[b]	74	0	80	0	12	8
1990	67	34	62	2	2	1
1992	89	26	70	2	0	3

[a] Syltefjord

[b] Syltefjord + Hornøy

Table 4.5 Monitoring counts of common guillemots, kittiwakes and puffins on selected sites on Hornøy, N. Norway, 1980-1993. N=no. of sites counted.

	C.guill. N=16	K'wake N=6	Puffin N=6
1980	967	(1848)*	-
1981	990	(1767)*	530
1982	990	1712	542
1983	1017	2123	540
1985	1006	1583	569
1987	154	1729	564
1988	145	1686	635
1989	146	1822	-
1990	158	1600	734
1991	168	1630	732
1992	195	1557	632
1993	194	1537	689

*Interpolations based on counts on 4 of the 6 sites

Table 5.1 Area comparison between sandeel and sprat fishery landings and seabird consumption. Landings of sandeels for 1984 and 1989 and sprat for 1985 are derived from Anon. (1992). Seabird consumption estimates are from Section 2.

Area	Sandeel Landings (x 1000 t)		Sandeel Consumption by Seabirds (x 1000 t)	Sprat Landings (t) 1985	Sprat Consumption by Seabirds (t)
	1984	1989			
IVa (west)	40.1	21.9	111.6	7,594	0
IVa (east)	32.4	234.9	16.3	24	5,200
IVb (west)	195.6	136.8	46.2	1,829	16,000
IVb (central)	245.0	409.6	14.9	0	6,600
IVb (east)	99.1	189.1	17.6	36,640	2,300
IVc	44.7	26.1	3.0	2,922	900

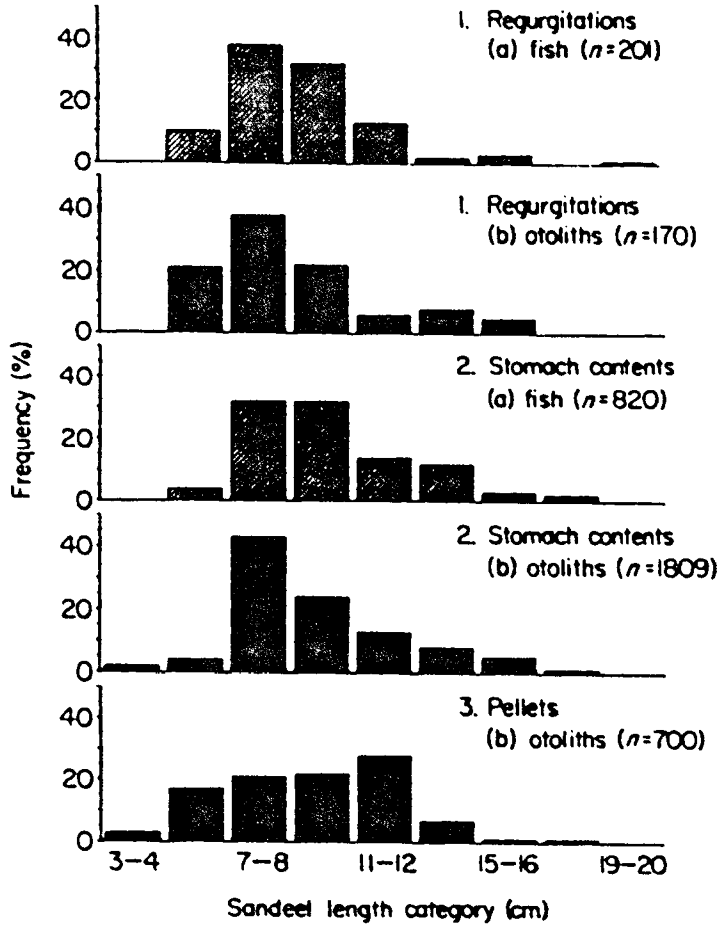


Figure 2.1 The distribution of lengths of sandeels from regurgitations (1) stomach contents (2) and pellets (3) of shags either measured directly (a) or back-calculated from otoliths measurements (b). Sample sizes are shown in parentheses (n). From Harris and Wanless (1993).

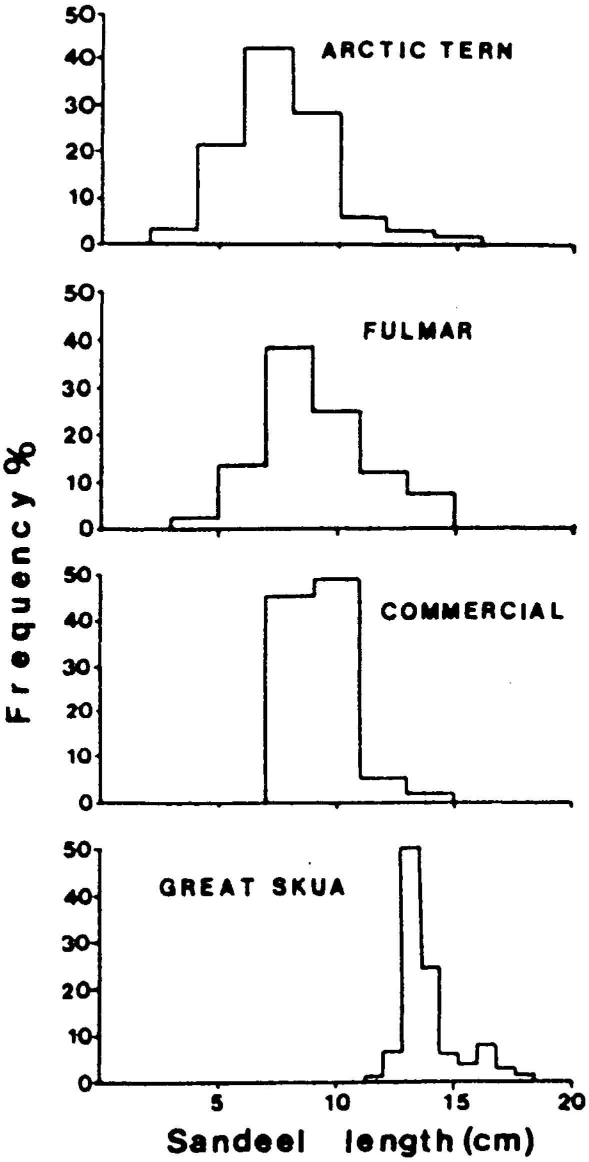


Figure 2.2 Frequency distribution of sandeel size classes reported in the diet of three species of Shetland seabirds compared with a commercial catch: Arctic tern, after Ewins (1985): fulmar, after Fouler and Dye (1987); great skua, after Furness and Hislop (1981).

Figure 2.3 Sub-regions in the North Sea used for this project, as based on ICES fishing areas Divisions IVa-c and IIIa.

