

Northern Gannets in the North Sea: foraging distribution and feeding techniques around the Bass Rock

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Abstract Field observations around the largest Northern Gannet *Morus bassanus* colony in the North Sea, the Bass Rock, showed that 66% of all Gannets foraged in areas with very low densities of conspecifics, more than 100 km from the colony. When one forager found prey, even distant Gannets responded by joining the finder to obtain a share of

the bounty but, because of the low densities of Gannets far from the colony, feeding opportunities were typically exploited by small flocks, with relatively few competing birds. Intraspecific competition was thus less intense than it would have been nearer the colony. Searching and feeding tactics of Gannets, as well as foraging associations with other top predators, were different between sea areas. Low numbers of Gannets per flock occurred within inshore multi-species feeding associations, where Gannets hampered feeding opportunities for other seabirds (and themselves) by plunge-diving into compact schools of small prey fish. Larger flocks of competing Gannets formed in situations where an escape response in prey fish was absent (discards behind commercial trawlers) or weakened (fish schools herded by marine mammals). The association of Gannets with marine mammals was typically an offshore phenomenon, despite the abundance of cetaceans in inshore waters. Behind trawlers, Gannets focused mostly on roundfish, between 22 and 30 cm in length. Discards were, however, a fairly unimportant source of food during the breeding season and natural feeding opportunities were widespread.



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Introduction

Northern Gannets *Morus bassanus* (hereafter simply ‘Gannets’) have shown a long-term population increase and range expansion in the North Atlantic (Nelson 2002). Their success may have been driven by a relaxation of direct exploitation (Fisher & Vevers 1951) and a concurrent increase in prey fish, for example as a result of the overfishing of competing predatory fish (Sherman *et al.* 1981; Furness 1982; Camphuysen & Garthe 2000). Within the North Sea, new colonies have been formed and breeding numbers at long-established sites have increased spectacularly (Wanless *et al.* 1986, 2005; Wanless 1987).

This population increase may have had important consequences on the foraging opportunities around colonies. Positive correlations between colony size and feeding-trip duration have been reported, suggesting that at larger colonies birds need to travel farther, or search longer, for prey. It is questionable whether seabirds could actually cause significant prey depletion around their colony (Birkhead & Furness 1985; Croxall 1987; Nelson 2002). However, Lewis *et al.* (2001) suggested that although schools of fish close to colonies were perhaps not entirely removed by predators, they would be more frequently attacked and disturbed by diving Gannets (thus becoming less available,

as a result of avoidance response behaviours by the fish) than fish schools farther away. In that situation, intraspecific competition among Gannets might make feeding more profitable in areas farther afield with rather lower densities of competitors.

An obvious question to ask is whether there is any evidence that Gannets trigger such an avoidance response in fish schools, with adverse effects on the birds’ own opportunities for profitable feeding. Nelson (2002) suggested that Gannets are ‘positively adapted to highly communal fishing’, perhaps because the species is commonly observed in (large) groups leaving and arriving at their colonies. Communal feeding is, however, difficult to understand in the context of a ‘prey-disturbance hypothesis’ where Gannets are assumed to disturb each other’s foraging opportunities rather than to enhance them.

So, how and where do Gannets feed around their colonies? For a spectacular seabird such as the Gannet, in a well-studied area such as the North Sea, there is remarkably little published material and first-hand documentation on their foraging behaviour at sea. Feeding Gannets are well known for their spectacular plunge-dives when targeting shoaling fish (Boddington 1959; Reinsch 1969; Nelson 1978, 2002), but they also



David Tipling

24. The Bass Rock gannetry, off the Lothian coast, July 2001.

commonly scavenge behind fishing vessels (Camphuysen *et al.* 1995b) and associate with prey-driving marine mammals (Evans 1982; Camphuysen *et al.* 1995a) or other seabirds (Camphuysen & Webb 1999; Camphuysen *et al.* 2006). Several atlases and papers have described distribution patterns based on ship-based surveys within the North Sea (Tasker *et al.* 1985; Skov *et al.* 1995; Stone *et al.* 1995) but none of these have been very specific with regard to spatial patterns in foraging activity, let alone behaviour. Recent studies using satellite transmitters and data loggers have been highly successful in tracking individual birds and their foraging activities around the Bass Rock (Hamer *et al.* 2000; Humphreys *et al.* 2004). These devices have produced unique and valuable information on location, depth (in the water) and prey ingestion of foraging individuals, and even on particular hydrographic properties of the areas these birds were feeding in. However, data on foraging interactions with other marine wildlife (including conspecifics) or on precise foraging and feeding techniques in relation to the foraging environment and specific feeding opportunities therein can be collected effectively only during visual observations at sea.

This paper describes the behaviour of Gannets at sea in multi-species feeding frenzies and elsewhere, from visual observations during ship-based surveys and sessions of experimental discarding on board fisheries research vessels in the North Sea.

Methods

The data from midsummer ship-based seabird surveys (carried out in June–July, for ten seasons between 1991 and 2004, in the northwestern North Sea – an area covering 54–59°N and 3°W–2°E) were analysed (see also Camphuysen 2005). These surveys covered most of the feeding range of Gannets nesting on the Bass Rock (Hamer *et al.* 2000; Nelson 2002). The work was conducted in conjunction with the annual acoustic herring survey of FRV *Tridens* (ten seasons between 1991 and 2004), and during a dedicated survey on board RV *Pelagia* in 2003, using strip-transect counts, which have been developed as a standard for the North Sea (Tasker *et al.* 1984; Camphuysen *et al.* 2004). Counts were conducted between the periods when the survey ship was fishing (these periods were well spaced, normally no more than 3–4 per day), when the number of ship-followers was low and could be controlled for and when the vessel travelled at full speed (8–10 knots). The observation platforms provided clear forward views (through 180°) at an altitude of 12–15 m above sea level. A total of 9,972 km² were surveyed, travelling a distance of 33,601 km, and 44,818 Gannets were observed during these surveys. A correction factor was not applied, with the assumption that all individual Gannets, either swimming or in flight, were detected effectively within the 300-m-wide strip transect (counts were discontinued in rough conditions, e.g. above wind force 6 on the Beaufort scale). The birds

were aged according to plumage characteristics (five immature plumage classes were distinguished, in addition to adult plumage).

To distinguish between foraging (searching for food), feeding and non-feeding birds, the behaviour of the Gannets observed was classified, recorded, coded and stored in a database. Inspired by Ashmole (1971), 20 types of feeding behaviour and 16 types of non-feeding behaviour were distinguished. The following behaviours were commonly observed in



25. The author, with co-observer Tanja Weichler, surveying seabirds from the observation platform of FRV *Tridens*, July 2001.



Mike Lane

26. A Northern Gannet *Morus bassanus* searching for prey (see text for differences between travelling and foraging birds) off the Bass Rock, August 2005.

Gannets: Actively searching, Deep plunging, Shallow plunging, Scooping prey, Surface seizing, Scavenging at fishing vessel, Resting or apparently asleep, Preening or bathing, Carrying nest material, and being Under attack by kleptoparasite (see descriptions in table 1; details in Camphuysen & Garthe 2004). In the case of Gannets, the difference between direct flight and searching for prey is obvious under field conditions. Travelling birds follow straight lines, with a fully stretched body and the bill pointing forward.

Searching Gannets have somewhat slower, 'bouncing' wingbeats, they often look down, follow a more or less meandering path and/or circle over a given location. An incidental peer down into the sea by a bird otherwise clearly travelling was not recorded as 'searching'. Birds associating with or apparently attracted by the research vessels have not been included in calculations of densities, patterns of relative abundance, or activity budgets.

