Distribution and foraging interactions of seabirds and marine mammals in the North Sea: a metapopulation analysis

Kees (C.J.) Camphuysen[1], Beth Scott[2] and Sarah Wanless[3]

[1]Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands
[2]Aberdeen University, Tillydrome Avenue, Aberdeen AB24 2TZ, UK
[3]CEH, Hill of Brathens, Banchory, Aberdeenshire, AB31 4BW, UK

The top-predator community off the British east coast consists of 50 species of seabirds and marine mammals, most of which are piscivorous. Sandeels are important prey for many species, but reduced sandeel abundance has had detectable consequences on breeding success for few, mostly surface feeding seabirds. Breeding success and population trends differ between species, suggesting species-specific responses on fluctuating prey stocks. The IMPRESS project aimed at a detailed evaluation of prey availability issues, believed to enhance sandeel intake rates of four common seabirds with contrasting foraging techniques and area usage in the Wee Bankie area, using a combination of advanced technology and field observations. To put these observations into perspective, a metapopulation study of top-predator distribution patterns and at-sea foraging interactions was conducted in the NW North Sea. With numerous predators utilising the same prey or a similar resource, issues as facilitation, interference and exploitation competition, and kleptoparasitism have to be considered. Four target species were studied in the Wee Bankie area, but more predators seemingly interact and none were excluded beforehand in the metapopulation study. It was found that Black-legged Kittiwakes and Common Guillemots utilised a zone of variable width up to 80 or 100km away from the coast. Kittiwakes relied substantially on prey facilitation by auks and on habitat characteristics that were predictable, but sparse and patchy. European Shags occupied a rather separate nearshore area, while Northern Gannets avoided intra-specific competition by dispersal over a long range, deploying different foraging strategies in near- and offshore habitats.

Sandeels are major prey for top-predators in the North Sea such as seabirds[1,2], cetaceans[3] and pinnipeds[4]. Severe effects of sandeel stock collapses have occurred[5]. The relationship between prey density and availability to predators is still poorly understood and although some seabirds fail to reproduce in years when sandeel stocks are particularly low[6], other species are able to adjust their foraging successfully or change prey[7]. The IMPRESS project studied prey availability issues, believed to enhance sandeel intake rates of four common seabirds in the Wee Bankie area, using a combination of advanced technology (data loggers on individual birds)[8,9,10] and field observations (colony and at sea). To put these observations into perspective, a metapopulation study of top-predator distribution patterns and at-sea foraging interactions was conducted in the NW North Sea (54-59°N, 2°E to the UK coast; **Fig. 1**) in 9 summers between 1991 and 2003. This part of the project aimed at intra- and interspecific interactions between predators in different sea areas (feeding assemblages rather than foraging individuals) and to evaluate breeding success with area usage in terms of foraging opportunities as derived from broad-scale habitat characteristics.

Top-predator community

The seabird breeding population between Banff and Humberside (54°-58°N) recently numbered 680,000 pairs, comprising 19 species, with common guillemot *Uria aalge* (30%), black-legged kittiwake *Rissa tridactyla* (25%), atlantic puffin *Fratercula arctica* (22%), and northern gannet *Morus bassanus* (7%) being most abundant[11]. The relative abundance of each of these species is mirrored at sea, but with additional shearwaters (2), storm-petrels (2), phalaropes (1), skuas (4) and gulls (3 species) as non-breeding summer visitors in rather small numbers. With summering divers, grebes and seaduck included[12], the offshore seabird community comprises 39 taxa. Harbour seals *Phoca vitulina* and grey seals *Halichoerus grypus* breed on the British east coast and the offshore marine mammal community includes at least nine cetaceans, with harbour porpoise *Phocoena phocoena*, white-beaked dolphin *Lagenorhynchus albirostris*, and minke whale *Balaenoptera acutorostrata* being most abundant and widespread.