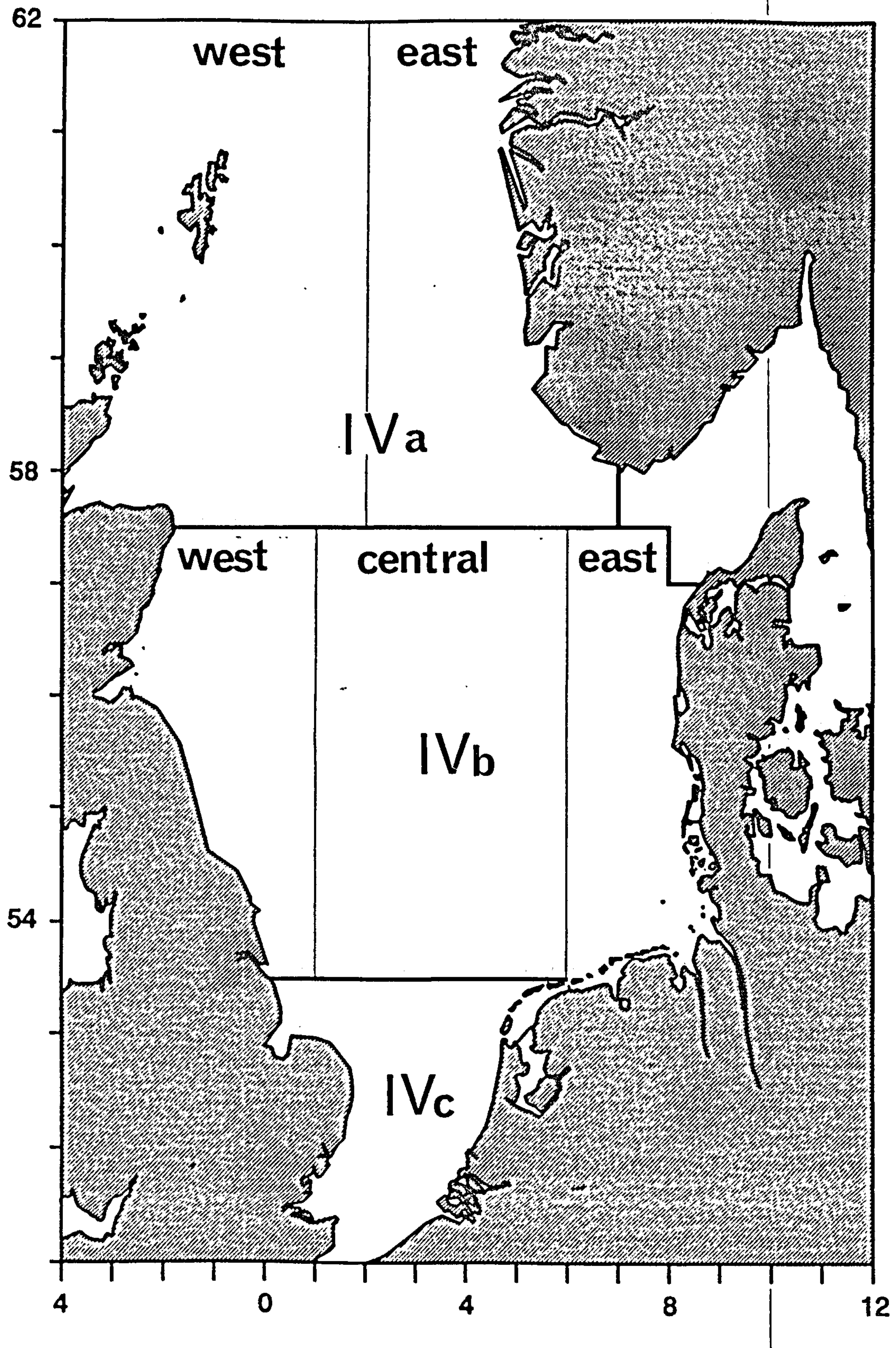


Figure 3.1 The total numbers of eiders counted in the 6 compartments of the Wadden Sea during the survey in January 1987. Swennen *et al.* (1989).