All birds, whether swimming or flying, that operated together in a particular area or movement were categorised as 'flocks'. Mean flock sizes and 95% confidence intervals were calculated after log transformation of the data to normalise the distributions and compared with the z-test ($z = d/\sigma$ where d is the deviation from the mean). The data were analysed in radius bands, or strata, of 20 km (covering the area 0–100 km from the colony) and 50 km (100–400 km from the colony) from the Bass Rock. Densities



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27. Northern Gannet *Morus bassanus* in flight approaching a feeding opportunity, June 2004.

Table 1. Types of Northern Gannet *Morus bassanus* behaviour recorded and logged at sea (see Camphuysen & Garthe 2004).

Direct(ed) flight	Straight flight with regular, powerful wingbeats and short glides in calm conditions, in higher winds, shortening wingspan and stroke, often banking and side-slipping. Head points straight forward during normal flight.
Actively searching	Reduced speed, often meandering course, head pointing down, more bouncing wingbeats, often circling to inspect situations or sea areas more closely.
Deep plunging	Headlong plunge-dive into the sea, bird disappears below surface.
Shallow plunging	Headlong plunge-dive into the sea, bird remains visible at surface.
Scooping prey	Sitting at the sea surface scooping up water and prey in the manner of a pelican.
Surface seizing	Sitting at the surface picking up (dead) prey from the surface.
Scavenging at fishing vessel	Any activity in association with a fishing vessel (searching, competing with other scavengers, feeding successfully).
Associated with MSFA	Feeding frenzy of more than one seabird species, including Gannets that either check out the situation (circling and approaching closely) or join in the foraging activity.
Associated with marine mammals	Cetaceans or seals followed at close range in persistent searching mode (see above), or actively feeding as a result of the surface activity of the mammals.
Resting or apparently asleep	Sitting at sea surface, no activity or sound asleep.
Preening or bathing	Sitting at sea surface, feather care.
Carrying nest material	In flight with seaweeds or plastics (excluding entangled birds).
Under attack by kleptoparasite	Aerial pursuit by a kleptoparasite, such as a skua or gull.

(Gannets per km²) were calculated for these strata and were transformed to total numbers of individuals at sea (density × surface area) to estimate how many individuals were involved.

Flocks comprising more than one seabird species were named 'multi-species (feeding) associations', or MSFAs. Small, short-lived MSFAs are an important mechanism for obtaining prey off the east coast of Britain for numerous species of piscivorous seabirds (details in Camphuysen & Webb 1999). Associations between seabirds and marine mammals involved birds that were actively drawn to cetaceans, whose foraging activities drive prey to the surface. Both the number of birds and the number (and species) of marine mammals involved were assessed and the type of behaviour was described and logged. Counts made during fishing operations of the research vessel (FRV *Tridens*) as well as counts made at nearby commercial trawlers were used to examine flock size at fishing vessels. The presence, age composition, flock size and the specific role (behaviour) of Gannets within MSFAs associated with both marine mammals and fishing

operations were recorded systematically.

Finally, as part of EC-funded research projects conducted in February 1993 and May, August and November 1994, the competitive strength and prey selection of Gannets in comparison with other scavenging seabirds was determined experimentally (Camphuysen *et al.* 1993, 1995b). During 536 sessions of experimental discarding (carried out throughout the North Sea survey area), in situations where Gannets were present, a total of 61,304 discards were individually identified, measured (fish only) and thrown in among other discards; these included 1,361 benthic invertebrates, 141 cephalopods (squid), 6 jellyfish, 7,735 particles of offal, 3,618 flatfish and 48,443 roundfish. The exact fate of each of these particular items (dropped and sunk, or picked up and swallowed by a scavenger) was determined, including identifications of the scavenger that picked up an item first, perhaps dropped it or had it stolen by another, until finally a morsel or fish was swallowed and could be tallied as being consumed successfully. From these experiments we could deduce prey-species and prey-size selection (composition of prey

taken versus composition of discards offered), as well as the competitive strength of each of the bird species present (number of prey items obtained and swallowed, including prey items stolen from others versus number of prey items dropped or lost as a result of kleptoparasitism by other scavengers). This competitive strength was calculated as a 'robbery index': the number of experimental discards stolen by a species divided by the number of discards stolen from that species (Camphuysen *et al.* 1995b). Observed consumption rates were compared with expectations based on the numerical abundance of scavengers at the trawl.

For each of the observations, since geographical coordinates were known, the distance (in km) from both the Bass Rock colony and the nearest part of the British coast was assessed. Water depth (m) was taken as the average depth within 10' latitude \times 20' longitude rectangles. Throughout the paper, means are accompanied by standard deviations (SD), derived means with 95% confidence intervals (CI), and significant test results refer to $P < 0.05$ or less.

Results

At-sea distribution

The at-sea distribution of Gannets could be described as a roughly bell-shaped form around the Bass Rock colony, with very similar declines in density with distance recorded in all directions (fig. 1). Mean densities of Gannets declined from 11.4 per km² within 20 km of the colony to

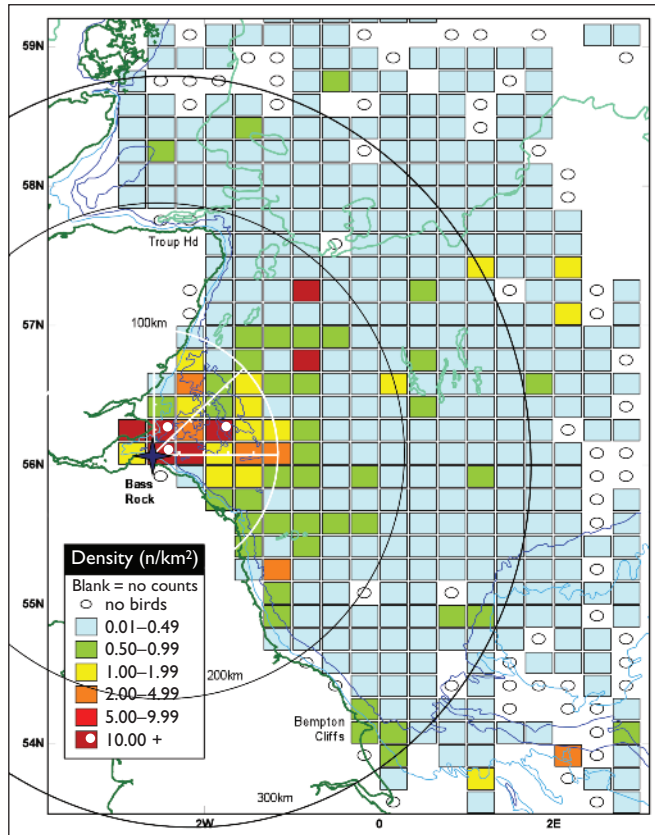


Fig. 1. Mean densities (number per km² per 10'-latitude \times 20'-longitude rectangle) of Northern Gannets *Morus bassanus* around the Bass Rock, based on June–July surveys 1991–2004. The circles indicate 100-km distance contours from the colony.

