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Distribution and foraging interactions of seabirds and marine mammals in the North Sea: multispecies foraging assemblages and habitat-specific feeding strategies

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The top-predator community in the northwest North Sea consists of 50 species of seabirds and marine mammals, most of which are piscivorous. Sandeels are important prey for many species, and reduced sandeel abundance has had detectable consequences for breeding success, most notably in surface-feeding seabirds. In recent years, breeding success and population trends of seabirds nesting along the east coast of Britain have differed among species, suggesting species-specific responses to fluctuating prey stocks. A large-scale, multi-disciplinary study of top-predator distribution patterns and at-sea foraging behaviour was conducted in the northwest North Sea to investigate some of the behavioural mechanisms underlying these species-specific population responses. This approach provided new insights into the ways in which marine predators utilize a shared prey resource. At-sea distributions of some of the smaller seabirds, such as black-legged kittiwakes, suggested individuals avoided feeding in inshore areas used by the larger *Larus* gulls. This resulted in an apparently counter-intuitive, positive relationship between annual breeding success and foraging range, with productivity tending to be lower in years when oceanographic conditions led to good foraging areas occurring closer inshore. Combining distributional data with information on activity patterns showed that northern gannets used different foraging strategies in nearshore and offshore habitats and that chick-rearing common guillemots utilized

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spatially segregated, colony-specific feeding areas. Many surface-feeding and plunge-diving seabirds relied heavily on facilitation by pursuit-diving predators, such as auks and cetaceans.

Sandeels Ammodytidae are major prey for top predators in the North Sea such as seabirds (Furness 1990, Lewis *et al.* 2001), cetaceans (Santos *et al.* 2004) and pinnipeds (Hammond & Fedak 1994). Severe effects of sandeel stock collapses on some species have been reported (Bailey *et al.* 1991), but the relationship between prey density and availability to predators remains poorly understood. Some seabirds fail to reproduce in years when sandeel stocks are low (Monaghan *et al.* 1992), while other species adjust their foraging successfully or change prey (Martin 1989). Rindorf *et al.* (2000) investigated the potential impact of the industrial sandeel fishery on seabirds, assuming that breeding success of seabirds depended on sandeel availability and that the fishery may have reduced sandeel availability to a level at which avian reproductive output is affected. It appeared that breeding success was significantly reduced when sandeel availability to the fishery in June was low, but also that the timing of peak sandeel availability influenced reproductive output such that success was lower when availability peaked early.

Recent studies of factors influencing the availability of sandeels to four common seabirds off the British east coast, using a combination of data loggers on individual birds (Hamer *et al.* (Chapter 16 in this volume), Daunt *et al.* (Chapter 12 in this volume)) and observations at the colony, have provided detailed insight into the foraging activities. Such studies are essentially single-species investigations, and to examine the complicated interplay between predators, a large-scale study of the at-sea distribution, foraging behaviour, feeding interactions and hydrographical characteristics of the feeding areas of all avian and mammalian top predators was conducted. In this chapter we present data from systematic surveys of the northwest North Sea (area surveyed 54° to 59° N, 2° E – British east coast, Fig. 6.1, Box 6.1) in nine summers between 1991 and 2003. We use these results to focus on intra- and interspecific interactions between predators in different areas, examine their tendency to participate in feeding assemblages and investigate area usage in terms of multispecies foraging opportunities and broad-scale habitat characteristics.

TOP-PREDATOR COMMUNITY AT SEA

The seabird breeding population at the mainland coast between Banff and Humberside (54° to 58° 30′ N) in 2000 was estimated at 680 000