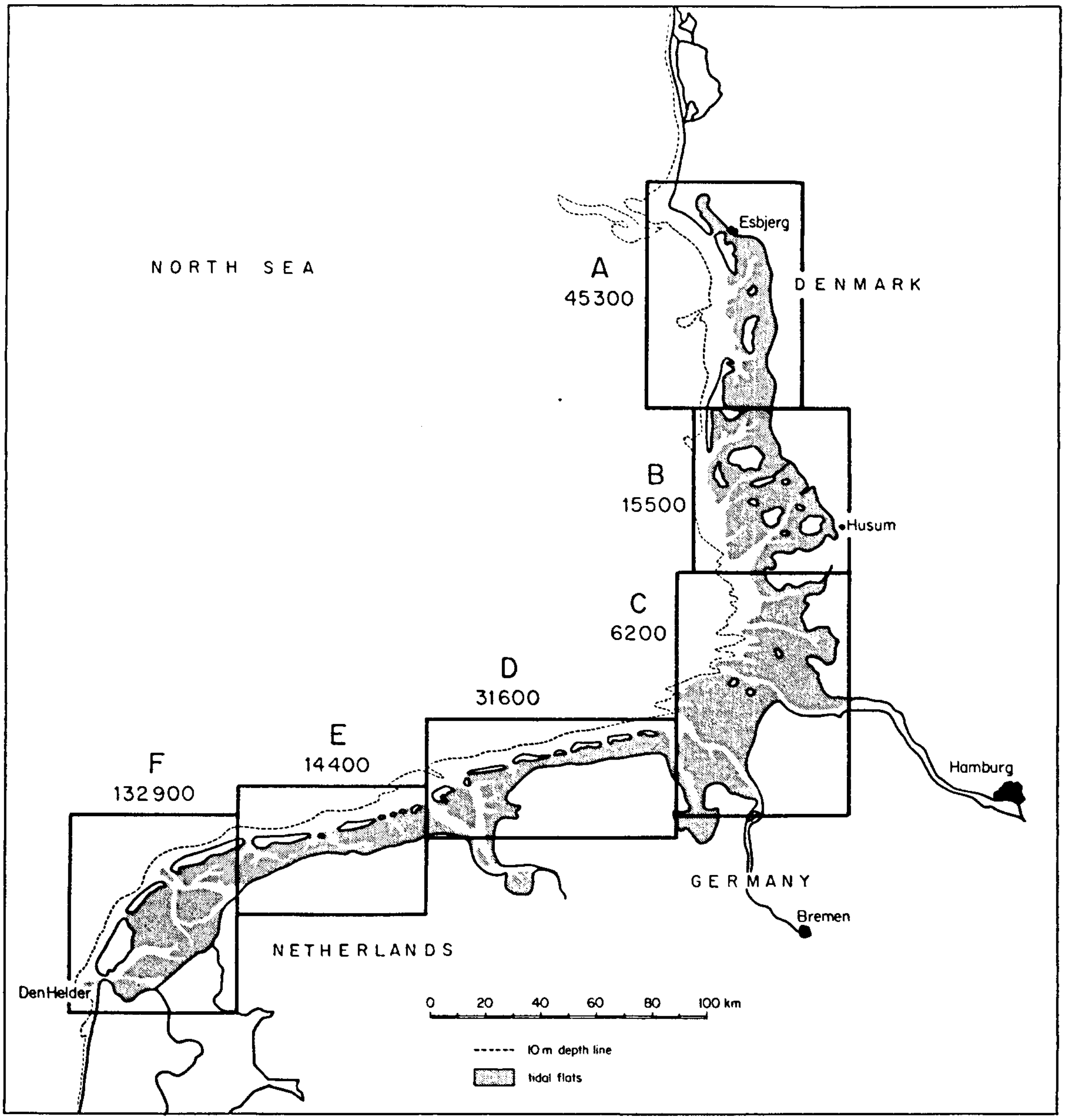
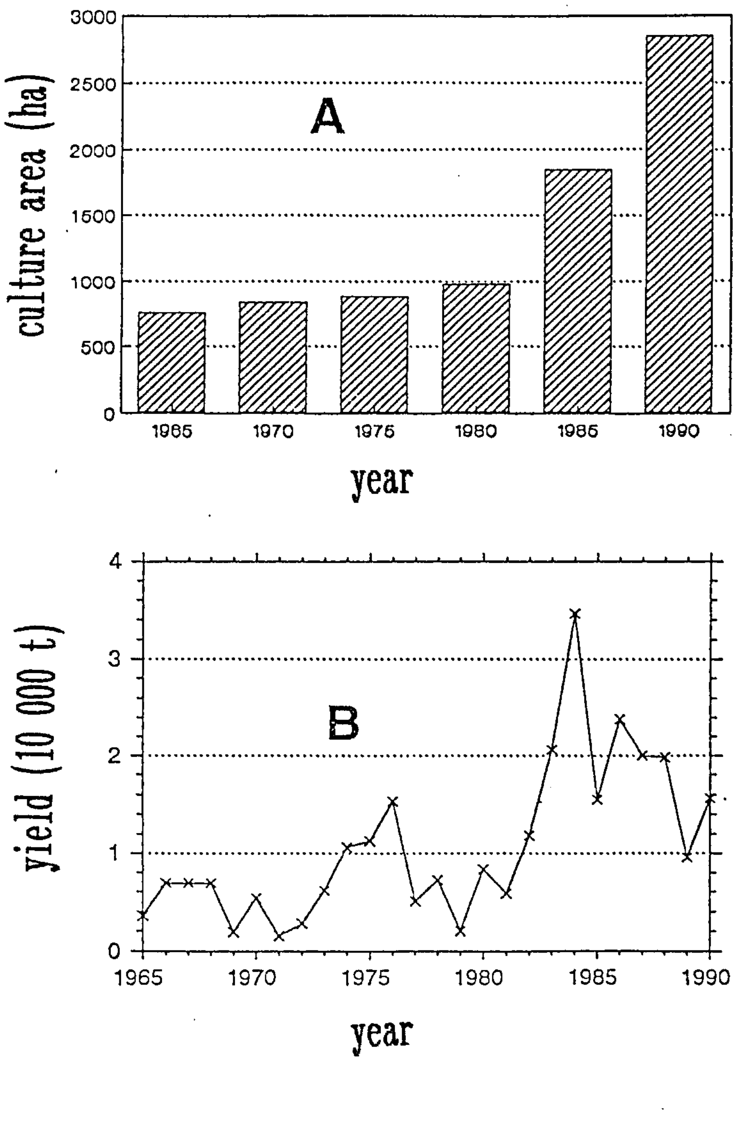


Figure 3.2 Temporal development of mussel culture plot area and mussel yield in the Wadden Sea of Schleswig-Holstein from 1965-1990 (Ruth, 1992).



