Summer sandeel consumption by seabirds breeding in the Firth of Forth, south-east Scotland

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The industrial fishery for lesser sandeels (*Ammodytes marinus*) is currently the largest single-species fishery in the North Sea and this species is also the main food of many seabirds breeding in colonies in this area. It has been suggested that inshore sandeel fisheries could have adverse consequences for local seabird populations. One potential area of concern is the fishing grounds on the banks (Wee Bankie and Marr Bank) which lie approximately 40 km off the coast of south-east Scotland, well within the feeding range of many seabirds breeding at colonies in and around the Firth of Forth. A bioenergetics model is used to estimate that seabirds associated with these colonies consumed 6000–17 000 t of sandeels during each of the summers of 1996 and 1997, with the majority of the fish being in the 1-group or older age categories. Distributions of birds at sea recorded during a systematic survey during the breeding season demonstrated that the Wee Bankie was an important feeding area for guillemot (*Uria aalge*), razorbill (*Alca torda*), and kittiwake (*Rissa tridactyla*) and to a lesser extent puffin (*Fratercula arctica*) indicating that the exploitation of sandeels by these species shows strong spatial overlap with the industrial fishery. In contrast, shags (*Phalacrocorax aristotelis*) and common/arctic terns (*Sterna hirundo/paradisaea*) showed predominantly inshore distributions while the North Atlantic gannet (*Morus bassanus*) probably fed mainly outside the area surveyed. Species-specific comparisons of the estimated size of the observed at-sea populations with those predicted from the number of individuals associated with colonies in the area suggests that during the chick-rearing period a high proportion of the Firth of Forth guillemot population was feeding in the surveyed area. However, for the other species the number observed at sea was consistently lower than predicted. The size of the sandeel stock associated with the Wee Bankie is currently unknown. Comparison of the size of the annual catch of the fishery and the amount taken by seabirds indicates that in most years the former has been consistently higher than the latter. Thus the potential for the fishery to affect seabirds is likely to be greater than the converse.

Key words: *Ammodytes marinus*, bioenergetics model, industrial fishery, resource partitioning, seabirds, wildlife-fisheries interactions, North Sea.

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Introduction

Seabirds are a highly visible component of the marine ecosystem and as such have a high conservation profile. Particularly during the spring and summer, sandeels (almost exclusively the lesser sandeel *Ammodytes marinus*) are the main food of many of the seabirds breeding in colonies on the coasts of the North Sea (e.g. Pearson, 1968; Cramp and Simmons, 1983). The industrial fishery for sandeels (again predominantly the lesser sandeel) is currently the largest single-species fishery in the North Sea; during the last 10 years annual landings have fluctuated between 579 000 and 1 039 000 t (ICES, 1997). The development of a sandeel fishery on the Wee Bankie, Scalp Bank, and Marr Bank, off the Firth of Forth, south-east Scotland, has caused concern for the

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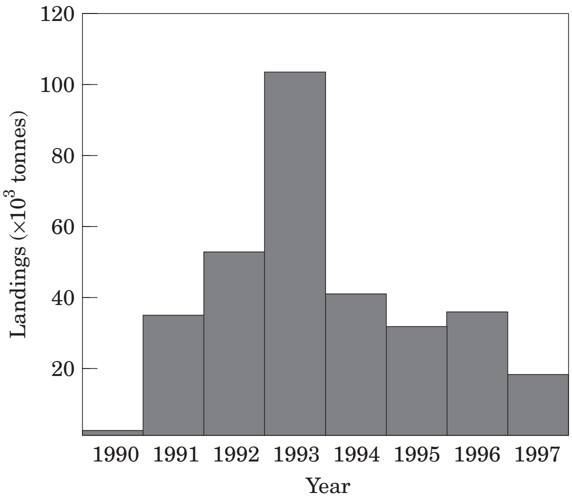

Figure 1. The annual reported landings of sandeels from the ICES fishery rectangles (41E7,41E8) surrounding the Wee Bankie (ICES 1995, updated by S. Pedersen using preliminary data from DIFRES).