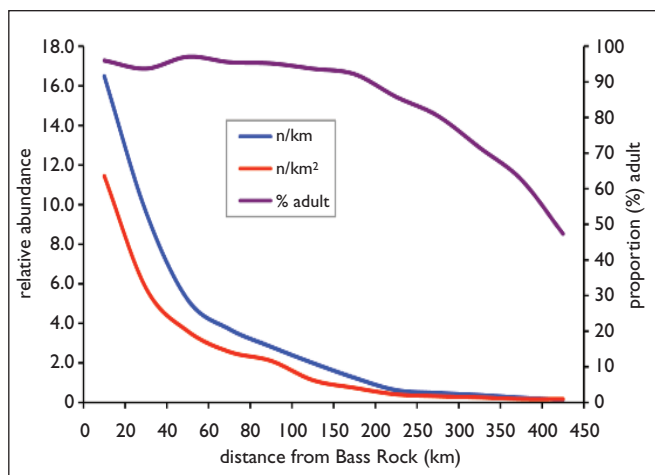


Fig. 2. Relative abundance (mean densities – n/km² – and number per km steamed – n/km) of Northern Gannets *Morus bassanus* and the proportion of adults with increasing distance around Bass Rock based on June–July surveys 1991–2004.

less than 0.17 per km² at over 400 km from the colony (fig. 2). About 350 km north of the Bass Rock, and within 150 km of the Scottish mainland, densities rose again, indicating an influence of the Shetland Gannet colonies on the numbers of birds at sea in that region. There was little or no discernible effect on at-sea densities around the smaller colonies at Troup Head (North-east Scotland) and Bempton Cliffs (Yorkshire), however.

Within 200 km of the Bass Rock, over 90% of the birds were adults (fig. 2) but the proportion of adults declined to less than 50% at 400 km or more from the colony. From extrapolated numbers of birds (based

on densities multiplied by sea surface area with increasing distance, but within 400 km of the colony), it can be estimated that about two-thirds of all adult Gannets at sea around the Bass Rock were recorded in areas where the mean densities (of Gannets) were very low (mean 0.53 per km²). From the age composition at sea, an uninterrupted zone of over 90% adult in all the Gannets observed extended up to 200 km around the Bass in nearly all directions, and up to 300 km from the colony to the ENE (fig. 3). Rather low percentages of mature birds were found directly off the North-east Scotland coast, in the Moray Firth area and around most of the

Dogger Bank (to the south-east).

Densities and flock size

Gannets travel in groups ('skeins') and clearly profit from the aerodynamics of V-shaped or linear flight formations, just as geese, swans or the (more closely related) pelicans do. Overall, group size declined with distance from the colony (fig. 4). Flocks of homeward-bound Gannets (max. flock size 199) were significantly larger than flocks leaving the colony (max. 47) in all distance strata within 250 km of the Bass Rock ($z = 2.60-7.49$, $P < 0.01$; $n = 6,623$ flocks; fig. 4).

Actively searching Gannets did not operate in cohesive flocks, but rather dispersed individually. Circling Gannets usually triggered an immediate response, even from distant conspecifics, but only

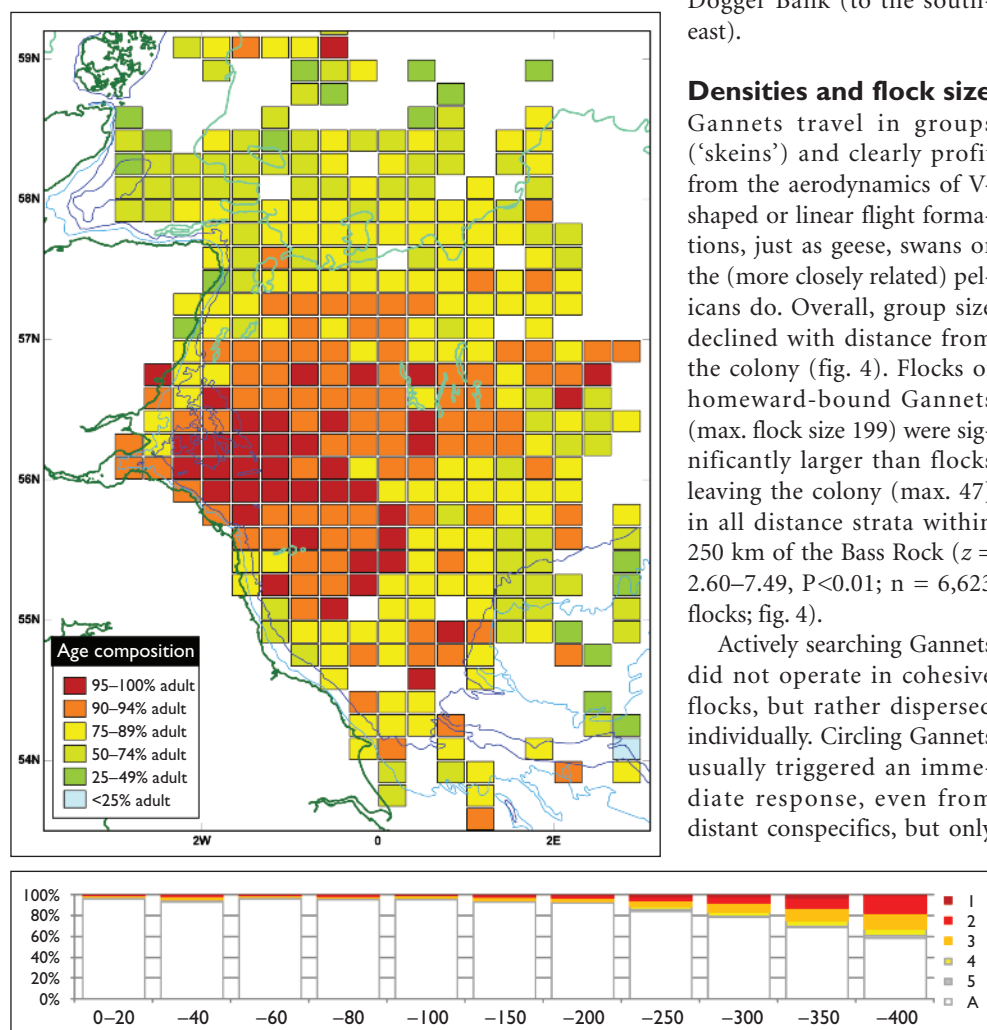


Fig. 3. Age composition (% adult per 10'-latitude x 20'-longitude rectangle) of Northern Gannets *Morus bassanus* around Bass Rock, based on June–July surveys 1991–2004. A proportion was calculated only if $n \geq 10$ per rectangle. Bottom graph: relative abundance of immature (plumage types 1–5) and adult Gannets with increasing distance from Bass Rock (km).

when that circling became more persistent would those 'neighbouring' birds come closer to form a flock. Foraging Gannets, in situations where a target (its prey) was not visible to the human observers, attracted few conspecifics to their searching area (mean flock size \pm 95% CI = 1.30 ± 1.05), and flocks did not grow significantly larger when such individuals began to dive (1.65 ± 1.09 , max. 112 per flock; fig. 5). Foraging opportunities were typically very short-lived after such an attack. Gannets participating in natural MSFAs also formed relatively small groups (1.70 ± 1.46 per flock for searching individuals, $z = 1.51$, ns; 1.76 ± 1.22 per flock when actively feeding, $z = 0.62$, ns; max. flock 35). Gannets were often the last species to arrive and join these frenzies, after which the feeding opportunities soon collapsed. Significantly larger flocks were observed searching over prey-driving dolphins and porpoises (1.91 ± 1.10 per flock searching, $z = 6.83$, $P < 0.001$; 2.96 ± 1.28 per flock feeding, $z = 4.51$, $P < 0.001$; max. flock 100 individuals) and, more particularly, near fishing vessels (1.76 ± 1.15 per flock searching, $z = 4.03$, $P < 0.001$; 4.63 ± 1.34 per flock feeding, $z = 6.77$, $P < 0.001$; max. flock 1,100 individuals).