Densities of seabirds and seals decline with distance to the coast, with rather low levels at over 100km from the shore (**Fig. 2a**). Seabird species richness drops markedly beyond 40km from the coast, from 33 ± 4.3 species within 20km, 25 ± 6.5 between 20 and 40km to *c.* 15 species in all further distance strata. By mass, the seabird community within 80km from the coast is dominated by pursuit diving auks, whereas deep plunging northern gannets and surface feeding northern fulmars gain importance further offshore (**Fig. 2b**). Top-predator groups of which >60% occurred within 40km from the coast include divers, grebes, cormorants, shearwaters, seaduck, skuas, *Larus*-gulls, terns, and seals. Of northern gannet, phalaropes, black-legged kittiwake, auks, whales and porpoises, over 70% occurred within 80 km from the coast. Some 50% of storm-petrels, 54% of dolphins, and nearly 75% of the northern fulmars occurred further offshore (>80km). Seabird biomass is dwarfed by the biomass of marine mammals in all areas (**Fig. 2c**).

Breeding populations and reproductive success

Overall trends in the breeding population of mainly sandeel consuming seabirds along the British east coast varied, ranging from pronounced long-term increases in Atlantic puffins and northern gannets to consistent declines in surface feeding black-legged kittiwakes, sandwich and arctic terns[11]. Populations of nesting razorbills and common guillemots generally thrived, while European shags declined locally or were stable at best. The breeding success of guillemots at the Isle of May throughout 1990s and early 21st century was generally high but gradually declining (1990-2003, mean ± SD 0.75 ± 0.07; range 0.63-0.85), whereas that of kittiwakes and shags fluctuated, largely in concert (r_S = 0.78, n = 14, P < 0.01), with particularly low reproductive success in 1990 and 1993 (both), 1998 (kittiwake) and 1999 (both). In the study area at large[13], roughly similar trends were found in each of these species. Surface feeding sandwich terns in NE Scotland experienced reproductive failures in 1991 and 1994-1997 (0.2-0.3) and rather high levels of success in other years (0.4-0.9 chicks fledged pair^{-1}), but birds breeding in NE England performed very different (complete failure 1993, successful 1995-1997. Arctic terns were different again, with relatively successful pairs in NE England and lower success in Scotland. Near-complete failures in SE Scotland were reported in 1990, 1993, and 2002.

Foraging range

Within approximately 80km from the British coast, huge numbers of foraging seabirds were observed (**Fig. 2a**). The outer boundary was usually abrupt, characterised by numerous multi-species feeding frenzies (MSFAs; **Box 1**) and peak densities of for example foraging kittiwakes and minke whales. The precise location varied between 5 and 100km from the coast. Averaging observations along 11 fixed transects perpendicular to the coast, peak densities in the outer boundary were found between 33 ± 12km (1998) and 60 ± 5km (1997) from the coast. In one year (1999), particularly high densities were rarely found and an outer boundary was difficult to recognize along any transects.

Prey transporting guillemots were observed up until 70 km from the nearest coast, a range that largely spans the area where densities peak. Based on homing directions, area segregation could be demonstrated between the major colonies. For example, guillemots from the Isle of May dominated on the westernmost feeding grounds at Wee Bankie, whereas Marr Bank was occupied mostly by guillemots from Berwickshire and Northumberland (e.g. Farne Islands and St Abbs) in the south and by birds from Kincardine and Deeside (e.g. Fowlsheugh) in the north. Extremes in each of these areas suggest a maximum range of about 50km for guillemots from the Isle of May as opposed to at least 110 km for the 3x larger colonies at Fowlsheugh. Kittiwakes utilised a similar zone along the coast, but directions of flight were useless to pinpoint probable colonies of origin in the Wee Bankie/Marr Bank area. Logger data confirmed, however, that breeding birds frequently foraged up to 70km away from the colony[10]. An analysis of northern gannet data confirmed findings from satellite telemetry studies that the entire study area and beyond was utilised by Bass Rock breeding birds (350km around the colony and more)[9], which were found to concentrate searching and feeding in areas with low densities of conspecifics[15]. European shags occurred in nearshore waters only (<10km).