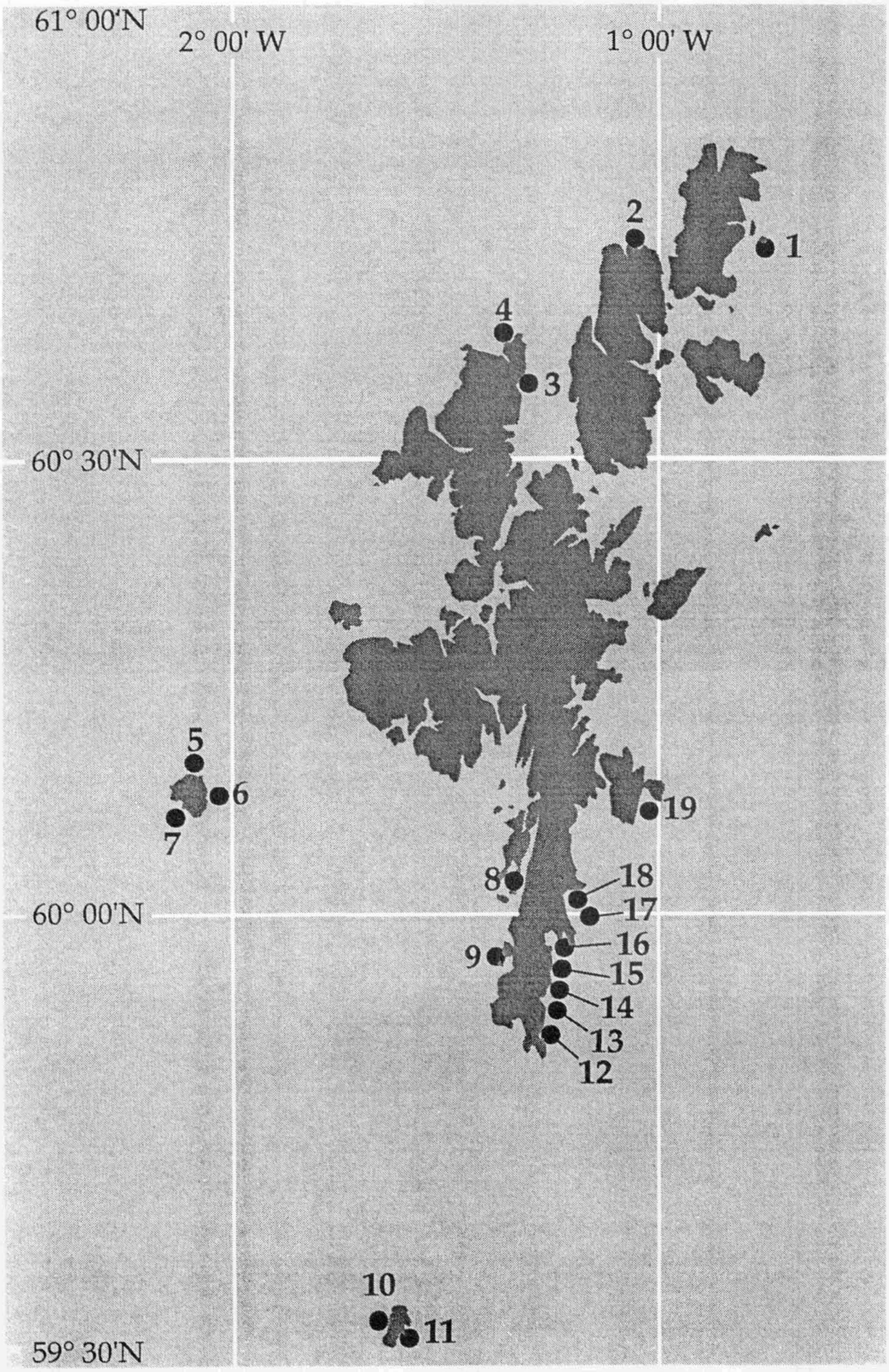
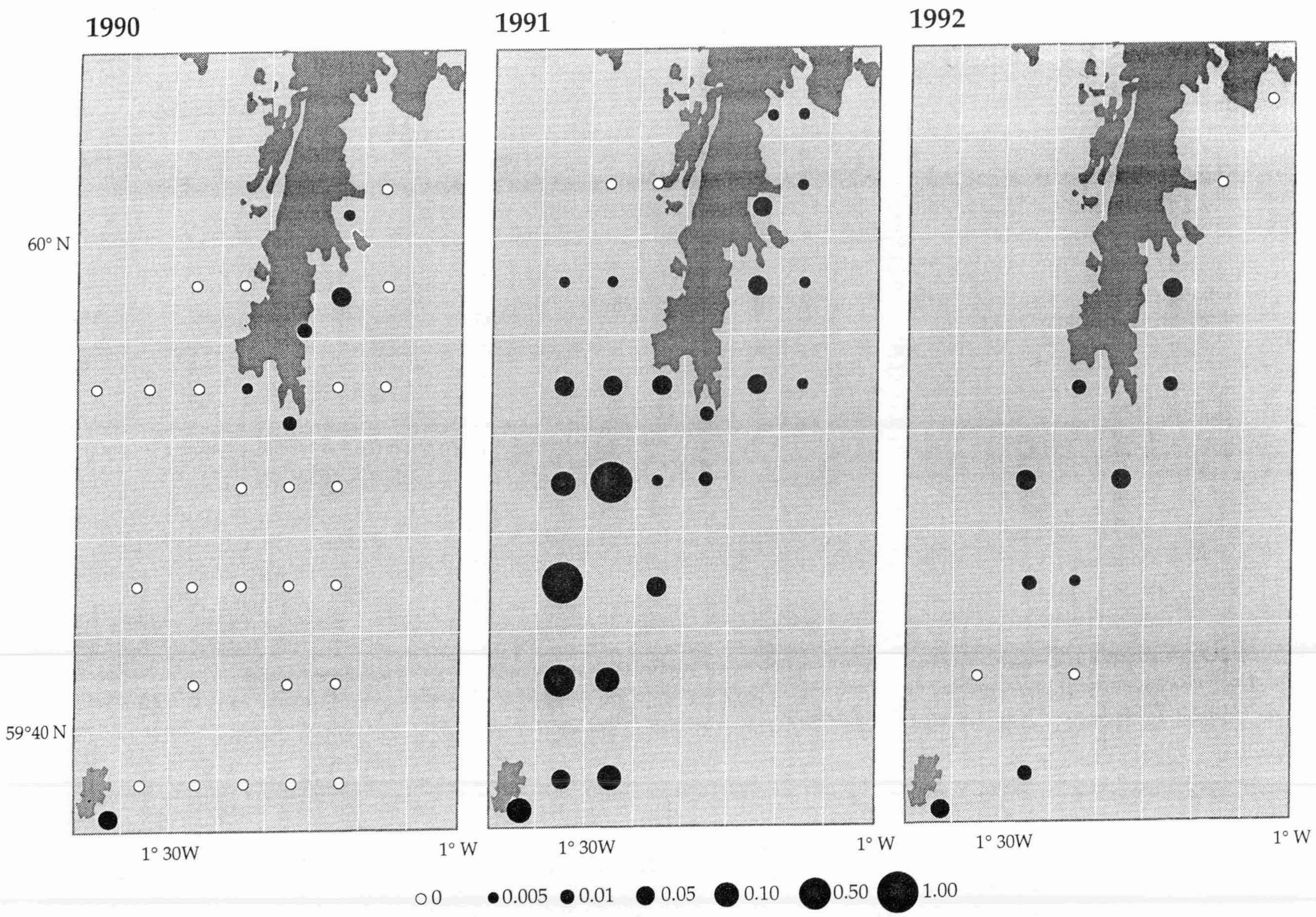


Figure 4.1 Chart showing locations of sandeel fishing grounds around Shetland

1. Balta
2. Breakin
3. Fethaland
4. Sand Voe
5. North Foula
6. Ham o'Foula
7. South Foula
8. Trink (Cliff Sound)
9. Colsay
10. West Fair Isle
11. East Fair Isle
12. Grutness
13. Boddam Voe
14. Clumlie Baas
15. Sandwick
16. Mousa Sound
17. Braeside
18. Helliness
19. South Sands

Figure 4.2 Comparison of sandeel density distribution around Shetland and Fair Isle based on acoustic surveys June-July, 1990, 1991 and 1992.