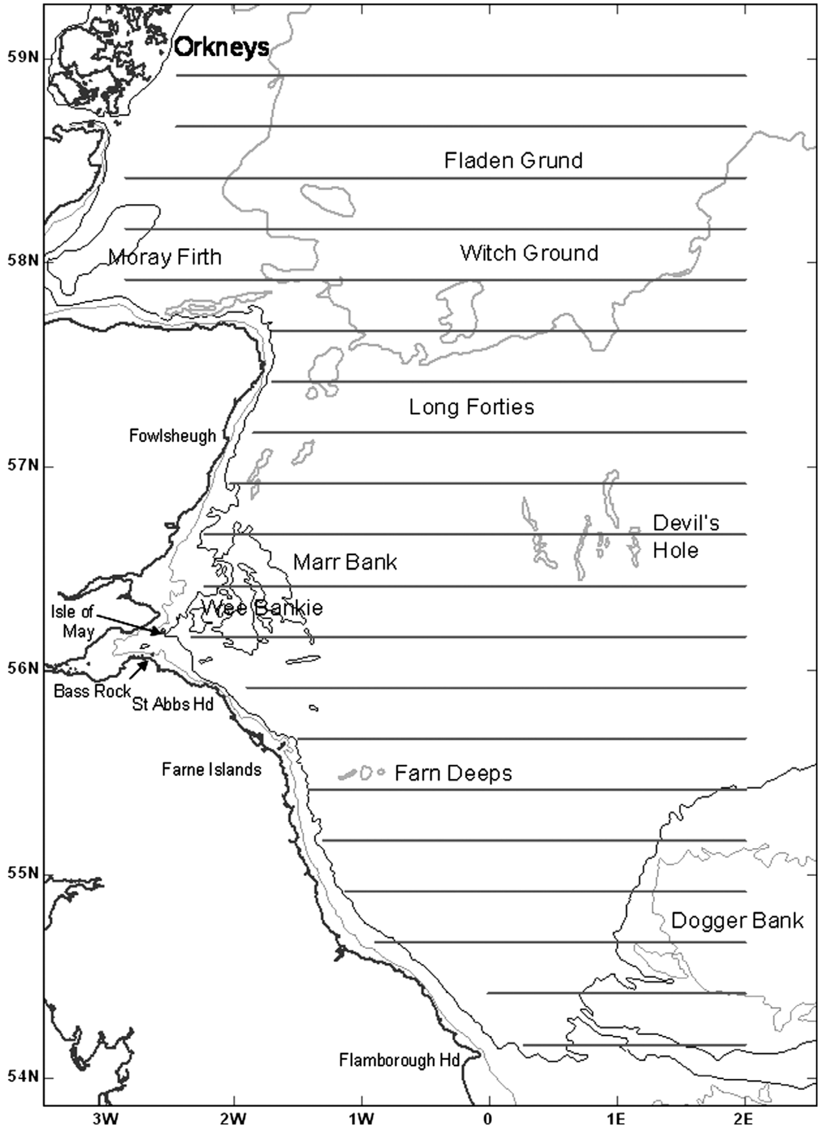

Fig. 6.1 Study area (54° to 59° N, 2° E to the coast) and locations of seabird colonies and oceanographic areas mentioned in the text. Isobaths for 30-, 50- and 100-m depths are shown, horizontal lines indicate ship-based transects (see Box 6.1).

Box 6.1 Recording seabirds and marine mammals at sea: general methods

At-sea densities of seabirds, seals, whales, dolphins and harbour porpoises were assessed during nine acoustics surveys by the fisheries research vessel *Tridens* in the northwest North Sea in June and July 1991–2003. Additional censuses were conducted on board RV *Pelagia* for a sub-sample of transects in the Wee Bankie area in June 2003. Census techniques were standardized strip-transect counts using 5- or 10-min intervals, and using a snap-shot for flying birds (Tasker *et al.* 1984) with special emphasis given to recording foraging behaviour and feeding assemblages (Camphuysen & Garthe 2004). Birds and mammals were detected by eye and identified by using 10 × 40 binoculars. Surveys were conducted along 20 transects perpendicular to the British east coast (Fig. 6.1), running from approximately 10 km from the coast out to a latitude of 2° E in the central North Sea. Additional data from CTD casts to sample water masses, and acoustic information on fish distribution, were collected during the 1999–2003 surveys.