Foraging behaviour, MSFA formation

Between seabird species, there was a very different tendency to participate in multi-species feeding (**Table 1**). The commonest type of MSFA formed over social feeding (herding) guillemots (%), razorbills (%) or harbour porpoises (%). Surface feeding gulls and skuas readily joined, with large gulls typically acting as surface seizing scroungers, skuas as peripheral (aerial) kleptoparasites and kittiwakes as dipping or shallow plunging catalysts. Most lightweight, fragile species such as storm-petrels and terns rarely joined feeding frenzies except at the periphery, perhaps because these species have little to gain and much to loose in direct competition with other predators. Auks, as producers, were normally joined by others and were seldom seen to fly into an existing frenzy (0.4%, n = 2286). A detailed analysis of the associations of kittiwakes and guillemots showed that associations formed in particular areas, with guillemot distribution being much more widespread. High densities of foraging kittiwakes typically occurred in areas where MSFAs were both prominent (size) and widespread (frequency), demonstrating the importance of prey facilitation by diving taxa for this surface feeding species. Nearshore MSFAs were often targeted by large *Larus* gulls, that excluded further access by catalysts upon arrival (28% within 20km (n = 2006), 24% within 40km from the coast (n = 2827), and MSFA forming kittiwakes peaked at greater distances where only 5-6% of MSFAs were targeted by large gulls. In these offshore waters (40-100km), northern gannets joined *c.* one out of ten MSFAs as scroungers (6-12%, n = 4683), ruining the foraging opportunities for all predators (gannets and driving auks included) within minutes. Feeding techniques of gannets included shallow plunge diving, scooping and pursuit diving. In offshore, thermally stratified waters of more than 50m depth, deep plunging gannets mainly profited from more stable fish shoals herded towards the surface by dolphins and porpoises[15].

Stratification and the formation of the shallow sea front within the North Sea

The physical characteristics of the shallow North Sea are dominated by tides, winds and solar radiation[16]. The main seasonal difference in the vertical characteristics of the water column are determined by depth and the speed of the tides[17]. During the winter months, low levels of radiation, stronger winds and tidal friction leave the water column completely mixed. In spring, with increasing amounts of sunlight and the lessening of winds do surface waters in areas which are deep enough (ie where the effect of tidal mixing does not reach the surface) begin to warm. This warming creates a difference in density between the upper and lower layers of the water column called stratification, the onset of which allows plankton to stay above the critical depth needed for population growth such that the timing of stratification is generally believed to herald the beginning of the seasonal flush of primary production called the ‘spring bloom’.

The locations of the areas that stratify within the North Sea change over the spring and summer months with increasing levels of radiation, less wind and the monthly and daily rhythm of tidal speeds.

Therefore the exact location that marks the frontal region between areas that remain mixed and those that are stratified is never static[18] and can be used to identify the locations of fronts.

The amount of primary production found within stratified regions also changes with the seasons. Nutrients are used up by primary produces in the upper water warmer layers such that after the spring bloom the areas of high primary production are confined to the regions where cooler, mixed, nutrient rich water is mixed into warmer stratified regions. This can occur at horizontal frontal areas between the stratified and more mixed regions or in the vertical at the boundary (pycnocline) between the upper warm layer and lower cool layer within stratified regions[19]. These frontal regions are areas with a marked increase abundance of higher trophic levels foraging on concentrations of fish, larvae and zooplankton within the fronts.

Foraging hotspots

The 'stratification index' is the difference between the bottom and surface density values (density being a function of both temperature and salinity). Values between 0.3–0.4 divide completely mixed and slightly stratified water with the beginnings of a pycnocline, values between 0.6 and 0.8 are locations where birds were found to be foraging in very high densities and where most MSFAs are formed; generally the outer boundary of the feeding range as discussed above[20], at the outer edge of thermally mixed coastal water. This Shallow Sea Front is normally within reach of both breeding kittiwakes[10] and guillemots, explaining the very high densities that are normally found here. Gannets occur within and beyond the front in numbers suggesting that the area is of secondary importance, but MSFAs at the front do attract them. For terns and large Larus gulls, the front is usually out of reach and densities there are generally rather low. Further hydrographical characteristics of patches within the front and occupied by MSFAs utilised by surface feeding kittiwakes include high near-surface chlorophyll fluorescence levels indicating primary productivity. Detailed studies in 2003 revealed that foraging hotspots may gain and lose importance during the day and that physical processes that drive prey towards the surface may be caused by the interaction between bathymetry and tidal currents (internal waves).