future of the seabirds breeding in the area many of which are known to feed on these banks (Tasker *et al.*, 1987; Wanless *et al.*, 1990; ICES, 1995; Gislason and Kirkegaard, 1997; Greenpeace, 1997; RSPB, 1997). The landings of this fishery, mainly 1-group or older fish (S. A. Petersen, pers. comm.) increased rapidly from its inception in 1990 to a recorded catch of over 100 000 t in 1993 (Fig. 1) but to date no estimate of the potential food requirements of the seabirds associated with the area has been published. This paper attempts to fill this gap as a first step in assessing whether the fishery is likely to have any impact on the seabirds.

Two lines of enquiry are pursued. First, what quantity of sandeels might be required by seabirds attending colonies in and around the Firth of Forth? Second, what degree of overlap is there between the areas used by the birds and the fishery? To address the first aim an approach adopted in previous studies is followed (e.g. Furness 1978; Croxall *et al.*, 1984; Furness and Barrett, 1985; Cairns *et al.*, 1991; Diamond *et al.*, 1993; Madenjian and Gabrey, 1995; Guinet *et al.*, 1996) and a simple bioenergetics model constructed which requires the following information: monthly totals of the number of seabirds attending colonies in the area, their breeding success, their daily energy requirements, the proportion of these requirements derived from sandeels, the size classes of sandeels taken and hence their energy content, and finally the birds' assimilation efficiency.

To address the second question and assess the extent to which birds from colonies in the Firth of Forth might be utilizing the Wee Bankie and the Marr Bank for feeding, a systematic survey was carried out of the seabirds at sea in the area to determine their spatial distribution. The size of the at-sea population of each species within the area around the banks was also compared with the numbers expected to be at sea at any one time, given the size of the breeding population, the non-breeding component and the colony attendance patterns in the Firth of Forth. This approach allows us to make a preliminary assessment of what proportion of the local population feeds within the Wee Bankie/Firth of Forth area. Such information has important conservation implications because it indicates the extent to which species may be dependent on the area exploited by the sandeel fishery.

Methods

Study area and species

The study area considered in this analysis consisted of all the seabird breeding colonies in the outer and inner Firth of Forth and the mainland colonies at Dunbar and St Abb's Head (Fig. 2). The area of sea surveyed ran from Dunbar (56°00′N) to the northern edge of the Tay Estuary (56°30′N) and extended 113 km east from the mouth of the Firth of Forth (03°00′W) to beyond the tip of the Marr Bank (01°10′W) – a total area of 4660 km^2.

Twelve species of seabird breed in the area but our analysis was restricted to the eight species known to rely heavily on the lesser sandeel during the breeding season. Thus the model includes European shag (*Phalacrocorax aristotelis*), North Atlantic gannet (*Morus bassanus*), black-legged kittiwake (*Rissa tridactyla*), common guillemot (*Uria aalge*), razorbill (*Alca torda*), Atlantic puffin (*Fratercula arctica*), common tern (*Sterna hirundo*), and arctic tern (*S. paradisaea*) (the latter two species were treated as a single unit due to the lack of information on interspecific differences in diet), but excludes great cormorant (*P. carbo*), herring gull (*Larus argentatus*) and lesser black-backed gull (*L. fuscus*). The authors did not include northern fulmar (*Fulmarus glacialis*) in the model because in this area there is no evidence that sandeels ever form an important item in the diet during the summer months (B. Zonfrillo, pers. comm.).

Sandeel consumption model

The model was initially parameterized using data collected during the 1997 field season. However, a second run was carried out using data for 1996 to determine inter-year differences.