pairs, comprising 19 species – with common guillemot *Uria aalge* (30% of the total population), black-legged kittiwake *Rissa tridactyla* (25%), Atlantic puffin *Fratercula arctica* (22%) and northern gannet *Morus bassanus* (7%) being most abundant (Mitchell *et al.* 2004). The relative abundances of seabirds recorded at the breeding colonies were mirrored in the numbers of birds seen within approximately 100 km of the coast. Small numbers of two species of *Puffinus* shearwaters, two storm-petrels Hydrobatidae, one *Phalaropus* phalarope, four skuas Stercorariidae and three *Larus* gulls occurred as non-breeding visitors. With divers Gaviidae, grebes Podicipedidae and seaduck Anatidae included, the overall summer seabird community comprised 39 species. Marine mammals present in the area included harbour seal *Phoca vitulina*, grey seal *Halichoerus grypus* and at least nine cetaceans, with harbour porpoise *Phocoena phocoena*, white-beaked dolphin *Lagenorhynchus albirostris* and minke whale *Balaenoptera acutorostrata* being the most abundant and widespread. Thus in total, the avian and mammalian top-predator community comprised at least 50 species.

Densities of both seabirds and seals declined with increasing distance from the coast, with values markedly lower beyond 100 km (Fig. 6.2a).

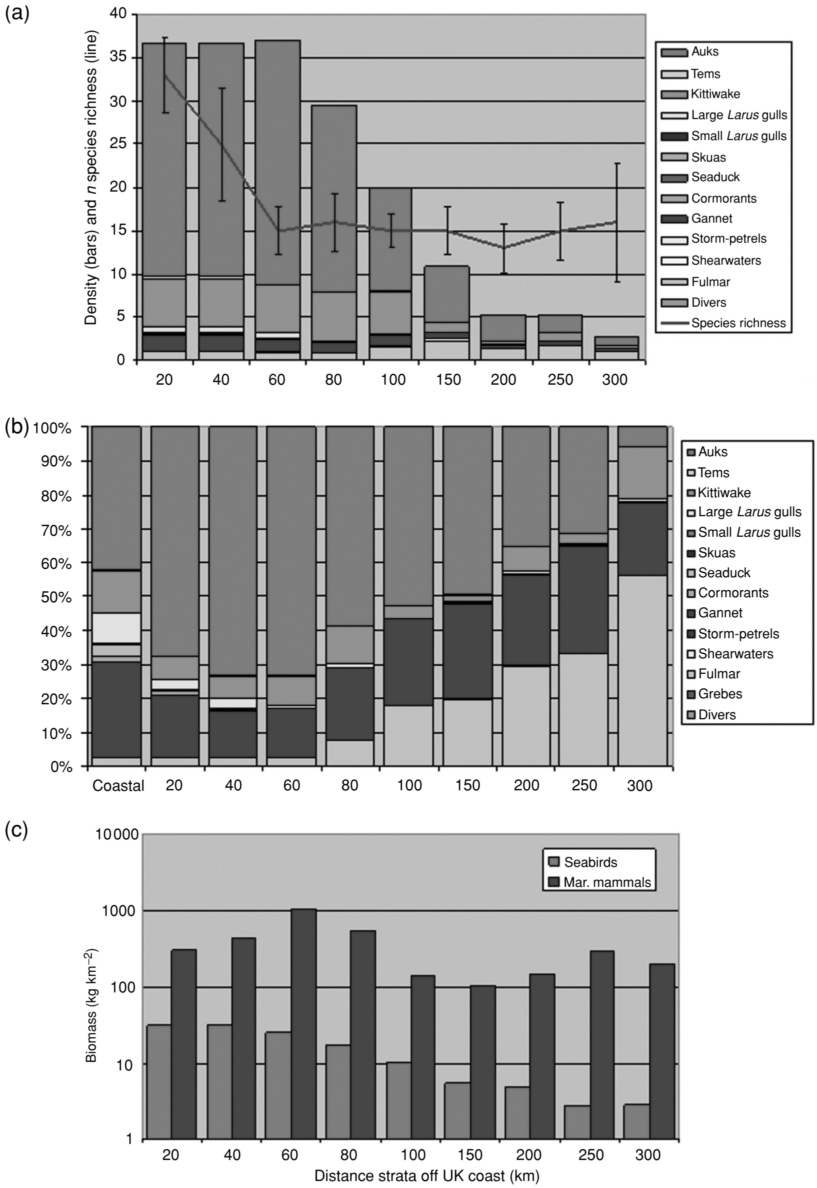

Fig. 6.2 Changes in top-predator community by distance from land. (a) Densities (n km^{-2}; stacked bars) and jack-knife estimate of species richness ($n \pm$ 95% Confidence interval; line). (b) Biomass as a percentage of total breeding population 1999–2003 (Mitchell *et al.* 2004) from summer censuses of divers Gaviidae and seaduck Anatidae in nearshore waters (Pollock & Barton 2004); percentage of the breeding population and counts of non-breeding bird species from the coast derived from ship-based surveys in June–July 1991–2003. (c) Biomass estimates for all seabirds and marine mammals (Mar. mammals; pinnipeds and cetaceans combined).