Discussion

The area studied is part of the Northeast Atlantic shelves province in the Atlantic coastal biome[21]. The distribution and abundance of (top-)predators is limited by the distribution and abundance of their prey and they will occupy a subset of the areas occupied by prey species at lower trophic levels[22]. Once stratification is reimposed in spring, tidal fronts at the boundary between mixed and thermally stratified water are quite predictable in location. These frontal regions are areas where concentrations of fish, larvae and zooplankton are found. Many of the top-predators observed in the area responded in one way or the other to the front[14], but the effect was probably most profound in black-legged kittiwakes, common guillemots, and minke whales.

Sandeels are abundant prey, targeted by numerous species using contrasting feeding techniques and in different parts of their range. Sandeels settled in the sand require different attack strategies than sandeels foraging in the water column and actively swimming older individuals are different from passive larvae. By biomass, the top-predator community off the Scottish east coast is overwhelmingly dominated by marine mammals (range 1:10 – 1:100 in different distance strata away from the coast; **Fig. 2c**), mainly whales and dolphins, animals that have no ties to a particular breeding site and that may target sandeels anywhere in the water column, including the sea floor. Together with predatory fish and (in some years) fisheries, marine mammals must be the most important consumers of sandeels in the region, but they do not necessarily target the same age classes as seabirds do.

Central place foraging, colony nesting seabirds are constrained by high energetic costs of long-distance flights and diving. Some birds can search the entire water column, others cannot and rely on other predators or temporal and spatial variations in the hydrographic structure to make prey available in the upper layers. It is in surface feeding seabirds that the effects of food shortages (lower prey stock) are usually most prominent[23]. Both the at-sea data and information derived from tagged individuals travelling in and out the colony suggest non-overlapping feeding areas between colonies, but the overall trends in breeding success in the area at large are broadly similar. In terns, sandeel specialists with rather different breeding results between colonies, most of the failures seemed related to specific problems within colonies (depredation, rain, floodings) on top of the effects of prey availability. A direct comparison between kittiwakes (erratic breeding results) and guillemots (more constant success) suggests that the former depends on more specific foraging opportunities (patchy, surface layers) than the latter (all the water column). Terns, that do not so much rely on prey facilitation by diving auks, are restricted to small feeding range, rely on their own searching capacities, and utilise a thin layer of (surface) water.

The sensitive kittiwake occupies a coastal area that is particularly rich in other predator species, but it travels further away from the coast than most. Between 20 and 60 km from the coast, kittiwakes and auks together account or 80% of the seabird biomass (**Fig. 1b**). The position of the Shallow Sea Front (backed up with CTD and XBT data[20]), usually indicated by the abrupt decline in feeding activity and seabird density, was normally well within range of birds breeding on the Scottish east coast (30-60km)[10]. The day to day position fluctuations require further study, however, as well as the observation that during the day feeding activity varied considerably, probably in response to the tidal phase. Using the mean positions of the front in 9 years of study, relatively poor breeding results coincided with seasons in which the feeding frenzies occurred relatively near the coast (<35km), whereas good results were recorded when peak densities occurred further out to sea (>35km; r_S 0.68, $n = 9$, $P < 0.05$). This counter-intuitive result may have resulted from inter-specific competition with large *Larus* gulls targeting MSFAs more frequently near the coast, or simply that a wider foraging range opened up a more varied mosaic of foraging opportunities between the colony and the front.