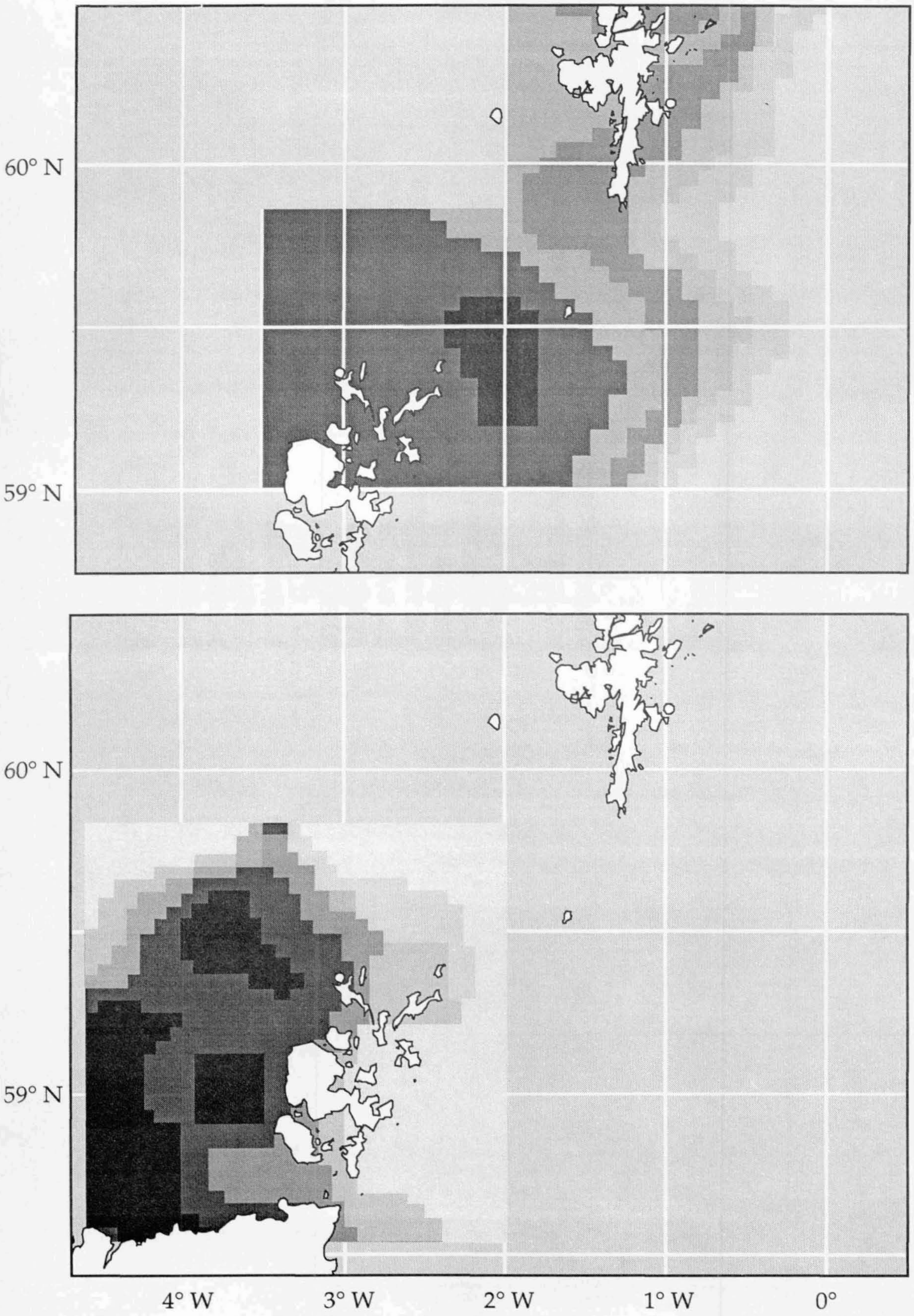


Figure 4.3 Larval sandeel distribution within the Shetland-Orkney regions. Larval density (m^{-2}) shown as logarithmically transformed contour plot of 0-10 d larvae between: a) 25 February - 5 March 1992, b) 18 - 27 March 1992. Contour shade range: >1000, 501-1000, 251-500, 51-250, 0-50.

Figure 4.4 Indices of 0-group sandeel recruitment at Faroe, 1974-1993.

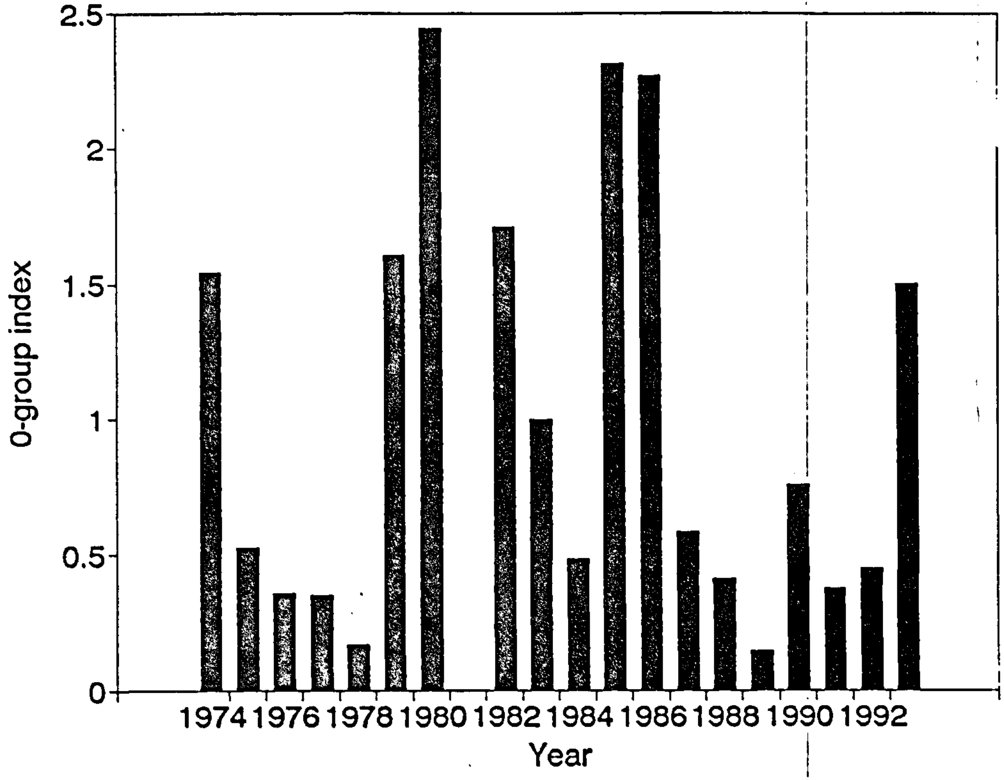


Figure 4.5 Faroese exports of seabird feathers, 1710-1910.

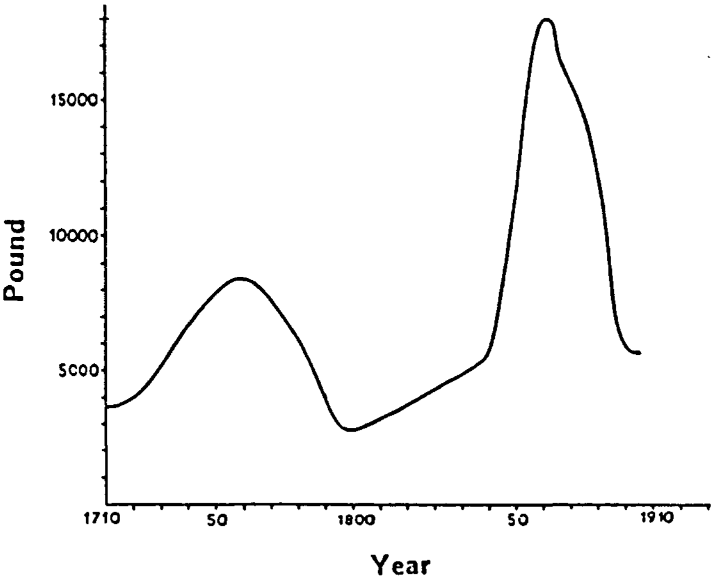
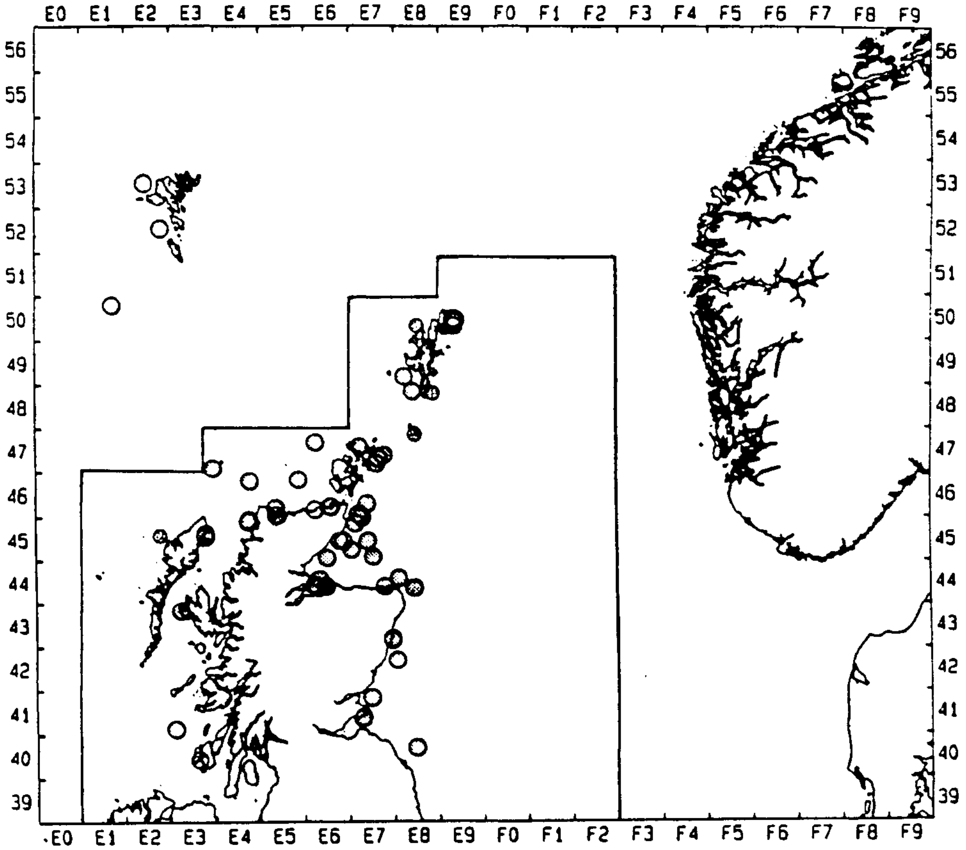