In the case of seabirds, species richness also declined substantially with distance (Fig. 6.2a). Predator groups for which >60% of individuals were recorded within 40 km of the coast included divers, grebes, cormorants, shearwaters, seaduck, skuas, *Larus* gulls, terns Sternidae and seals. Groups with a slightly more offshore distribution (>70% of individuals recorded within 80 km of the coast) included northern gannet, phalaropes, black-legged kittiwake, auks, whales and harbour porpoise. Predators found furthest away from the coast (50% to 75% of individuals recorded >80 km from land) included European storm-petrel *Hydrobates pelagicus*, dolphins and North Atlantic fulmar *Fulmarus glacialis*. In biomass terms, the seabird community within 80 km of the coast was dominated by pursuit-diving auks, whereas deep-plunging northern gannets and surface-feeding northern fulmars were most important further offshore (Fig. 6.2b). However, marine mammal biomass greatly exceeded that of seabirds in all areas (Fig. 6.2c).

FORAGING RANGE

In general, the highest densities of foraging seabirds between the Farne Islands and Moray Firth/Witch Ground were observed within 100 km of the coast (Figs 6.1 and 6.2a). The offshore boundary of this feeding zone was typically quite abrupt, being characterized by high densities of black-legged kittiwakes, common guillemots and razorbills *Alca torda*. A comparison of annual observations along 11 transects running perpendicular to the coast between the Farn Deeps and the Moray Firth (Fig. 6.1), indicated that the mean (±SE) of this boundary occurred between 33 ± 12 km (1998) and 60 ± 5 km (1997) of the coast (range 5 to 100 km for individual transects). In 1999, the boundary was difficult to identify, with high densities of foraging seabirds recorded 35 km from the coast on one of the transects, but with the transition zone between high and low feeding densities being diffuse on the other 10 transects.

Concurrent with these surveys, the foraging locations of several seabird species were recorded using data loggers deployed on breeding adults (Daunt *et al.* (Chapter 12 in this volume), Hamer *et al.* (Chapter 16 in this volume)). This provided a unique opportunity to compare findings from ship-based surveys with data from seabirds of known origin and breeding status. In the case of common guillemots, birds carrying fish – presumably back to the colony either to feed chicks or for display – were frequently recorded during survey transects. Flight directions of individuals heading towards land suggested that breeders from different colonies were using spatially discrete foraging areas. Comparing these results with information on diving locations, obtained using activity loggers deployed on chick-rearing adults on the Isle of May in 2003, showed that there was close agreement between the two methods, with birds feeding predominantly on the western side of the Wee Bankie. In addition, the at-sea surveys suggested that common guillemots from the Farne Islands and St Abb's Head were using the southern part of the Marr Bank, while birds from Fowlsheugh foraged mainly in the northern part (Fig. 6.1). These results indicate maximum foraging ranges of 50 km for common guillemots from the Isle of May, 55 km for St Abb's Head, 70 km for the Farne Islands and at least 110 km for Fowlsheugh.