Foraging behaviour and feeding distribution

Most Gannets were recorded foraging and feeding in areas with relatively low densities of conspecifics (fig. 6). From extrapolated numbers it is clear that within 400 km of the colony 66.1% of Gannets were feeding in low-density areas (< 1 Gannet per km^2 ; > 100 km from Bass Rock), 25.8% in areas with moderate densities (1–5 Gannets per km^2 ;

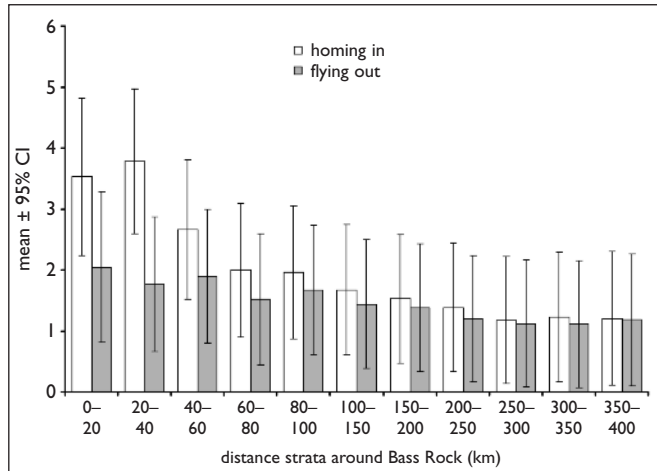


Fig. 4. Flock size (derived mean \pm 95% CI) of Northern Gannets *Morus bassanus* returning to (white) and leaving (grey) the Bass Rock with increasing distance from the colony ($n = 6,623$ flocks).

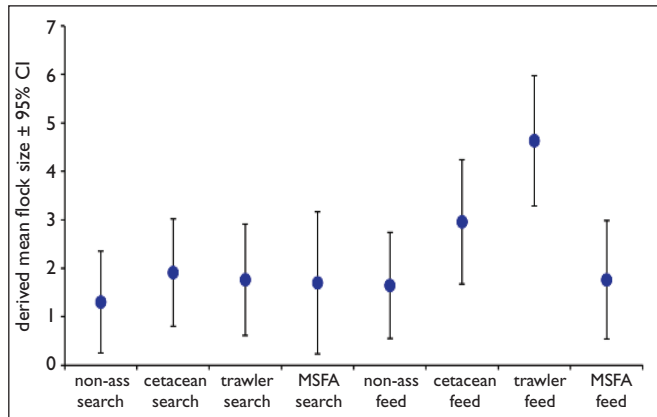


Fig. 5. Derived mean flock size (\pm 95% CI) of foraging Northern Gannets *Morus bassanus*, including searching and actively feeding individuals in different situations: only with conspecifics (non-ass), associated with cetaceans (cetacean), associated with fishing vessels (trawler) and when joining multi-species foraging associations (MSFA).

40–100 km from Bass Rock), and only 8.1% in high-density areas (> 5 Gannets per km^2 ; < 40 km from Bass Rock). However, while most Gannets were observed feeding > 100 km from the colony, the number of attacks (dives) per km^2 declined markedly with distance, after a maximum intensity between 20 and 40 km from the colony. Nonetheless, foraging activity expressed as the proportion of Gannets seen was lowest immediately around the colony.

The type of feeding behaviour was characteristic for the situation the Gannets were in, as summarised below.

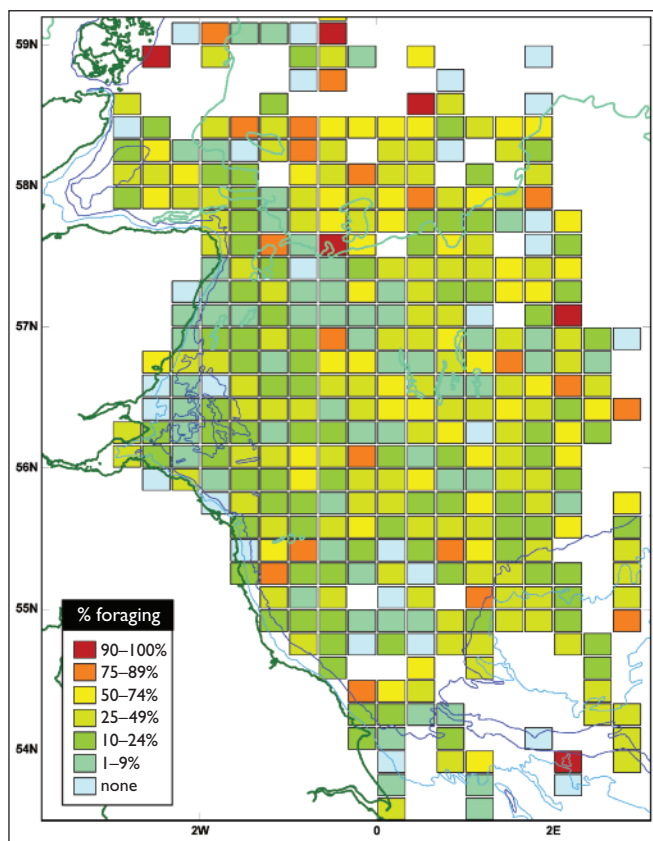


Fig. 6. Frequency of foraging (% searching for prey or feeding) of all birds observed per 10'-latitude x 20'-longitude rectangle) of Northern Gannets *Morus bassanus* around the Bass Rock, based on June–July surveys, 1991–2004. A percentage was calculated only if $n \geq 10$ per rectangle.



28. A feeding frenzy, with the Northern Gannets *Morus bassanus* being joined here by Fulmars *Fulmarus glacialis* and Great Skuas *Stercorarius skua*, south of Orkney, June 2004.

Gannets feeding on their own

Foraging Gannets away from other predators or fishing vessels were normally (deep) plunge-diving. In deeper (clear) waters far from the coast, many of these plunge-dives were from spectacular heights, suggesting that the birds needed to venture deep into the water and that fish prey could be observed at considerable depth.

Gannets joining MSFAs

Gannets would join the relatively small feeding frenzies of other seabirds by plunging into the sea at an angle (thus a relatively shallow plunge-dive), or straight into the feeding frenzy where auks (Common Guillemots *Uria aalge* and Razorbills *Alca torda*) had driven small prey, mostly sandeels *Ammodytes*, to the surface. When the specific role of seabird species within a feeding frenzy could be assessed (initiators, joiners or scroungers), Gannets were generally seen to *join* established feeding frenzies and they were never recorded as initiators. After joining (usually with a plunge-dive), they would position themselves on the water surface in the midst of the feeding opportunity, scooping up small fish fry for as long as this was within reach. Scooping (in 'pelican fashion') was an unexpected type of behaviour, perhaps first recorded with certainty during the surveys reported here, and this only after years of studying MSFAs, but one that has been seen commonly ever since it was first detected. The presence of Gannets

forced smaller (aerial) seabirds such as Kittiwakes *Rissa tridactyla* to position themselves at the periphery of the feeding frenzy and typically prompted the auks to give up driving fish towards the surface, so that the