Figure 5.1 Chart showing locations of adult sandeel (*Ammodytes marinus*) concentrations in Scottish waters, based on bottom trawls within the box indicated. Data collected between 1922 and 1980 by the Marine Laboratory, Aberdeen.



APPENDIX 1

Working Paper for the ICES Seabirds/Fish Interaction Study Group

Simon P.R. Greenstreet

'Industrial' Fish, Fish Predators and Fisheries: A Question of Supply and Demand

Introduction

This working document presents some results of recent work, carried out as part of the E.C. MAST European Regional Seas Ecosystem Model(ERSEM) project; to determine the total quantity of each type of food eaten by fish predators in the North Sea. In particular, the impact of fish predators on 'Industrial' species (Norway pout, sprat, herring and sandeels) is detailed here. I then consider whether the production rates of 'Industrial' Fish species are high enough to sustain the estimated levels of exploitation by both fish predators and the 'Industrial' fishery. The availability of 'Industrial' fish prey to seabird and marine mammal predators is discussed in the light of these results.

Results

DEMAND

Based on their feeding ecology, the fish species recorded in the North Sea by Sparholt (1990) were assigned to one of four foraging guilds; Demersal Piscivores, Demersal Benthivores, Pelagic Piscivores and Pelagic Planktivores (see Annex 1) The consumption of food by all fish belonging to each guild was estimated from published information on fish biomass, diet and food consumption. Daily food consumption rates, as a percentage of predator body-weight, were determined. Knowing their standing crop biomass, the total quantity of food consumed each day by each predatory fish species could therefore be calculated. Diet information, as a percentage of wet weight of food consumed, allowed these total food consumption rates to be broken down into estimates of the daily consumption of each prey. Only the two piscivore guilds had any significant impact on industrial fish species.

The diets of four species, cod, haddock, whiting and saithe, were estimated with reference to Cranmer (1986), Daan (1973; 1989), Hislop *et al.* (1983; 1991), Robb (1981), Robb and Hislop (1980) and Vea Salvanes (1986). Daily rations were determined by applying Jones' (1974) digestion model to stomach weight data given in Daan (1989). Sea temperature was assumed to be 6°C in quarter 1, 7°C in quarter 2, 10°C in quarter 3, and 8°C in quarter 4 (Daan 1989). Output from the Multi-Species Virtual Population Analysis (MSVPA) program was used to determine the mean weight, length and proportion of biomass at age in each quarter. The input values used were similar to those used for the 'key run' of the 1990 meeting of the ICES Multi-Species Working Group (Anon., 1991a; P.A. Kunzlik, Pers. Comm.). These four species make up between 75% and 80% of the total biomass of the Demersal Piscivore guild throughout the year (Sparholt, 1990). The remaining species within this guild were assumed to have diets and consumption rates, as a proportion of predator biomass, equal to the average of the four gadoids.

The Pelagic Piscivore guild consists of only two species, mackerel and horse mackerel; their diets were estimated with reference to Daan (1989), Dahl and Kirkegaard (1986; 1987) and Kirkegaard et al. (1987). Mackerel daily food consumption was calculated by applying Mehl and Westgard's (1983a; 1983b) digestion model to mean stomach weight data given in Daan (1989). Mean weight at age and the proportion of the total mackerel biomass belonging to each age group in each quarter were obtained from the MSVPA output. Horse mackerel daily consumption rates observed in a Danish study carried out in autumn (Dahl and Kirkegaard, 1986; 1987; Kirkegaard *et al.*, 1987) were extrapolated to the whole North Sea population and considered to vary seasonally in a similar manner to mackerel.

The annual consumption of 'Industrial' fish by each of the major predator species, and by all other piscivorous fish is shown in Figure 1. The combined consumption by all fish predators is also shown for comparison with the weight landed by the fishery (Anon., 1991b). Full details of the procedures involved in deriving the consumption data are described elsewhere (Greenstreet, In Preparation, manuscript available on request).

The consumption of sprat and Norway pout by fish predators far exceeds the take of the fishery. This is not the case for sandeels where the fishery is a more serious competitor for the resource taking over half as much sandeel biomass as all the fish predators combined. Herring is not normally regarded as an 'Industrial' species, but have been included here because, historically, young herring used to be caught for industrial purposes, and today small herring might be included in the 'Industrial' fishery bycatch. Since there is also a directed herring fishery for human consumption, and given that the adult size of herring means that few fish predators will be able to handle older fish, it is not surprising, that the herring catch is much larger, relative to fish predation, when compared with the other 'Industrial' species.

In making these comparisons it must be born in mind that Jones' (1974) digestion model was used to determine the daily ration of gadoid and 'other fish' predators. Jones' (1974) model produces daily ration estimates which are approximately twice as high as those produced by Daan's (1973) digestion model when both models are applied to the same set of stomach contents weight data (Hislop *et al.*, 1991). MSVPA studies have traditionally used Daan's (1973) digestion model to determine fish natural mortality due to predation by other fish. The estimates of fish consumption by fish shown here are therefore approximately twice those of estimates based on MSVPA output (eg. Bax, 1991). Jones' (1974) digestion model produces estimates of daily food consumption which are similar to estimates of fish daily energy requirements (Jones and Hislop, 1978; Hislop *et al.*, 1991), and similar to rates of food consumption observed in field studies (eg. Daan, 1973; Basimi and Grove, 1985). The figures given here might, therefore, be regarded as likely maximum predation rates; possible minimum rates could be as low as half these values.