Box 1. Multi-species feeding associations (MSFAs)

Small, short-lived multi-species foraging assemblages are an important mechanism to obtain prey off the British east coast for numerous species of seabirds[14]. Typically, small social feeding flocks of auks (mainly guillemots or razorbills) drive a dense ball of fish towards the surface in a concerted effort and exploit this resource from below (producers; **Fig. I**). Actively searching kittiwakes are normally the first to discover such a situation and start exploiting from above. Their behaviour (dipping or shallow plunging) ensures that the producers can continue feeding and when the auks surface for air, the activity of the kittiwakes normally ceases, to be resumed as soon as the auks dive again. Kittiwakes act as catalysts for conspecifics as well as for other predators and scroungers arrive soon. Typical scroungers near the coast are herring gulls and great black-backed gulls. Northern gannets as scroungers are more widespread. Scroungers attack the fish ball forcefully, such that driving auks soon give up and swim away, and typically exclude the catalysts from further access to the feeding frenzy by their aggression (inter-specific interference competition). Intake rates of catalysts that only attract conspecifics probably decline with increasing numbers of birds at the scene. In situations where only conspecifics were attracted, kittiwakes outnumbered producers with a factor 2 over both guillemots (mean flock size ± SE: 9.7 ± 0.9 kittiwakes versus 4.7 ± 0.3 auks) and razorbills (3.9 ± 0.7 versus 2.4 ± 0.2), while equal numbers occurred with atlantic puffins (1.9 ± 0.1 versus 1.8 ± 0.1). Only Atlantic puffins were frequently kleptoparasitised by kittiwakes under these circumstances and evidence for their herding capacities is weak. The mechanism of facilitation, where surface feeders gain access to fish that would normally be to deep in the water column, is particularly common near the frontal boundary between stratified central North Sea water and mixed coastal water and over bank edges in the Wee Bankie area.

Fig. I. Schematic representation of a multi-species feeding association with driving auks and facilitated surface feeders.

References

1. 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.
2. Lewis, S., Wanless, S., Wright, P.J., Harris, M.P., Bull, J. and Elston, D.A. (2001) Diet and breeding performance of Black-legged Kittiwakes Rissa tridactyla at a North Sea colony. Mar. Ecol. Progr. Ser. 221: 277-284.
3. Santos, M.B., Pierce, G.J., Learmonth, J.A., Reid, R.J. , Ross, H.M., Patterson, I.A.P., Reid, D.G., and Beare, D., (2004) Variability in the diet of Harbor Porpoises (*Phocoena phocoena*) in Scottish waters 1992-2003. Mar. Mamm. Sc. 20: 1-27.
4. Hammond, P.S. and Fedak, M.A., (eds) (1994) Grey seals in the North Sea and their interactions with fisheries. MF 0503, Final Report to the Ministry of Agriculture, Fisheries and Food, Sea Mammal Research Unit, Cambridge, 157pp.
5. Bailey, R.S., Furness, R.W., Gauld, J.A. and 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.
6. Monaghan, P., Uttley, J.D. and Burns, M.D. (1992) Effect of changes in food availability on reproductive effort in arctic terns *Sterna paradisaea*. Ardea 80: 71-81.
7. Martin, A.R. (1989) The diet of Atlantic Puffin *Fratercula arctica* and Northern Gannet *Sula bassana* chicks at a Shetland colony during a period of changing prey availability. Bird Study 36: 170-180.
8. Humphreys E.M. (this volume), Foraging behaviour of the Northern gannets: insights using data loggers.
9. Hamer K. (this volume) Foraging gannets: colony size, prey patchiness and foraging area fidelity.
10. Daunt F., Wanless S., Peters, G., Benvenuti S., Sharples J., Grémillet D. & Scott B. (this volume) Impacts of oceanography on the foraging dynamics of seabirds in the North Sea.
11. Mitchell, P.I., Newton, S.F., Ratcliffe, N. and Dunn, T.E. (2004) Seabird populations in Britain and Ireland. T. & A.D. Poyser, London, 511pp.
12. Pollock, C. and Barton, C. (2004) Review of divers, grebes & seaduck distribution and abundance in the SEA 5 area. Poster presentation 8th Intern. Seabird Group Conference, King's College Conference Centre, Aberdeen University, 2-4 April 2004, Aberdeen.
13. Seabird numbers and breeding success in Britain and Ireland, 1991-2002 [in series]. UK Nature Conservation Nos. 6-27, Joint Nature Conservation Committee, Aberdeen
14. Camphuysen, C.J. and Webb, A. (1999) Multi-species feeding associations in North Sea seabirds: jointly exploiting a patchy environment. Ardea 87(2): 177-198.
15. Camphuysen, C.J. (2004) Area-specific feeding behaviour of central place foraging Northern Gannets *Morus bassanus* from the Bass Rock (North Sea). Oral presentation 8th Intern. Seabird Group Conference, King's College Conference Centre, Aberdeen University, 2-4 April 2004, Aberdeen.
16. Simpson, J.H. and Hunter J.R. (1974)Fronts in the Irish Sea. Nature 250:404-406.