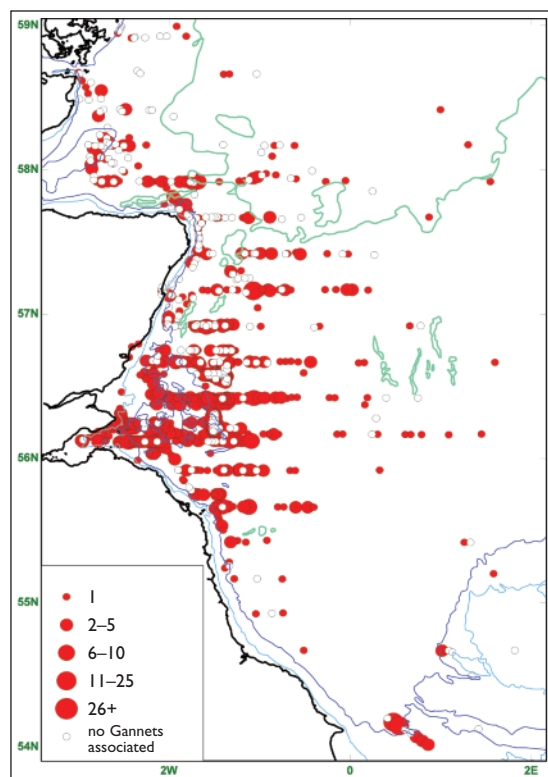


Fig. 7. MSFAs with (red circles) and without (white circles) Northern Gannets *Morus bassanus* in the northwest North Sea around the Bass Rock colony. Total number of MSFAs recorded was 2,080, of which 442 (21%) contained Gannets.

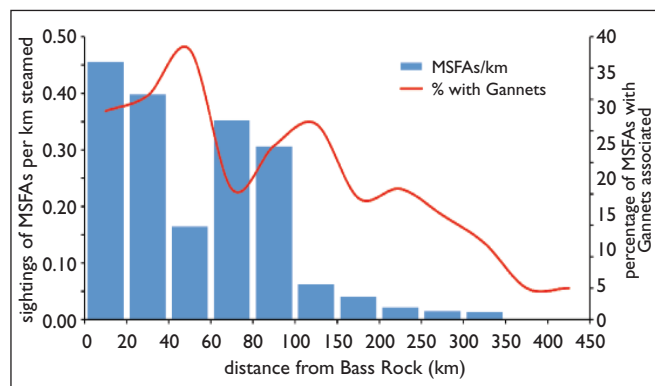


Fig. 8. Sightings of multi-species feeding associations (MSFAs) – number of sightings per km steamed – and the frequency (percentage) of MSFAs containing Northern Gannets *Morus bassanus*, with distance from the Bass Rock gannetry.

feeding possibility collapsed within seconds. So quick would feeding opportunities develop and collapse in these MSFAs that, even from a passing ship at speed, much of the evolution of individual frenzies could be recorded, time and time again, including the role and effect of each of the participating species (see Camphuysen & Webb 1999 for details). MSFA participation as described here typically occurred within 100 km of the Bass Rock, and particularly within 80 km of the coast (fig. 7). Therefore, the frequency with which MSFAs were joined by Gannets reflected the possibilities at sea (fig. 8). Within that sea area, the proportion of adult Gannets outside MSFAs amounted to 95.6% ($n = 11,093$), whereas within MSFAs the proportion of mature birds was significantly lower (93.7%, $n = 1,715$; $G_{adj} = 11.67$, $df = 1$, $P < 0.001$).

Gannets associated with cetaceans

Gannets joining cetaceans were usually deep plunge-diving, but often seemed reluctant to do so in the immediate presence of the hunting mammals. Cetaceans (certainly dolphins) often herded fish prey at speed and it appeared that Gannets needed to position themselves very carefully to profit most from the opportunities. On many occasions, the birds were merely seen to circle closer and closer above the mammals, trying to keep up with them during their regular disappearances deep underwater.

During the ship-based surveys, cetaceans were encountered 1,825 times (eight different species, 5,565 individuals in total). On 286 occasions (15.7%), Gannets were seen to begin searching for prey or actively feeding in association with these mammals (table 2). Gannets were never seen to join the (rarely encountered) coastal dolphins (Bottlenose Dolphin *Tursiops truncatus* and Risso's Dolphin *Grampus griseus*), and they seldom expressed interest in baleen

Table 2. Sightings of cetaceans (number of sightings, number of animals and mean pod size), and sightings where Northern Gannets *Morus bassanus* were joining the animals while searching for prey or actively feeding (number and frequency (%) of sightings) within 400 km of the Bass Rock, based on June–July surveys, 1991–2004.

	Sightings	Animals	Pod size	Sightings with Gannets
Common Dolphin <i>Delphinus delphis</i>	5	138	27.6	3 (60.0%)
White-sided Dolphin <i>Lagenorhynchus acutus</i>	26	402	15.5	13 (50.0%)
White-beaked Dolphin <i>Lagenorhynchus albirostris</i>	369	1,897	5.1	117 (31.7%)
Harbour Porpoise <i>Phocoena phocoena</i>	910	2,514	2.8	145 (15.9%)
Unidentified dolphin	36	79	2.2	3 (8.3%)
Minke Whale <i>Balaenoptera acutorostrata</i>	462	590	1.3	5 (1.1%)
Unidentified whale	11	11	1.0	–
Fin Whale <i>Balaenoptera physalus</i>	2	2	1.0	–
Bottlenose Dolphin <i>Tursiops truncatus</i>	3	19	6.3	–
Risso's Dolphin <i>Grampus griseus</i>	1	3	3.0	–
	1,825	5,655	3.1	286 (15.7%)

whales (only five associations with Minke Whales *Balaenoptera acutorostrata*, out of 462 encounters with this species at sea). The most abundant cetacean, Harbour Porpoise *Phocoena phocoena*, was joined by Gannets in 145 of 910 encounters (15.9%), while offshore dolphins of various species were most frequently 'targeted' (table 2).

The frequency of association with certain cetacean species was strongly correlated with the mean pod size of that species (table 2). Furthermore, the mean pod size of the commonest cetaceans joined by Gannets (White-beaked Dolphin *Lagenorhynchus albirostris*, 7.5 (± 6.1) animals and Harbour Porpoise, 3.4 (± 3.1) animals) was significantly larger than that of pods of the same cetacean species where Gannets were either not nearby or did not show an interest (pod size 4.0 ± 3.2 , $t_{365} = 7.24$, $P < 0.001$ and 2.6 ± 3.5 , $t_{908} = 2.61$, $P < 0.01$, respectively).

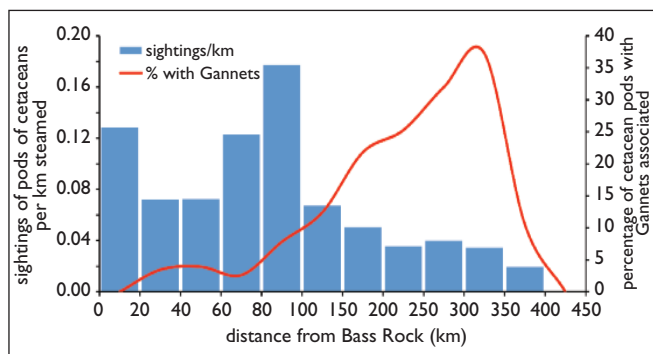


Fig. 9. Sightings of cetaceans (number of sightings per km steamed) and the frequency of association with Northern Gannets *Morus bassanus* (percentage of pods with associated Gannets), with distance from the Bass Rock gannetry.