Table I gives the average daily consumption and catch rates in each quarter of the year on which the total annual removals shown in Figure 1 are based. These daily values take into account seasonal variation in predator biomass, diet, feeding activity, and water temperature (Greenstreet, In Preparation). Sparholt's (1990) estimates of fish biomass in the North Sea were used for Quarters 1 and 4; linear change over time was assumed in estimating biomass values for Quarters 2 and 3. These biomass values are given in Table II. To determine the level of "pressure" on 'Industrial' fish species, the total quantity of each species taken daily by predatory fish and fishermen in each quarter of the year was converted into daily exploitation rates (Table III). Some of these exploitation rates seem impossibly high; for example, a daily exploitation of over 1% among sprats in Quarter 1 would imply that fish predation and exploitation by man, in the absence of any growth, accounts for the entire sprat population during the late winter to early spring period!

SUPPLY

Output from the MSVPA model (using input values similar to those used for the key-run of the 1990 meeting of the ICES Multi-Species Working Group; Anon., 1991a. P.A. Kunzlik, Personal Communication) was used to estimate specific growth rates at age for each of the 'Industrial' Fish species in each quarter of the year. Applying these to biomass at age data, potential population production in the absence of exploitation could be estimated (Table IV). Growth rates as high as 1% body-weight per day seem readily achievable (Checkley, 1984; Hall, 1988; Hawkins *et al.*, 1985; Tytler and Calow, 1985)

As a check on these figures, estimates of the quantity of food consumed daily in each quarter of the year by each 'Industrial' species (Table V) were derived from review of the literature. Diets were estimated with reference to Albert (1991), Hardy (1924), Last (1982; 1989), Macer (1966), Raitt and Adams (1965), Robb (1981), Robb and Hislop (1980), Savage (1937) and Wilson and Bailey (1991). Albert's (1991) diet and stomach weight data for Norway pout were all given as dry weight values; these were converted to wet weights using suitable water content values (Bamstedt, 1981; O'Mori, 1969; Raymont *et al.*, 1971; Rumohr *et al.*, 1987). Herring diet was described as a percentage by number contribution of each prey item (Last, 1989). However, the relative weight of each prey item could be inferred from the data presented, allowing percentage by wet weight contributions to be calculated. Jones' (1984) digestion model was applied to the Norway pout mean stomach content wet weight values to estimate daily food consumption rates. Herring stomach contents weights were obtained from Koster et al. (1990) and Daan's (1973) digestion model was used to estimate daily consumption rates. A gastric emptying time of 12h was assumed (Koster *et al.*, 1990), atlthough times as fast as 6h have been observed (Daan *et al.*, 1985). Sprats and sandeels were considered to have the same daily consumption rate (as a percentage of the total population biomass) as that part of the herring population up to 15 cm in length. These food consumption estimates were based on the population standing crop biomass figures shown in Table II (see Greenstreet, In Preparation for more details). Assuming production/food-consumption ratios of 0.2 (eg. Jones 1982; 1984), daily production could be estimated (Table V). These values are lower, and less seasonally variable, than those derived from the MSVPA output.

Figure II shows, for each set of production figures, the daily production - exploitation balance for each 'Industrial' Fish species in each quarter of the year. Clearly production estimates based on the estimated food consumption of industrial fish fail to support the estimated exploitation rates of fish predators and fishermen. When balanced over the year however, the MSVPA derived production estimates are, more or less, sufficient to support these levels of exploitation; but there is strong seasonal variation. In Quarter 4, when fish production rates are very low (actually negative for all species but Norway pout, according to the MSVPA data), the estimated levels of exploitation would appear to cause significant depletion of the standing crop biomass. At other times of the year production is approximately sufficient to support the level of exploitation by fish predators and fishing activities estimated above, perhaps even sufficient to leave some excess available for exploitation by other top predators.

Discussion

Considering the MSVPA derived 'Industrial' Fish species production estimates, one point is immediately obvious. In Quarter 4, daily exploitation through exploitation by fish predators and fishermen significantly exceeds production. Figure II suggests that the standing crops of Norway pout, sandeels, sprat and herring would be expected to decline from Quarter 4 to Quarter 1 by 36%, 43%, 76% and 31.6%, respectively. Sparholt's (1990) data indicates that the biomass of these populations does indeed decline over this period. Examination of Table II indicates respective reductions of 34%, 25%, 43% and 40%. Only in the case of sprat is there a large discrepancy between these two sets of figures.

Over Quarters 1 to 3, daily production of all four of the 'Industrial' Fish species showed net gains over exploitation losses resulting from predation by fish and fishing activities. In the case of Norway pout this gain was 113%, far in excess of the 36% winter decline in standing crop biomass. Over the whole year this suggests a large surplus of Norway pout production with plenty available for exploitation by other top predators. In the case of sandeels the net gain in biomass of 56.7% over Quarters 1 to 3 only just exceeds the winter decline of 43%, however, this difference suggests that up to a quarter of a million tonnes of sandeel production might be available for exploitation by seabirds and marine mammals over the year. In the case of herring the spring and summer increase in standing crop biomass, at 31.4%, is almost identical to the 31.6% winter decline. Fish predators and fishing account for the entire annual production of this species, little, or none, is available for exploitation by other predators. Sprats are the only species where there is an apparent problem. The Quarter 4 deficit of exploitation over production, at 76%, significantly exceeds the net production gain of 25% over Quarters 1 to 3. These figures suggest that the sprat population should be in marked decline and this appears to have been the case during the 1980s (Anon., 1991a).

It would seem, therefore, that even the maximum estimates of consumption of 'Industrial' Fish by fish predators, and estimated losses through fishing, can be sustained by estimated levels of production over the year. Seasonal variation in the population biomass of 'Industrial' Fish species can be explained by seasonal variation in the net balance of production over exploitation. The exception to this is sprats which are over exploited by fish predators, particularly during the winter period. With the exception of Norway pout, little 'Industrial' Fish production appears to be available for exploitation by seabirds and marine mammals. However, this could be resolved if only marginally lower daily consumption rates by fish predators were adopted. In addition, it is worth noting at this point that, if the natural mortality rates of 'Industrial' species have been underestimated in the MSVPA through the use of Daan's (1973) digestion model rather than Jones' (1974) model, then adjusting the natural mortality parameter would result in larger population biomass estimates. Daily exploitation rates by fish predators and fishermen, as a percentage of standing crop biomass, would then decline, while the same daily production rate would generate more biomass each day.