17. Pingree , R.D., Bowman, M.J. and Esaias, W.E.(1978) Headland fronts, pp.78-86 In. M.J. Bowman and W.E. Esaias (Eds) Oceanic Fronts in Coastal Processes. Springer-Verlag, Berlin.
18. Simpson, JH. (1981) The shelf-sea fronts: implications of their existence and behaviour. Phil. Trans. R. Soc. Lond. A 302:531-546.
19. Pingree, R.D, Pugh, P.R. Holligan, P.M. and Forster, G.R. (1975) Summer phytoplankton blooms and red tides along tidal fronts in the approaches to the English Channel. Nature 258:672-677.
20. Ollason J.G. (ed.) 2000. Modelling the Impact of Fisheries on Seabirds. Final Report CFP 96-079, University of Aberdeen, Aberdeen.
21. Longhurst A.R. 1999. Ecological Geography of the Sea. Academic Press.
22. Holt, R.D. (1997) From metapopulation dynamics to community structure: some consequences of spatial heterogeneity. In: Hanski, I.A. and Gilpnin, M.E. (eds) Metapopulation biology: 149-165. Academic Press, California.
23. Rindorf A., Wanless S. & Harris M.P. 2000. Effects of changes in sandeel availability on the reproductive output of seabirds. Mar. Ecol. Progr. Ser. 202: 241-252.

Table 1. Participation of surface feeding and plunge diving seabirds in multi-species foraging associations within 100km from the coast (numbers of individuals seen feeding or searching for prey within and outside MSFAs) and behavioural characteristics within such groups (see also Box 1).

Species	Mono-specific	MSFA	%MSFA	MSFA behaviour
Arctic Skua	4	56	93	kleptoparasite, joining
Great Skua	7	54	89	kleptoparasite, joining
Herring Gull	224	1971	90	klepto / surface seizing, scrounger
Great Black-backed Gull	8	61	88	klepto / surface seizing, scrounger
Lesser Black-backed Gull	24	149	86	klepto / surface seizing, scrounger
Manx shearwater	10	61	86	pursuit plunging, joining
Kittiwake	6150	15673	72	dipping, catalyst
Northern Gannet	1418	2279	62	deep plunging, scooping, scrounger
Northern Fulmar	633	554	47	surface pecking, scrounger
Arctic Tern	600	372	38	shallow plunging, catalyst
Sandwich Tern	214	61	22	shallow plunging, catalyst
Common Tern	173	17	9	shallow plunging, catalyst
Storm-Petrel	334	3	1	dipping, joining
Black-headed Gull	145	1	1	dipping, joining