Associations with cetaceans occurred mainly well offshore (more than 60 km from the colony), and typically over deeper waters (fig. 9). The latter seemed to reflect a genuine preference for cetaceans in deeper, thermally stratified seawater given that these animals were widespread and occurred in high numbers closer to the colony. Cetaceans were most commonly encountered within 100 km of the Bass Rock, while records of Gannets associating with cetaceans were most frequent at greater distances (fig. 10). Offshore feeding assemblages more than 80 km from the coast that involved cetaceans normally attracted Gannets as the only bird species (90.7%, $n = 237$). The age composition of all Gannets encountered >80 km from the coast and >100 km from the Bass Rock comprised 90.5% adults ($n = 18,036$); in the same distance class, taking solely those associated with cetaceans, the proportion of mature

birds was significantly lower (84.9%, $n = 2,335$; $G_{adj} = 62.14$, $df = 1$, $P < 0.001$).

Gannets and fishing vessels

Fishing vessels were joined irregularly and, with declining fishery effort between 1991 and 2003, this association became increasingly rare during the study. Birds scavenging at trawlers would enter the water with a deep or a shallow plunge-dive and use a variety of techniques to

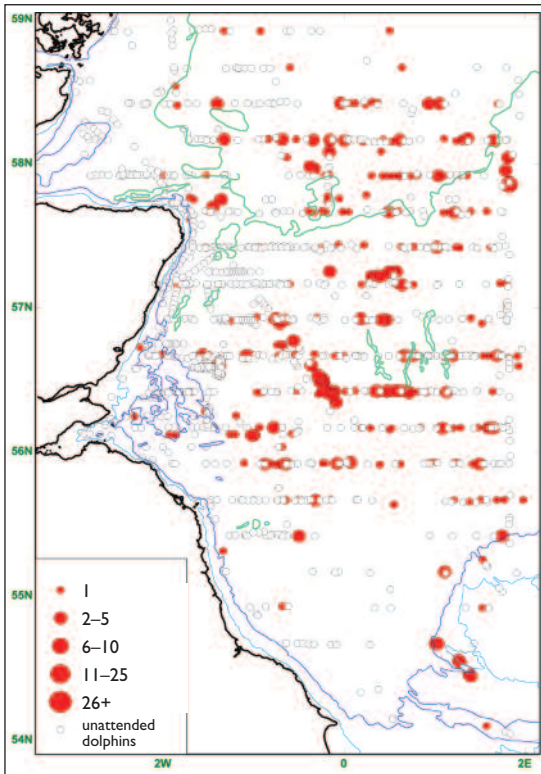


Fig. 10. Pods of small cetaceans with (red circles) and without (white circles) Northern Gannets *Morus bassanus* in the northwest North Sea around the Bass Rock colony. The total number of pods of cetaceans observed was 1,825, of which 286 had associated Gannets.



29. A feeding frenzy behind a trawler – note the 'impact' (the underwater white 'plume') that marks the entry of a plunge-diving Northern Gannet *Morus bassanus*, July 2002.

obtain discards after that initial dive. Scavenging Gannets were sometimes engaged in surface pecking, swallowing dead fish floating at the surface. However, they often continued with their normal strategy of deep plunging. Gannets joining a session of discarding at a fishing vessel would typically dive deep into the water, select and swallow one or two sinking fish in the water column, resurface, take off, circle around the boat, and deep-plunge again, until satiated. At the surface (or indeed sometimes while still underwater), Gannets would readily steal fish from competing conspecifics or from other seabirds. Flatfish were often ignored and offal was seldom taken.

Groups of Gannets around commercial fishing vessels could be very large (over 1,000 birds at times), but only when vessels were actively discarding fishery waste. It is important to note, although it was hard to quantify, that Gannets very often ignored the activity of nearby fishing vessels, even when suitable prey was released in large quantities (for example, released from the survey vessel itself during periods of fishing), to continue on their foraging trips farther away (see also Camphuysen *et al.* 1995b).

At trawlers in the North Sea, Gannets were found to be the largest and most powerful scavenging predators (cetaceans excluded), equalled in apparent strength and foraging success only by Great Black-backed Gulls *Larus marinus*. Gannets took much less offal (liver and guts from gutted fish) than expected from the numerical abundance during discard experiments. In contrast, their feeding success was very high for roundfish, notably gadoids and particularly in early summer, and they were observed to swallow significantly more of these fish than expected from their numerical abundance during the experiments. Experiments showed that Gannets focused more on larger roundfish (22–30 cm long) than any of the other birds joining fishing vessels, which is consistent with their own overall size

and swallowing capacity (fig. 11). Gannets also preferred smooth fish species (gadoids, clupeids) over spiny species (gurnards).

The overall robbery index of Gannets (17.9 for all categories, 18.3 for roundfish; Camphuysen *et al.* 1995b) over a total of 536 sessions of experimental discarding was higher than in any other seabird species and the species' competitive strength was most pronounced in summer and in the northwest and west of the North Sea basin. The age composition of all Gannets encountered more than 150 km from the Bass Rock (where all records of birds associating with fishing vessels occurred) comprised 87.7% adults ($n = 18,654$), whereas for those associated with fishing vessels the proportion of mature birds was significantly higher (96.7%, $n = 1,764$; $G_{adj} = 171.4$, $df = 1$, $P < 0.001$).

Gannets disturbing fish schools?

The effect of a Gannet attack on a fish shoal could be observed only in cases of surface-driven fish schools. As MSFA participants, targeting surface-driven 'balls' of sandeels, Gannets normally attacked the fish from above while swimming at the surface (typi-

cally after surfacing from a fruitless plunge-dive). The driving auks normally quickly abandoned their herding when Gannets joined in, and fish 'balls' driven to the surface by the auks were seen to disintegrate and sink deeper within seconds of a Gannet attack. Gannets were seen to reach deeper and deeper into the water until they gave up feeding, indicating that soon after their arrival the herded fish would disperse into waters too deep for the birds to have access to from the surface. Late arrivals (Gannets or other seabirds) would, as a rule, have no access to the fish and intake rates for those birds were zero.

Discussion

During the fieldwork described here, individual adult Gannets breeding on the Bass Rock were tracked with satellite transmitters, GPS, time–depth recorders and other devices to study the foraging behaviour of breeding birds and to log individual foraging trips (Hamer *et al.* 2000; Humphreys *et al.* 2004). The ship-based surveys showed that Gannets dispersed widely around the colony, with high densities near the colony and low densities over vast areas 100–450 km from the Bass

(fig. 1). The telemetry studies confirmed that this entire range and beyond is used by breeding birds from the Bass Rock colony. They revealed that the maximum foraging range was 540 km from the colony, and that the mean farthest distance from the colony on any one trip was 232 km. Foraging trips lasted between 13 and 84 hours. Destinations of foraging trips mapped with satellite transmitters and GPS data loggers covered a wide area of the North Sea, with a non-random distribution and a higher-than-expected proportion of trips to the northeast (generally in the vicinity of Buchan Deep and Halibut Bank) and to the southeast (mostly between Farne

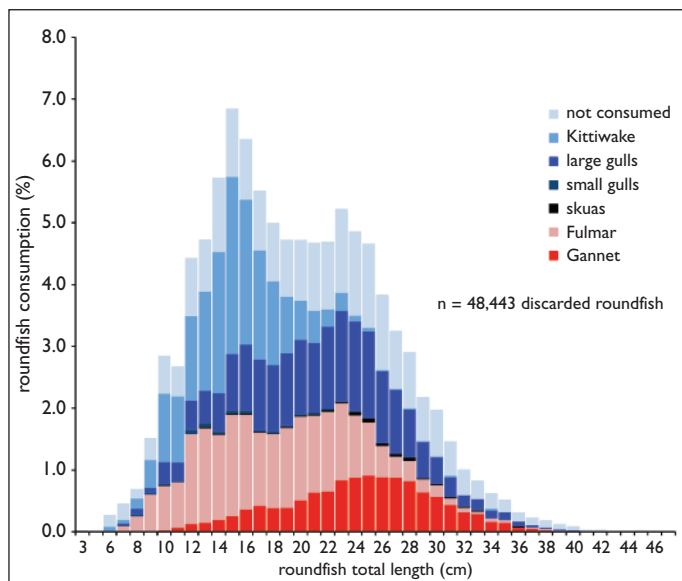


Fig. 11. Roundfish consumption (% of total discarded) by seabirds during experimental discarding from fisheries research vessels in the North Sea with Northern Gannet *Morus bassanus* consumptions in red (from data collected in 1993–94; Camphuysen *et al.* 1993, 1995b). Bars indicate the frequency discarded for each size class (cm total fish length), colours represent the fraction successfully swallowed by each of the main groups of seabirds.