Seabird numbers

The number of seabirds breeding in the study area was derived mainly from counts summarized in Andrews (1997a,b) following methods described in Walsh *et al.*

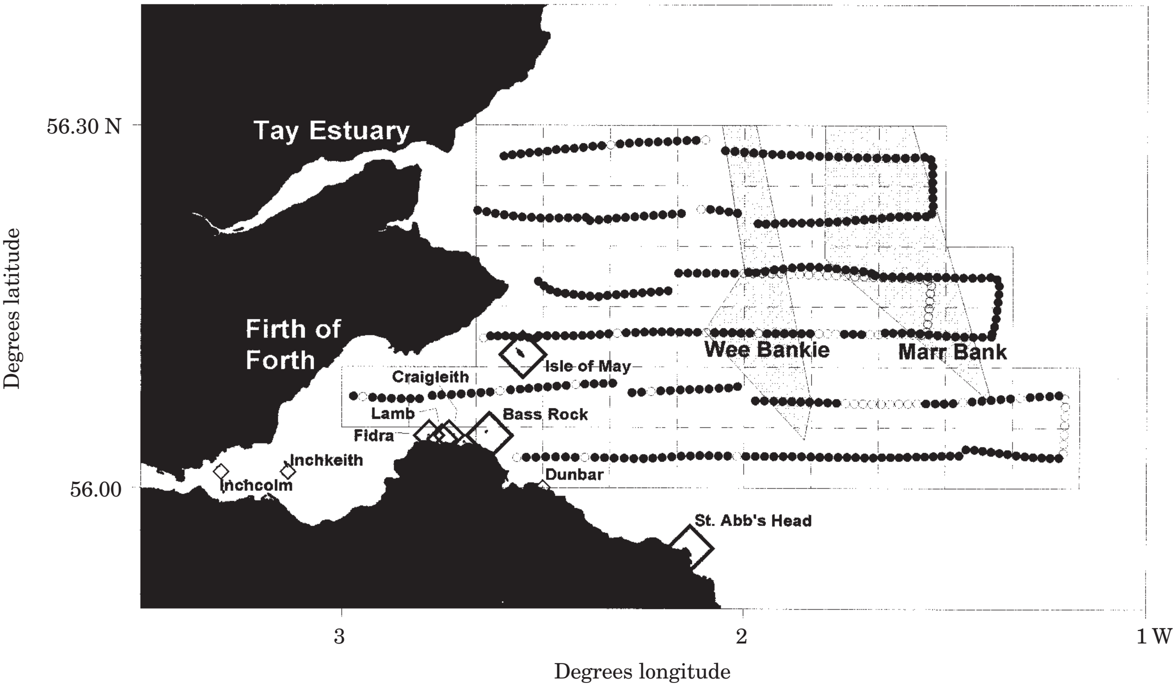

Figure 2. Map of the Firth of Forth study area showing the Wee Bankie and Marr Bank. The locations of the major seabird colonies are shown (diamonds) and three colony size classes are indicated; large symbols, >40 000 pairs; medium symbols, 1000–10 000 pairs; and small symbols, <1000 pairs. The vessel survey track is indicated. The mid-point locations of 5 min survey periods are shown; open circles, no seabird counts; solid circles, seabird counts made. The extent of the sea area over which species-specific at-sea population estimates have been made is indicated by the non-blanked out region, and the division of the study area into 5′ latitude by 10′ longitude rectangles is illustrated.

(1995). Where data were lacking, for example for gannets on the Bass Rock, values were extrapolated from the most recent complete census and the current rate of population change (Murray and Wanless, 1997; Rideout and Patterson, 1996, 1997; personal records). In addition to breeding birds, colonies are also attended by many immature individuals and a smaller number of non-breeding adults. Empirical data on this component of the population are scarce but values can be estimated from life table and colony attendance data. Generally we followed Cairns *et al.* (1991) and Madenjian and Gabrey (1995) and assumed that this component of the population comprised 30% of the total number of adults. Exceptions to this were: guillemot, razorbill, puffin, and kittiwake in April (when virtually no non-breeders are present) and puffin and kittiwake in August (20% present). Adults were assumed to attend the colonies from 1 April (1 May for terns) until 31 July for razorbill, guillemot, and terns, 10 August for kittiwake and puffin, and 31 August for shag and gannet. The model also takes account of the number of chicks present in the colonies. Information on breeding success (chicks reared per breeding pair) was available for most species in 1996 and 1997 (Harris, 1996; Harris and Wanless, 1997a; Rideout and Patterson, 1996, 1997). The main omission was for the gannet for which a value from the 1970s had to be used (Nelson, 1978). The food requirements of chicks which died before fledging were ignored.