FORAGING-HABITAT CHARACTERISTICS

The study area is part of the Northeast Atlantic shelves province of the Atlantic coastal biome (Longhurst 1999) and contains two distinct hydrographic regions: North Atlantic waters, which occupy most of the central North Sea, and Scottish coastal waters (Otto *et al.* 1990, Scott *et al.* (Chapter 4 in this volume)). During the winter months, lower levels of solar radiation combined with stronger winds and tidal friction leave the water column throughout the North Sea completely mixed. Only in the spring does the surface layer in deeper areas begin to warm due to increasing amounts of sunlight and decreasing winds. This warming creates a difference in density between the upper and lower layers of the water column and the onset of the resulting stratification allows plankton to stay above the critical depth needed for population growth and marks the beginning of seasonal primary production (Scott *et al.* (Chapter 4 in this volume)). In shelf seas, shallow sea fronts, also known as tidal mixing fronts, separate inshore areas that are permanently vertically mixed due to their shallow depth and/or strong tidal currents, from areas that stratify due to deeper depths and/or weaker tidal currents (Simpson 1981, Scott *et al.* this volume). Top predators frequently congregate around these shallow sea fronts that are associated with increased abundances of fish, larvae and zooplankton (Pingree *et al.* 1975, Pingree & Griffiths 1978, Richardson *et al.* 1986). The exact locations of the fronts change over the spring and summer months in response to weather conditions, and the monthly and daily rhythm of tidal speeds. A 'stratification index', defined as the difference in density between the sea surface and the bottom, can be used to identify the locations of fronts (Heath & Brander 2001). The offshore boundary of the area used by many seabirds and marine mammals repeatedly identified from at-sea surveys, typically coincided with this frontal zone, where the stratification index ranged from 0.6 to 0.8 (cf. Ollason 2000).

FORAGING BEHAVIOUR AND MULTISPECIES FEEDING ASSOCIATIONS (MSFAs)

Small, short-lived MSFAs (Box 6.2) were frequently recorded in the coastal foraging zone, particularly around the shallow sea front. The tendency to participate in such MSFAs differed among the various species (Table 6.1). Black-legged kittiwakes frequently acted as catalysts or initiators in MSFA formation, large gulls and skuas quickly joined in, with the former acting as scroungers or suppressors, while the latter were peripheral, aerial kleptoparasites (see Box 6.2 for definitions of these terms). Small species such as storm-petrels and terns rarely joined feeding aggregations, except at the periphery, possibly because such birds are likely to lose out in direct competition with other predators. Auks were normally joined by other seabirds and rarely joined existing aggregations (0.3% of cases, $n = 3277$ MSFAs recorded within 100 km of the coast). The most common type of MSFA in coastal waters formed over groups of feeding common guillemots and/or razorbills (76%, $n = 3277$), puffins (13%) or harbour porpoises (3%). Within 40 km of the coast, about one-quarter of MSFAs (26%, $n = 1518$) were targeted by large *Larus* gulls, and the arrival of these species rapidly prevented further access by catalysts. In contrast, only 6% ($n = 1759$) of MSFAs more than 40 km from land were targeted by large gulls, and black-legged kittiwake foraging activities tended to be concentrated in these aggregations. The apparent avoidance by black-legged kittiwakes of the inshore areas used by the large gulls resulted in a counter-intuitive, positive relationship between kittiwake annual breeding success and foraging range ($r_S = 0.68$, $n = 9$, $p < 0.05$) such that success tended to be lower in years when the shallow sea front occurred closer inshore. Northern gannets joined 18% of MSFAs ($n = 3277$), and their arrival typically rapidly disrupted the foraging opportunities of all the other participants, including other gannets and auks.

Large differences in feeding activity, as well as in the frequency of occurrence of MSFAs, were recorded when comparing transects crossing the shallow sea front. On some occasions only large flocks of inactive (resting or preening) seabirds were encountered while on others high numbers of birds and MSFAs were recorded. A dedicated cruise in 2003 revealed that foraging activity in these areas varied during the day in relation to changes in tidal currents, suggesting that physical processes may help drive prey towards the

Table 6.1. Proportion of surface-feeding and plunge-diving seabirds participating in MSFAs[a], behavioural characteristics and role within MSFAs (see Box 6.2), main feeding area[b] and the type of diving predator producing the MSFA (see Box 6.2)