Deep, Dogger Bank and Outer Silver Pit) of the colony. The authors of these telemetry studies have suggested that Gannets breeding at the Bass Rock focused their activity on bathymetric features that were probably associated with high primary production. From the at-sea surveys described in this paper, a preference for destinations to the northeast and south-east of the colony is more difficult to detect in the overall distribution map (fig. 1), but could be inferred from the recorded age composition of Gannets at sea around the colony (fig. 3). However, an association of foraging activities with bathymetric features is not clear from ship-based survey results (fig. 6), and, in fact, foraging is a seemingly random process, certainly so if the type of feeding is ignored.

The observations summarised in this paper show that different feeding areas are visited during long-distance trips, requiring different foraging techniques and probably yielding different prey. Gannets

commonly deployed three rather different types of feeding in the North Sea: (1) deep plunge-diving, presumably mainly for large, shoaling fish; (2) surface feeding for small fish (scooping up prey); and (3) scavenging behind fishing vessels. Deep plunging was observed in monospecific feeding events, in MSFAs, at trawlers and when associated with cetaceans. Surface feeding (including scooping) was characteristic within coastal MSFAs and at fishing vessels. Monospecific feeding bouts were seldom seen to build up large congregations of birds, but were nevertheless generally short-lived (several minutes).

There was no evidence to suggest that Gannets joining inshore MSFAs (<80 km from the coast) were targeting anything but small shoaling fish (notably sandeels), whereas birds joining cetaceans or trawlers were clearly targeting larger prey. The inshore MSFAs probably formed fairly predictable feeding opportunities relatively close to the colony (Camphuysen *et al.* 2006). The development of MSFAs was a characteristic



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30 & 31. Northern Gannets *Morus bassanus* and Fulmars *Fulmarus glacialis* gathering above hunting cetaceans – in this case Killer Whales *Orcinus orca* in the northern part of the North Sea study area, June 2003.

phenomenon in mixed coastal waters inshore of the shallow sea front (the separation zone between mixed coastal waters and thermally stratified waters). However, Gannets were encountered both in mixed coastal waters and in deeper, stratified waters farther out. They used different foraging techniques in the two areas and, in contrast to the case for many other seabirds, the shallow sea front was relatively unimportant as a feeding area for Gannets. High primary production is associated with oceanic fronts, so the suggestion (from the analysis of logger data) that Gannets focused their activity on features that were associated with high primary production (Hamer *et al.* 2000) could not be confirmed.

Prey (fish schools) occurs in discrete patches, which are probably non-randomly distributed and difficult to find. In offshore waters, Gannets often fed on fish schools that were herded towards the surface by dolphins or porpoises. The location of cetacean activity probably varies unpredictably but is at least highly visible at the surface, and could thus be

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32 & 33. Plunge-diving Northern Gannet *Morus bassanus* in Shetland waters, June 2008.

a good guide for Gannets searching for accessible prey patches. Otherwise, the potential to respond to the behaviour of even very distant conspecifics will enhance feeding opportunities at greater distances from land. Actively searching Gannets did so mainly individually, while simultaneously monitoring the behaviour of conspecifics, such that when one forager found a patch, other individuals soon joined the finder. The signalling function of the bright white plumage of Gannets was certainly appreciated by the ship-based observers, who were able to detect Gannets at much greater distances than they could all other species of seabirds. The majority of Gannets foraged in areas with low densities of conspecifics, so that the typically short-lived feeding bouts attracted relatively few competitors. These observations provide further support to the hypothesis formulated by Lewis *et al.* (2001) that intraspecific competition drives birds from large colonies farther afield.

Lewis *et al.* (2001) suggested that schools of fish attacked by diving Gannets would become temporarily unavailable as a result of an avoidance response. The question that remained was whether evidence could be provided that Gannets would indeed trigger such an avoidance response in fish schools, with adverse effects on their own opportunities for profitable feeding. The response of a fish school was rarely observed directly, but the short duration of most feeding events suggests that feeding was no longer profitable soon after an attack by one or just a few Gannets. Moreover, an attack-avoidance response by surface-driven fish within some MSFAs could actually be observed after Gannets entered the scene.

Gannet flock sizes were significantly larger over prey-herding cetaceans (even though this took place mainly in areas with very low densities of Gannets) and near trawlers. In each of these situations, an attack-avoidance response by prey fish was either blocked (herding mammals) or non-existent (discards), and feeding bouts were apparently relatively longer-lived, attracting more birds. Field observations thus support the prediction that feeding frenzies over persistent prey patches grow larger than those over small, easily disturbed fish schools and seem to support the assertion that Gannets could be

important in inducing an avoidance response by their prey in certain conditions.

Competition for prey is probably most intense behind fishing vessels, where numerous species congregate and large flocks may be formed. The competitive strength of scavenging Gannets at trawlers is considerable and the species has been identified as a highly successful kleptoparasite, being capable of stealing 18 times more items from other seabirds than were lost by them through robbery (Hudson & Furness 1989; Camphuysen *et al.* 1995b; Garthe & Hüppop 1998; this paper). A combination of brute force and aggression, the ability to swallow even the largest discards, plus an ability to dive to reach sinking (dead) prey makes Gannets highly successful competitors in these situations. The same avian competitors meet one another in MSFAs targeting fish balls driven towards the surface by auks. Here, the same ranking in the dominance hierarchy was established. Smaller, surface-feeding seabirds gave way when Gannets arrived on the scene. An important difference was that the prey facilitation mechanism collapsed when Gannets arrived (auks gave up driving) and the attack-avoidance response by the fish prompted them to swim down, beyond reach. The scooping behaviour of Gannets at fish balls appears to be a new discovery and the visual observations of this has elucidated some hitherto unexplained findings from studies employing time-depth activity recorders and stomach-temperature loggers (Humphreys *et al.* 2004).

Where intake rates are expected to fall with increasing numbers of competitors (Stephens & Krebs 1986), it does not pay to arrive late in a feeding frenzy. Where an attack would trigger an immediate avoidance response by the prey, it may be predicted that only the first few predators experience a profitable feeding bout.

Widespread feeding in a patchy environment with very low densities of competitors may thus be a sensible option for an aerial and highly mobile species such as the Gannet. Feeding individuals can be quickly joined even if they are several kilometres away, while large flocks of competitors over feeding patches are unlikely to develop, simply because the birds are too far apart. A feeding bout is thus profitable but short-lived. Recent studies using instrumentation to track individual Gannets have supported the suggestion of wide (individual) dispersal of foraging birds over large distances at sea.