Diet

Information on seabird diets, and in particular the percentage contributed by sandeels, comes from Harding (1996), Harris (1996), Harris and Wanless (1997a,b), Hemsley (1997), Tasker and Furness (1996) and the authors' own unpublished records. Most data refer to the food of chicks and it was assumed that adult diets were similar. Therefore, most information on the species and size of prey taken was derived either from food loads directly observed being fed to chicks (e.g. guillemot, razorbill, puffin, terns) or from otoliths extracted from regurgitations, either from adults with chicks or the chicks themselves (e.g. kittiwake, shag, gannet).

Sandeels in the north-west North Sea rarely attain a length of more than 11 cm in the first year of life (Wright and Bailey, 1996; P. J. Wright, unpubl. data). Therefore it is assumed that all sandeels equal to, or less than, this length were 0-group. Samples obtained from kittiwakes and to a lesser extent shags and gannets, rarely contain whole measurable fish. Sandeels in such samples were aged by the absence (0-group) or presence (1-group or older) of annual growth rings in otoliths extracted by digestion of the food sample (details in Harris and Wanless, 1997b). In the North Sea, 0-group lesser sandeels do not metamorphose until the end of May (Wright and Bailey, 1996). Before this they are either too small to be of interest to foraging seabirds or too translucent for easy detection (e.g. Gallego and Heath, 1994). It was assumed, therefore, that all sandeels consumed in April and May were at least 1-year-old and empirical data for the kittiwake during 1997 supported this assumption (Harris and Wanless, unpubl. data). All elements of the diet were converted to energetic values using information and equations in Harris and Hislop (1978) and Hislop *et al.* (1991) before the contributions of 0-group and older sandeels to the diet were calculated.

Energy requirements

The authors used values for the energy needs of full-grown birds presented in Tasker and Furness (1996) and Furness and Tasker (1997), as part of their assessment of seabird consumption of sandeels in the North Sea. The requirements of chicks from hatching to leaving the colony were either measured directly from observed daily food intakes (auks, Harris and Wanless, 1986; gannet, Montevecchi *et al.*, 1984) or calculated using formulae in Weathers (1992). A digestive efficiency of 75% (Tasker and Furness, 1996) was assumed and values of 4.9 and 7.5 kJ g^{-1} wet weight was used for 0-group (average length 7.5 cm) and older (14.5 cm) sandeels, respectively (Hislop *et al.*, 1991).

Seabirds at sea model

Survey data

Seabirds were counted from the FRV "Clupea" over the period 21–25 June 1997 using a slight modification of the standard shipboard transect survey methods proposed by Tasker *et al.* (1984) and Webb and Durink (1992). Instead of using a fixed transect width of 300 m and determining "correction factors" to adjust counts of seabirds on the water to account for birds "missed" at various distances out from the vessel's line of travel, a variable transect width was employed. Transect width was adjusted depending upon prevailing sea conditions to reduce as far as possible the chances of missing seabirds sitting on the water surface, yet at the same time attempting to maximize the area surveyed. This avoided the necessity of determining and using correction factors which would have been inappropriate in examining variation in the numbers and distribution of seabirds at the spatial resolution considered in this paper. The maximum transect width employed was 300 m as problems with species identification multiplied enormously beyond this distance. Generally a transect width of 300 m could be used in sea states of up to two or three. Transect width was reduced in steps of 50 m as sea states worsened, until in sea states of around five, the transect width was reduced to 150 m. Transect width was never less than 150 m and seabird survey was abandoned in sea states of six and above. Flying birds were surveyed using the same variable transect width, but with a fixed scan distance ahead of the ship of 300 m. With the vessel travelling at 10 knots, this meant that one count of flying birds per minute was required to survey flying birds in the transect strip. Counts were recorded over 5-min intervals and the position of the vessel at the start/end of each 5-min recording period, obtained from the vessel's Differential Global Positioning System was stored automatically by computer. Density estimates for each 5-min count period were obtained by dividing the count of each species by the area covered within the transect strip.