Species	MSFA (%)	Feeding behaviour and MSFA role	Distance	Producer
Arctic skua (*Stercorarius parasiticus*)	93	Kleptoparasite, joining	Nearshore	—
Great skua (*S. skua*)	89	Kleptoparasite, joining	Nearshore	—
Herring gull (*Larus argentatus*)	90	Klepto/surface-seizing, suppressor	Nearshore	Auks
Great black-backed gull (*L. marinus*)	88	Klepto/surface-seizing, scrounger	Nearshore	Auks
Lesser black-backed gull (*L. fuscus*)	86	Klepto/surface-seizing, scrounger	Nearshore	Auks
Manx shearwater (*Puffinus puffinus*)	86	Pursuit-plunging, joining	Nearshore	Auks
Black-legged kittiwake (*Rissa tridactyla*)	72	Dipping, catalyst	Offshore	Auks
Northern gannet (*Morus bassanus*)	62	Plunge-diving, scooping, suppressor	Offshore	Cetaceans
North Atlantic fulmar (*Fulmarus glacialis*)	47	Surface-pecking, joining	Pelagic	—
Arctic tern (*Sterna paradisaea*)	38	Shallow-plunging, catalyst	Nearshore	—
Sandwich tern (*S. sandvicensis*)	22	Shallow-plunging, catalyst	Nearshore	—
Common tern (*S. hirundo*)	9	Shallow-plunging, catalyst	Nearshore	—
European storm-petrel (*Hydrobates pelagicus*)	1	Dipping, joining	Pelagic	—
Black-headed gull (*L. ridibundus*)	1	Dipping, joining	Nearshore	—

[a] Individuals foraging within MSFAs as a percentage of total observed feeding.
[b] Feeding distances: nearshore, <40 km; offshore, 40–80 km; pelagic, >80 km.

Box 6.2 Multispecies feeding associations (MSFAs)

Small, short-lived MSFAs are an important strategy used by numerous species of seabirds to obtain prey (Camphuysen & Webb 1999). Typically, small, social-feeding flocks of auks drive a dense ball of fish towards the surface in a concerted effort and exploit this resource from below ('producers'; see Fig. 6.3). The term 'social feeding' is used, because the auks dive and surface simultaneously and cooperate in their attempts to drive a fish ball towards the surface. Actively searching black-legged kittiwakes are normally the first to discover and exploit the fish ball from above by dipping or shallow-plunging. As long as only small, surface-feeders such as black-legged kittiwakes are involved, even when the size of the flock increases substantially (to 10 to 20 individuals) the producers can continue feeding seemingly undisturbed. When the auks simultaneously surface for air, the activity of the black-legged kittiwakes normally ceases, but resumes as soon as the auks dive again. Black-legged kittiwakes act as 'catalysts' or 'initiators' of MSFAs by attracting other predators. Herring gulls *Larus argentatus*, great black-backed gulls *Larus marinus* and northern gannets *Morus bassanus* arriving on the scene typically act as 'scroungers' or 'suppressors' by taking over the surface-feeding opportunities from smaller species (interspecific interference competition). Suppressors attack the fish ball forcefully, causing producers to swim away and the MSFA breaks down shortly after. Catalysts normally outnumber producers by a factor of 2; for example, mean flock size ($\pm$SE) for black-legged kittiwakes was 9.7 ± 0.9 compared with 4.7 ± 0.3 for common guillemots, and 3.9 ± 0.7 for black-legged kittiwakes versus 2.4 ± 0.2 for razorbills. A second common type of MSFA for seabirds is generated by hunting pods of dolphins or harbour porpoises.

surface (Camphuysen & Scott 2003). Inactive periods were recorded more frequently in black-legged kittiwakes than in common guillemots (Fig. 6.4), with the latter continuing to feed at certain phases of the tide when black-legged kittiwakes had stopped entirely. Common guillemot feeding activity was more evenly spread over the day than that of kittiwakes. Clearly more surveys are needed to investigate these interspecific differences further.

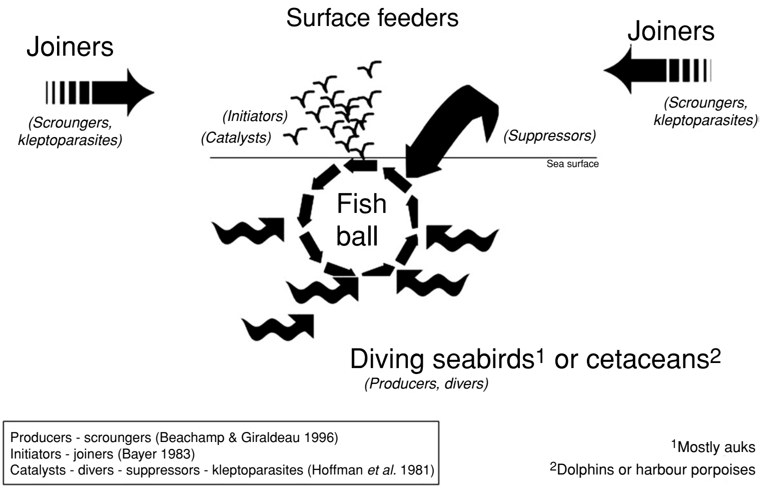

Fig. 6.3 Schematic representation of an MSFA with diving auks and facilitated surface-feeders. (Redrawn from Camphuysen and Webb (1999).)