Acknowledgments

The work was funded by EC projects EC DG XIV research contracts 92/3505 and BIOECO/93/10, 'Interactions between the marine environment, predators and prey: implications for sustainable sandeel fisheries (IMPRESS; QRRS 2000-30864)' and 'Modelling the impact of fisheries on seabirds (MIFOS; CFP 96-079)'. I would like to thank numerous co-observers and crews of FRV *Tridens* and RV *Pelagia* for help in the field. This work benefited from fruitful discussions with all partners of the IMPRESS and MIFOS projects. Stefan Garthe, Mardik Leopold and Theunis Piersma kindly commented on earlier drafts of this paper.

References

- Ashmole, N. P. 1963. The regulation of numbers of tropical oceanic birds. *Ibis* 103b: 458–473.
- 1971. Sea bird ecology and the marine environment. In: Farner, D. S., & King, J. R. (eds.), *Avian Biology I*, pp. 224–286. Academic Press, New York.
- Birkhead, T. R., & Furness, R. W. 1985. Regulation of



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34. A multi-species feeding frenzy (MSFA) – Northern Gannets *Morus bassanus* have entered the scene and are scooping prey (one of the key findings in this study), Kittiwakes *Rissa tridactyla* have been displaced and Common Guillemots *Uria aalge* (top), which had been driving prey fish to the surface, swim off away from the scene; July 2002.

- seabird populations. In: Sibly, R. M., & Smith, R. H. (eds.), *Behavioural Ecology, Ecological Consequences of Adaptive Behaviour*, pp. 147–167. Blackwell Science, London.
- 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. Progr. Ser.* 40: 205–208.
- Boddington, D. 1959. Feeding behaviour of Gannets and Great Black-backed Gull with Mackerel schools. *Brit. Birds* 52: 383–384.
- Camphuysen, C. J. 2005. Seabirds at sea in summer in the northwest North Sea. *Brit. Birds* 98: 2–19.
- & Garthe, S. 2000. Seabirds and commercial fisheries: population trends of piscivorous seabirds explained? In: Kaiser, M. J., & Groot, S. J. de (eds.), *Effects of Fishing on Non-target Species and Habitats: biological, conservation and socio-economic issues*, pp. 163–184. Blackwell Science, Oxford.
- & — 2004. Recording foraging seabirds at sea: standardised recording and coding of foraging behaviour and multi-species foraging associations. *Atlantic Seabirds* 6: 1–32.
- & Webb, A. 1999. Multi-species feeding associations in North Sea seabirds: jointly exploiting a patchy environment. *Ardea* 87: 177–198.
- , Scott, B., & Wanless, S. 2006. Distribution and foraging interactions of seabirds and marine mammals in the North Sea: multi-species foraging assemblages and habitat-specific feeding strategies. In: Boyd, I. J., Wanless, S., & Camphuysen, C. J. (eds.), *Top Predators in Marine Ecosystems: monitoring change in upper trophic levels*, pp. 82–97. Cambridge Univ. Press, Cambridge.
- , Heessen, H. J. L., & Winter, C. J. N. 1995a. Distant feeding and associations with cetaceans of Gannets *Morus bassanus* from Bass Rock, May 1994. *Seabird* 17: 36–43.
- , Calvo, B., Durinck, J., Ensor, K., Follestad, A., Furness, R. W., Garthe, S., Leaper, G., Skov, H., Tasker, M. L., & Winter, C. J. N. 1995b. *Consumption of Discards by Seabirds in the North Sea*. NIOZ-Report 1995–5. Netherlands Institute for Sea Research, Texel.
- , Fox, A. D., Leopold, M. F., & Petersen, I. K. 2004. *Towards Standardised Seabirds at Sea Census Techniques in Connection with Environmental Impact Assessments for Offshore Wind Farms in the UK*. Royal Netherlands Institute for Sea Research, Texel.
- , Ensor, K., Furness, R. W., Garthe, S., Hüppop, O., Leaper, G., Offringa, H., & Tasker, M. L. 1993. *Seabirds Feeding on Discards in Winter in the North Sea*. NIOZ-Report 1993–8, Netherlands Institute for Sea Research, Texel.
- Croxall, J. P. (ed.) 1987. *Seabirds: feeding ecology and role in marine ecosystems*. Cambridge University Press, Cambridge.
- Evans, P. G. H. 1982. Associations between seabirds and cetaceans: a review. *Mamm. Rev.* 12: 187–206.
- Fisher, J., & Vevers, H. G. 1951. The present population of the North Atlantic Gannet (*Sula bassana*). *Proc. Int. Orn. Congr.* 10: 463–467.
- Furness, R. W. 1982. Competition between fisheries and seabird communities. *Adv. Mar. Biol.* 20: 225–307.
- Garthe, S., & Hüppop, O. 1998. Foraging success, kleptoparasitism and feeding techniques in scavenging seabirds: does crime pay? *Helgol. Meeresunters.* 52: 187–196.
- Hamer, K., Phillips, R., Wanless, S., Harris, M. P., & Wood, A. 2000. Foraging ranges, diets and feeding locations of Gannets *Morus bassanus* in the North Sea: evidence from satellite telemetry. *Mar. Ecol. Progr. Ser.* 200: 257–264.
- Hudson, A. V., & Furness, R. W. 1989. The behaviour of seabirds foraging at fishing boats around Shetland. *Ibis* 131: 225–237.
- Humphreys, E. M., Hennicke, J. C., Hamer, K. C., Garthe, S., Peters, G., Grémillet, D., & Wanless, S. 2004. Foraging behaviour of Northern Gannets: new insights from remote-sensing. Oral presentation *Management of Marine Ecosystems: monitoring change in upper trophic levels*. Zoological Society of London Conference, April 2004.
- Lewis, S., Sherratt, T. N., Hamer, K. C., & Wanless, S. 2001. Evidence of intra-specific competition for food in a pelagic seabird. *Nature* 412: 816–819.
- Nelson, J. B. 1978. *The Gannet*. Poyser, Berkhamsted.
- 2002. *The Atlantic Gannet*. Fenix Books, Great Yarmouth.
- Reinsch, H. H. 1969. *Der Basstölpel*. Wittenberg Lutherstadt: Neue Brehm-Bücherei 412.
- 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: 487–489.
- Skov, H., Durinck, J., Leopold, M. F., & Tasker, M. L. 1995. *Important Bird Areas for Seabirds in the North Sea, including the Channel and the Kattegat*. BirdLife International, Cambridge.
- Stephens, D. W., & Krebs, J. R. 1986. *Foraging Theory*. Princeton University Press, Princeton.
- Stone, C. J., Webb, A., Barton, C., Ratcliffe, N., Reed, T. C., Tasker, M. L., Camphuysen, C. J., & Pienkowski, M. W. 1995. *An Atlas of Seabird Distribution in North-west European Waters*. JNCC, Peterborough.
- Tasker, M. L., Jones, P. H., Dixon, T. J., & Blake, B. F. 1984. Counting seabirds at sea from ships: a review of methods employed and a suggestion for a standardised approach. *Auk* 101: 567–577.
- , —, Blake, B. F., & Dixon, T. J. 1985. The marine distribution of the Gannet in the North Sea. *Bird Study* 32: 82–90.
- Wanless, S. 1987. *A Survey of the Numbers and Breeding Distribution of the North Atlantic Gannet Sula bassana and an Assessment of the Changes Which Have Occurred Since Operation Seafarer 1969/70*. NCC, Peterborough.
- , Murray, S., & Harris, M. P. 1986. Gannets – a boom in numbers and distribution. *BTO News* 145: 8.
- , — & — 2005. The status of Northern Gannet in Britain & Ireland in 2003/04. *Brit. Birds* 98: 280–294.

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