The study area was divided into 50 rectangles measuring 5′ latitude by 10′ longitude (9.27 by 10.30 km) (Fig. 2). Six main (east/west) transects were steamed through the centre of each rectangle. The mid-point location of each 5-min seabird count period was determined enabling all 5-min observations to be assigned to a particular rectangle. All 50 rectangles were covered to some extent by the survey. The average density of each species of seabird in each rectangle was calculated by dividing the species' totals over all 5-min observation periods assigned to a particular rectangle by the total transect area surveyed in each rectangle. Multiplying this by the rectangle's area, and then summing over all rectangles provided an estimate of the total number of each species present in the study area. Spatial distribution plots for the species were based on the mean densities in each rectangle ($n=50$). These were smoothed in SURFER (Golden Software Inc., Golden, Colorado, USA) using a multiquadric radial basis function with $R^2=0.00236$ for all species except shag and common/arctic terns where R^2 was set to zero (Carlson and Foley, 1991). Low values of R^2 were used to force the almost exact interpolation of the data. In the case of shags and terns exact interpolation was desired since such a high proportion of the data consisted of zero values.

Expected at-sea populations

Expected at-sea populations were derived from the same population data used in the prey consumption model. In all of the seabird species considered here, both members of the pair provision the brood and, with the exception of the puffin, one adult is normally present at the site to protect the young. Non-breeders also spend a considerable part of the day at the colony, although empirical data to quantify this are generally lacking. Here it is assumed that all birds spend 40% of each day at sea, except in the case of the burrow-nesting puffin which spends markedly less time at the colony than the cliff- and ground-nesting species, where it is assumed that birds were away for 80% of the time.

Results

Prey consumption models

The authors estimated that approximately 154 000 pairs of the eight sandeel-eating species of seabirds bred at colonies in the Firth of Forth in 1997 (Table 1). The most numerous species were gannet (40 200, all on the Bass Rock), guillemot (53 600, mainly on the Isle of May and at St Abb's Head), puffin (28 000, mainly at the Isle of May), and kittiwake (25 500, mainly at St Abb's Head, Isle of May, and Dunbar). The total energy requirement of these species (breeders, non-breeders, and chicks combined) during the summer was 117×10^9 kJ, of which 61.3% was accounted for by gannets and 22.7% by guillemots (Table 1).

These energy values were converted to food consumption requirements and integrated with information on diet in order to estimate the total demand for sandeels by seabirds (Table 2). As expected, the dietary data collected indicated that sandeels were taken by all the species included in the model (Table 2). However, the degree of reliance and the age classes taken showed considerable interspecific variation. No direct assessment of gannet diet was made but Nelson (1978, pers. comm.) recorded that large sandeels were frequently regurgitated by gannets on the Bass Rock between March and May, and some regurgitations from the chick-rearing period were also composed of sandeels. The authors therefore follow Furness and Tasker (1997) and assume that 30% of the diet of gannets consisted of 1-group and older sandeels and that no 0-group sandeels were eaten.

In energetic terms, sandeels were estimated to account for about 46% of the total food consumed by Firth of Forth seabirds during the breeding season, with the demand for 1-group and older sandeels being more than five times greater than for 0-group fish (41% of total energy compared to 5%). In biomass terms, seabirds were estimated to need 1452 t of 0-group sandeels and 8616 t of older fish between the start of April and their departure from the colonies in late July or August. The model was run again using similar input data collected in 1996. Sandeel consumption by seabirds in this season was estimated at 1600 t and 5600 t of 0-group and older sandeels, respectively. The difference between the years was due to (1) guillemots in 1996 feeding their young mainly on clupeids rather than on sandeels, and (2) higher colony counts of most species in 1997.