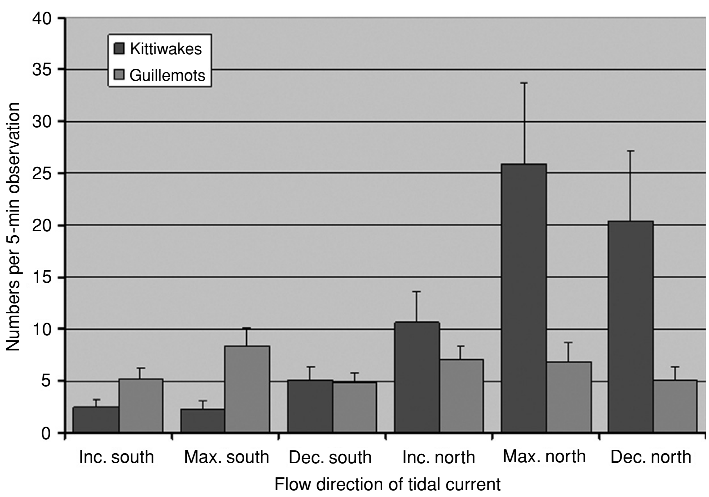

Fig. 6.4 Foraging black-legged kittiwakes and common guillemots (number ± SE per 5-min observation) with changing tide during continuous surveys in the Marr Bank area (the full tidal cycle was surveyed twice, 12–13 June 2003; 56° 15′ N, 01° 30′ W). On the *x*-axis, indications of currents running south (ebb: increasing (Inc.), maximum (Max.) and decreasing (Dec.)) and north (flood) during six tidal stages.

Northern gannets were encountered both inshore of the shallow sea front in mixed coastal waters and further offshore in the deeper, more stratified regions of the central North Sea. They used contrasting foraging techniques in the two regions but, unlike many of the other seabirds, the shallow sea front was less important as a feeding area. In inshore areas, northern gannets appeared to profit from MSFAs produced by prey-driving common guillemots and razorbills, with birds alighting or making shallow, oblique plunge-dives into the frenzy and scooping up sandeels while they were swimming. In contrast, in offshore waters, gannets usually fed on fish shoals that were herded towards the surface by dolphins or harbour porpoises and made vertical, deep plunge-dives (Camphuysen 2004). Of 496 herds of cetaceans recorded in the offshore region, northern gannets targeted 43.3%, a significantly higher frequency than that recorded inshore (16.2% of 723; $G_{\mathrm{adj}} = 108.6$, d.f. $= 1$, $p < 0.001$). Thus in inshore regions, northern gannets relied on feeding opportunities created by other seabird species while in offshore regions they were mainly associated with marine mammals, predominantly cetaceans.

DISCUSSION

In terms of biomass, the endotherm component of the top-predator community in the northwest North Sea is dominated by marine mammals, primarily cetaceans (Fig. 6.2c). Together with predatory fish and, in some years, an industrial sandeel fishery, marine mammals are likely to be the major consumers of sandeels in the region. The largest species, the minke whale, increased during the study period from average densities of 0.001 km^{-1} surveyed in 1991–5, to 0.002 km^{-1} in 1997–9, and to 0.005 km^{-1} in 2001–3. However, the lack of dietary information and consumption rates for minke whales makes it impossible to assess their impact with any certainty.

Of the 50 predator species studied during the ship-based surveys reported here, many were strictly coastal, some were far-ranging, while others showed intermediate distribution patterns. Near the coast, where densities of birds and seals were greater and avian species richness was also higher, interspecific interference competition was presumably most intense. Many of the top predators were associated with the shallow sea front marking the transition zone between mixed coastal waters and thermally stratified offshore waters. Black-legged kittiwakes, razorbills, common guillemots, harbour porpoises and minke whales were all most abundant in this frontal region. Offshore of the shallow sea front, densities of seabirds remained high although species richness declined. However, with relatively high densities of marine mammals, notably minke whales (Fig. 6.2), exploitation competition may have been more important in this part of the North Sea.