One problem remains, the discrepancy between the estimates of 'Industrial' Fish daily production when derived from MSVPA output, or from production/food consumption ratios. In order to achieve the higher MSVPA-derived production values, 'Industrial' Fish species must either eat two to three times more food than is currently estimated (Greenstreet In Prep.), or their production/food consumption ratio must be higher than 0.2. The former possibility is under current investigation, the latter seems unlikely (Jones, 1982; 1984)

References

Albert, O.T. (1991). Biology and ecology of Norway pout *Trisopterus esmarki* in the Norwegian Deep. ICES Document, CM1991/G:44

Anon (1991)a. Report of the Multi-Species Working Group. ICES Document CM1991/Assess:7

Anon (1991)b. Report on the Meetings of the STCF Working Group on Improvements of the Exploitation Pattern of North Sea Fish Stocks. STCF Document, September 1991.

Bamstedt, U. (1981). Water and organic content of boreal macrozooplankton and their significance for the energy content. Sarsia, 66, 59-66.

Basimi, R.A. and Grove, D.J. (1985). Studies on feeding, growth and production of a recruited inshore population of Pleuronectes platessa (L.) at east Anglesey, North Wales. Journal of Fish Biology, 27, 765-783.

Bax, N.J. (1991). A comparison of the fish biomass flow to fish, fisheries, and mammals in six marine ecosystems. ICES Marine Science Symposia, 193, 217-224.

Checkley, D.M. (1984). Relation of growth to ingestion for larvae of Atlantic herring Clupea harengus and other fish. Marine Ecology - Progress Series, 18, 215-224.

Cranmer, G.J. (1986). The food of the haddock (Melanogrammus aeglefinus) in the North Sea. ICES Document, CM1986/G:86.

Daan, N. (1973). A quantitative analysis of the food intake of North Sea cod, Gadus morhua. Netherlands Journal of Sea Research, 6, 479-517.

Daan, N. (1989). Database report of the stomach sampling project 1981. ICES Cooperative Research Report, 164, 144pp.

Daan, N., Rijnsdorp, A.D. & van Overbeeke, G.R. (1985). Predation by North Sea herring Clupea harengus on eggs of plaice Pleuronectes platessa and cod Gadus morhua. Transactions of the American Fisheries Society, 114, 499-506.

Dahl, K. & Kirkegaard, E. (1986). Stomach contents of mackerel, horse mackerel and whiting in the eastern part of the North Sea in July 1985. ICES Document CM1986/H:68.

Dahl, K. & Kirkegaard, E. (1987). The diet and consumption of horse mackerel (Trachurus trachurus) in the eastern North Sea, August 1986. ICES Document CM1987/H:43.

Greenstreet, S.P.R. (In Preparation). Estimation of the daily consumption of food by fish in the North Sea.

Hall, S.J. (1988). The effects of reversal of seasonal changes in photoperiod on the growth and food consumption of cod, Gadus morhua L. Journal of Fish Biology, 32, 783--792.

Hardy, A.C. (1924). The herring in relation to its animate environment. Fisheries Investigations, Series II, 7, 1-53.

Hawkins, A.D., Soofiani, N.M. & Smith, G.W. (1985). Growth and feeding of juvenile cod (Gadus morhua L.). Journal du Conseil international pour l' Exploration de la Mer, 42, 11-32.

Hislop, J.R.G., Robb, A.P., Brown, M.A. & Armstrong, D.W. (1983). A preliminary report on the analysis of the whiting stomachs collected during the 1981 North Sea stomach sampling project. ICES Document CM1983/G:59.

Hislop, J.R.G., Robb, A.P., Bell, M.A. & Armstrong, D.W. (1991). The diet and food consumption of whiting (Merlangius merlangus) in the North Sea. ICES Journal of Marine Science, 48, 139-156.

Jones, R. (1974). The rate of elimination of food from the stomachs of haddock Melanogrammus aeglefinus, cod Gadus morhua, and whiting Merlangius merlangus. Journal du Conseil international pour Exploration de le Mer, 35, 225-243.

Jones, R. (1982). Species interactions in the North Sea. Canadian Special Publication of Fisheries and Aquatic Sciences, 59, 48-63.

Jones, R. (1984). Some observations on energy transfer through the North Sea and Georges Bank food webs. Rapp. P.-v. Reun. Cons. int. Explor. Mer., 183, 204-217.

Jones, R. & Hislop, J.R.G. (1978). Further observations on the relation between food uptake and growth of gadoids in captivity. Journal du Conseil international pour Exploration de le Mer, 38, 244-251.

Kirkegaard, E., Lewy, P. & Staehr, K.J. (1987). The Danish acoustical survey in division IIIa and eastern North Sea August 1986. ICES Document CM1987/H42.

Koster, F.W., Schober, W., Korves, A. & Schneider, R. (1990). Tank experiments on board: a useful tool for the estimation of stomach evacuation rates? ICES Document CM1990/G:34.

Last, J.M. (1982). The food of juvenile sprat Sprattus sprattus (Linnaeus 1758) and herring Clupea harengus (Linnaeus 1758) in inshore waters of the southern North Sea. ICES Document CM1982/H:12.

Last, J.M. (1989). The food of herring, Clupea harengus, in the North Sea, 1983-1986. Journal of Fish Biology, 34, 489-501.

Macer, C.T. (1966). Sandeels (Ammodytidae) in the south-western North Sea; their biology and fishery. MAFF Fishery Investigations, London, Series II, 24, 1-55.

Mehl, S. & Westergard, T. (1983)a. Gastric evacuation rate in mackerel (Scomber scombrus L.). ICES Document, CM1983/H:33.

Mehl, S. & Westergard, T. (1983)b. The diet and consumption of mackerel in the North Sea (A preliminary report). ICES Document, CM1983/H:34.

Raitt, D.F.S. and Adams, J.A. (1965). The food and feeding of Tricopterus esmarkii (Nilsson) in the northern North Sea. Marine Research, 3, 28pp.

Raymont, J.E.G., Strinivasagam, R.T. & Raymont, J.K.B. (1971). Biochemical studies on marine zooplankton - VIII. Further investigations on Meganyctiphanes norvegica (M. Sars). Deep-Sea Research, 18, 1167-1178.

Robb, A.P. (1981). Observations on the food and diel feeding behaviour of pelagic O-group gadoids in the northern North Sea. Journal of Fish Biology, 18, 184-194.

Robb, A.P. and Hislop, J.R.G. (1980). The food of five gadoid species during the pelagic O-group phasein the northern North Sea. Journal of Fish Biology, 16, 199-217.

Rumohr, H., Brey, T. & Ankar, S. (1987). A compilation of biometric conversion factors for benthic invertebrates of the Baltic Sea. The Baltic Marine Biologists Publication, 9, 56pp.

Savage, R.E. (1937). The food of the North Sea herring in 1930-1934. Fisheries Investigations London Series II, 15(5), 1-60.

Sparholt, H. (1990). An estimate of the total biomass of fish in the North Sea. Journal du Conseil international pour Exploration de le Mer, 46, 200-210.

Tytler, P. & Calow, P. (1985). Fish Energetics. Croome and Helm.

Vea Salvanes, A.G. (1986). Preliminary report from a comparitive study of the diet of four gadoid fishes in a fjord in western Norway. ICES Document, CM1986/G:71.

Wilson, M. & Bailey, R.S. (1991). A literature survey of sandeel biology. Unpublished SOAFD Literature Review.