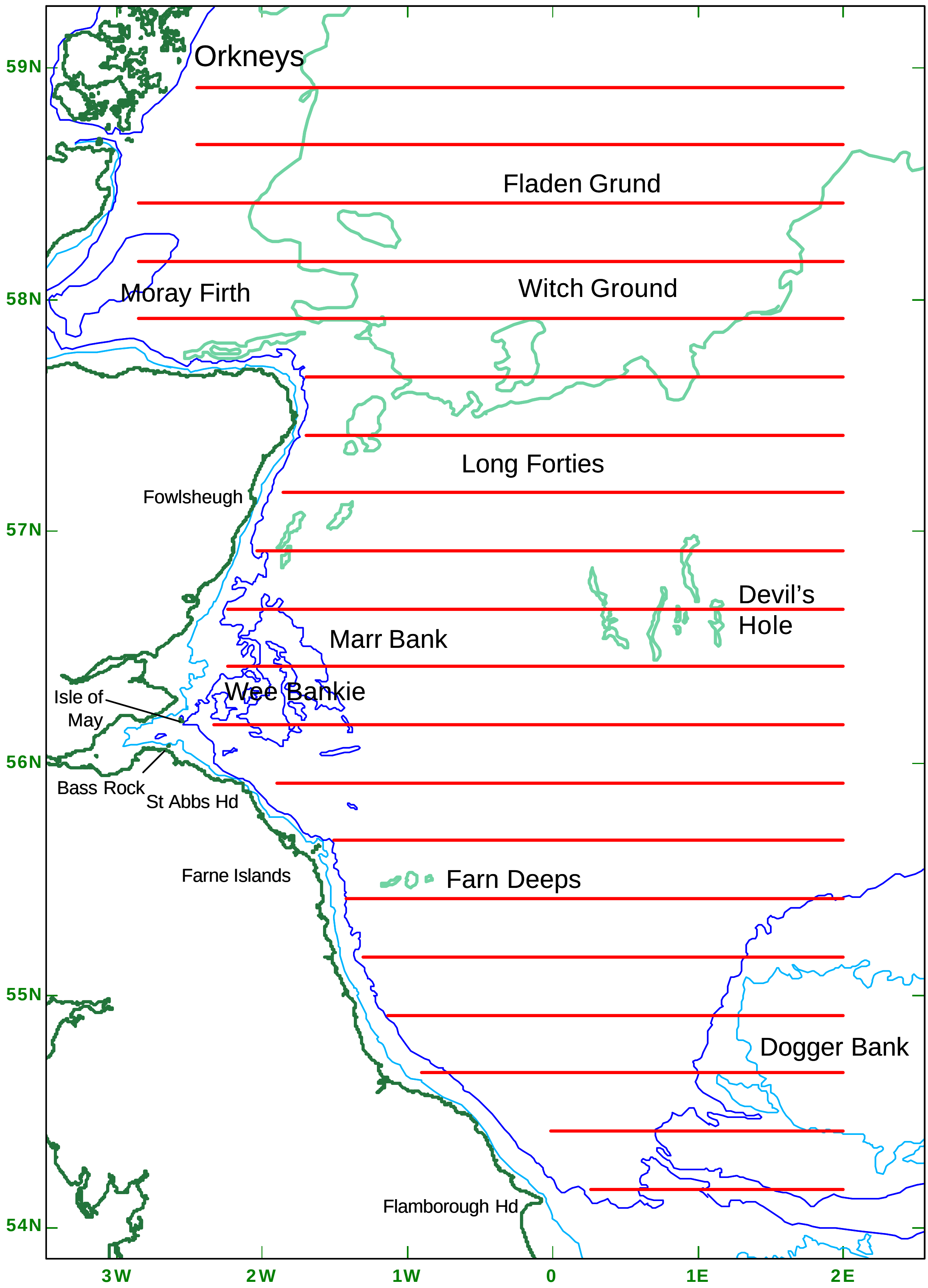

Fig. 1. Study area (54°-59°N, 2°E-coast) and locations mentioned in the text. Depth contours indicate 30, 50 and 100m depth, horizontal lines indicate transects perpendicular to the coast.