Water depth throughout most of the study area is less than 60 m and thus European shags *Phalacrocorax aristotelis*, razorbills, common guillemots, Atlantic puffins and all the marine mammals potentially have access to the entire water column within their respective foraging ranges. Terns, black-legged kittiwakes, northern fulmars and storm-petrels rely on the presence of prey near the water surface, while northern gannets are unlikely to dive deeper than 20 to 25m (Garthe *et al.* 2000). These differences in foraging capabilities have implications as to how prey stocks can be utilized by each predator. Piscivorous seabirds in most of the world's oceans exploit fish schools in multispecies flocks and the importance of these assemblages cannot be over-emphasized (Hoffman *et al.* 1981, Camphuysen & Webb 1999). Between 20 and 60 km off the coast, black-legged kittiwakes, common guillemots and razorbills together accounted for 80% of the seabird biomass (Fig. 6.2b). In this region, black-legged kittiwakes readily joined, and profited from, small flocks of common guillemots and razorbills driving sandeels and other fish in balls to the surface. Schooling by small fish does not apparently function as a deterrent to avian predators in the same way as it does for predatory fish (Brock & Riffenburg 1959). Most MSFAs included species that used complementary tactics when feeding together (e.g. pursuit-diving, plunge-diving, dipping, scooping, surface-pecking and aerial-pursuit; see Box 6.2). However, some of the large aerial species tended to exclude smaller species thereby preventing further access to the MSFA. Unexpectedly, northern gannets that joined these feeding frenzies obtained prey by scooping items from the surface rather than by plunge-diving. Some species – e.g. arctic terns *Sterna paradisaea* and European storm-petrels *Hydrobates pelagicus* – rarely, if ever, joined MSFAs; however, for at least eight other surface-feeding species, MSFAs must have contributed significantly to their daily prey intake (Table 6.1). In the case of black-legged kittiwakes, at-sea surveys suggested that birds avoided foraging in MSFAs near to the coast where they were more likely to be adversely affected by *Larus* gulls and where kleptoparasites such as skuas were most abundant.

Changes in numbers of many North Sea seabirds over the last 15 to 20 years have varied from long-term increases – e.g. in Atlantic puffins, common guillemots, razorbills and northern gannets – to declines, e.g. in black-legged kittiwakes, terns and European shags (Mitchell *et al.* 2004). Interestingly, while the reproductive success of sandeel specialists such as black-legged kittiwakes and shags in eastern Britain fluctuated in parallel ($r_S = 0.78$, $n = 14$, $p < 0.001$), their foraging habits and at-sea distribution differ radically. In contrast, while distributions of black-legged kittiwakes and common guillemots in this area appear to overlap, their breeding success was not correlated ($r_S = -0.05$, $n = 14$, not significant). Effects of reduced prey availability on breeding success are often more pronounced in surface-feeding seabirds such as black-legged kittiwakes and terns (Monaghan *et al.*, 1992, Rindorf *et al.*, 2000). These findings have led to suggestions that these species are most sensitive to changes in prey availability, particularly sandeels (Furness & Tasker 2000). Our survey work has emphasized the importance of the shallow sea fronts for black-legged kittiwake foraging and indicates that it also forms an outer barrier for birds breeding down the east coast of Britain (see also Daunt *et al.* (Chapter 12 in this volume)). In addition, combining information on at-sea distribution and activity with oceanographic data has highlighted the potentially complex interplay between seabird breeding success, feeding location and interspecific competition.

Given the increasing pressures on the North Sea ecosystem from both fisheries and climate change (Edwards & Richardson 2004, Huntington *et al.* 2004), using top predators to monitor ecosystem health is an attractive concept (Boyd & Murray 2001). However, as the results presented here clearly indicate, we are still a long way from having all the background knowledge required for such an approach. Only through multi-disciplinary projects such as those described here, will we start to understand the functional links between marine predators, their prey and the marine climate – and thus move towards ecosystem-based fisheries management.

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