At-sea abundance

The at-sea transect survey estimated that about 111 500 individuals of the eight species of seabird were present in the study area in late June 1997 (Table 3), and indicated that high densities of guillemot, razorbill, puffin, and kittiwake were associated with the Wee Bankie (Fig. 3). Concentrations of all species, except gannet, were also present around the Isle of May. Shag and common/arctic terns both had strongly coastal distributions and were almost completely restricted to the inner Firth of Forth, with no individuals recorded in areas to the east of the Isle of May. The gannet distribution plot showed two "hot spots", one off Fife Ness between the Firth of Forth and the Tay Estuary and another around the breeding colony on the Bass Rock on the south side of the Firth of Forth.

Species-specific comparisons of the estimated at-sea populations and expected totals derived from the numbers of breeding and non-breeding individuals associated with colonies in the Firth of Forth indicated that for guillemots there was only a 5% difference between the two estimates (Table 3). However, for the other species the number observed at sea was consistently lower than the number expected from the colony totals with the discrepancy being greatest for the inshore feeding species (terns, 78%; shag, 81%).

Discussion

The prey consumption model indicates that during the breeding seasons of 1996 and 1997, 35% and 46% of the diet of seabirds associated with colonies in the Firth of Forth was made up of sandeels, and this consisted of 1600 t and 1452 t of 0-group sandeels, and 5600 t and 8618 t of 1-group and older sandeels, respectively.

These estimates are subject to various sources of error, most of which are unquantifiable. While counts of the number of breeding birds will, in general, be reasonably accurate, estimation of the non-breeding component is more problematic. Most of the data on diet composition are based on observations of prey brought back for the chicks and there are few empirical data, either from our own studies or the literature, documenting the food consumed directly by adult birds or non-breeders. This could inflate the relative significance of 1-year-old and older sandeels particularly if birds were selecting larger prey items to bring back to the nest. However, the single largest potential source of error in the model is the lack of up-to-date data on the diet of the gannet since this species is both the largest and most abundant breeding seabird in the area. Studies in Shetland indicate that the importance of sandeels in the diet of gannets varies from year-to-year e.g. from 91% of prey regurgitated by chicks in 1981 to only 6% in 1988 (Martin, 1989). During the 1980s there was some evidence of an increase

Table 1. Species-specific population and energetic values used to parameterize the sandeel consumption model for seabird populations in the Firth of Forth in 1997.

	Breeding population (pairs)	Period attending colony (breeders)	Breeders and non-breeders: Colony attendance (bird days × 10^4)*	Breeders and non-breeders: Daily energy requirements (kJ d^{-1})†	Breeders and non-breeders: Total energy requirements (kJ × 10^7)	Chicks: Chicks reared per pair	Chicks: Energy requirements per chick (kJ × 10^3)	Chicks: Total energy required by chicks (kJ × 10^6)	All birds: Total energy requirements of population (kJ × 10^6)	All birds: Percentage
Shag	1114	1 Apr–31 Aug	42.3	2980	126.1	0.85	64	60.6	1321.6	1.1
Gannet	40 200	1 Apr–31 Aug	1526.8	4407	6728.8	0.75†	145	4371.8	71 659.6	61.3
Kittiwake	25 500	1 Apr–10 Aug	808.4	909	734.4	0.60	12.8	195.8	7541.3	6.5
Common/arctic tern	1702	1 May–31 Jul	39.7	347	13.8	0.35	4.4	2.62	140.4	0.1
Razorbill	4100	1 Apr–31 Jul	108.4	1299	140.8	0.71	2.9	8.4	1416.2	1.2
Guillemot	53 600	1 Apr–31 Jul	1417.2	1853	2625.4	0.77	7.2	297.2	26 551.0	22.7
Puffin	28 000	1 Apr–10 Aug	891.6	909	810.2	0.65	13.0	236.6	8338.8	7.1

*Includes correction for non-breeding component of the population (see Methods).
†Based on basal metabolic rates given by Furness and Tasker (1997) multiplied by 3.9.
‡From Nelson (1978).