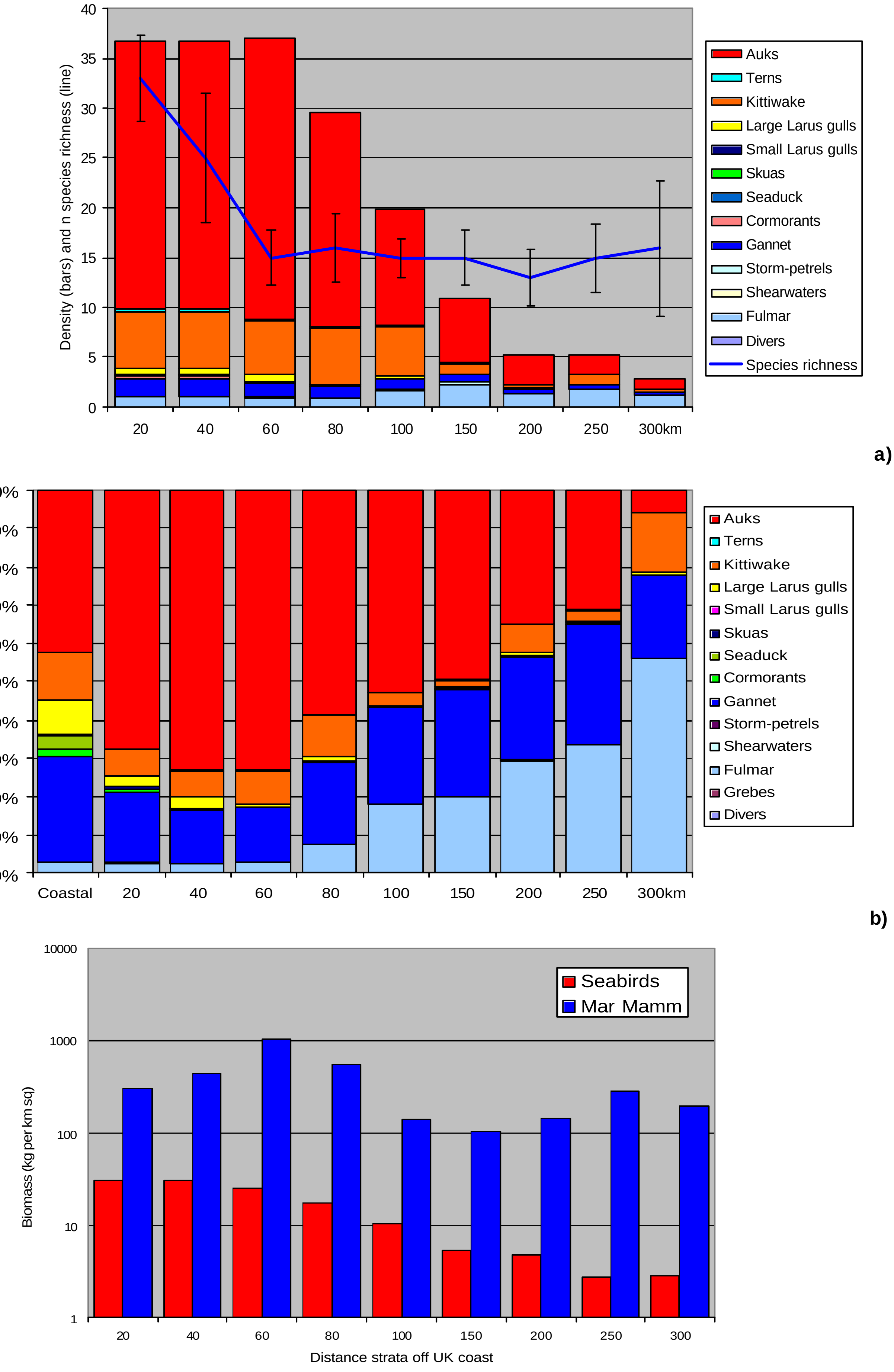

Fig. 2. Top-predator community as (**a**) densities (n km^{-2}; stacked bars) and jackknife estimate of species richness (n ± 95% CI; line), (**b**) % biomass with distance off the British east coast, from breeding population estimates 1999-2003[8], summer censuses of divers and seaduck[9] (coastal data), and ship-based surveys in June-July 1991-2003 (distance strata), and (**c**) biomass estimates for the total seabird community and marine mammals (seals, whales, dolphins, and porpoises combined; log scale).