Table 2. Estimates of the fish required to satisfy the energy requirements of seabirds breeding in the Firth of Forth, the proportions (in energy terms) of 0-group and older sandeels in the diet and the mass of sandeels calculated to have been consumed. Figures refer to 1997.

	Total energy needed to be supplied by fish (kJ × 10^6)*	Proportion of sandeels in diet		Weight of sandeels tonnes‡	
		0-group	Older	0-group	Older
Shag	1762.2	0.01	0.99	4	233
Gannet	95 546.2	0	0.30†	0	3822
Kittiwake	10 055.1	0.27	0.61	554	818
Common/arctic tern	187.1	0.25	0.20	10	5
Razorbill	1888.7	0.45	0.47	173	118
Guillimot	35 401.4	0.02	0.61	144	2879
Puffin	11 118.5	0.25	0.50	567	741
Total				1452	8616

*Assuming a digestive efficiency of 75%.
†No empirical data collected.
‡Assumes average calorific values of 4.9 and 7.5 kJ g^{-1} wet weight for 0-group and older sandeels, respectively.

Table 3. Comparison of the number of seabirds specializing on sandeels estimated in the at-sea survey (0) with the total numbers of breeding, immature, and non-breeding birds associated with colonies in and around the Firth of Forth which were expected to be at sea (E).

Species	Individuals counted at sea (0)	Individuals at colonies*	Individuals at sea at any one time† (E)	Difference between observed and expected [(0 − E)/E] × 100
Guillimot	52 802	139 360	55 744	− 5%
Razorbill	2417	10 530	4212	− 43%
Puffin	24 115	72 800	58 240	− 59%
Kittiwake	13 499	66 300	26 520	− 49%
Gannet	18 008	104 520	41 808	− 57%
Common/arctic tern	384	4425	1770	− 78%
Shag	226	2896	1159	− 81%

*Two individuals per breeding pair (see Table 1) plus 30% to allow for other birds attending the colony (see text).
†Assumes 40% of the population at sea at any one time for all species except puffin (where 80% were assumed to be away).

in the biomass of sandeels in the North Sea and a coincident decrease in the amount of clupeid fish (Corten, 1990; Bailey *et al.*, 1991; Turrell, 1992), conditions which might tend to increase the proportion of sandeels taken by gannets. Assuming that sandeels currently make up 90% of the diet, rather than the conservative value of 30% used in our original calculations, increases the estimated sandeel consumption of gannets to 11 500 t, which approximately doubles the total sandeel consumption by birds in the area. Taking account of these possible extreme scenarios, it is suggested that the sandeel consumption by seabirds at colonies in and near the Firth of Forth is of the order of 1000–2000 t of 0-group and 5000–15 000 t of older sandeels. Thus 1-group and older sandeels constitute the greater fraction of sandeel prey in the diet of seabirds. This age group is also the one predominantly exploited by the sandeel fishery on the Wee Bankie and Marr Bank and consequently the birds and fishery are potentially competing for the same resource.

The at-sea distribution plots highlight the importance of the Wee Bankie for several species of seabird that feed on sandeels, particularly guillemot but also razorbill, kittiwake, and, to a lesser extent, puffin. These results accord well with previous and concurrent radiotracking studies (Wanless *et al.*, 1990, personal data) and previous at-sea surveys (Tasker *et al.*, 1985; Stone *et al.*, 1995) and thus provide a strong body of evidence that the exploitation of sandeels by auks, kittiwakes, and the industrial fishery in this part of the North Sea shows considerable spatial overlap. In contrast, shag and common/arctic terns showed predominantly inshore

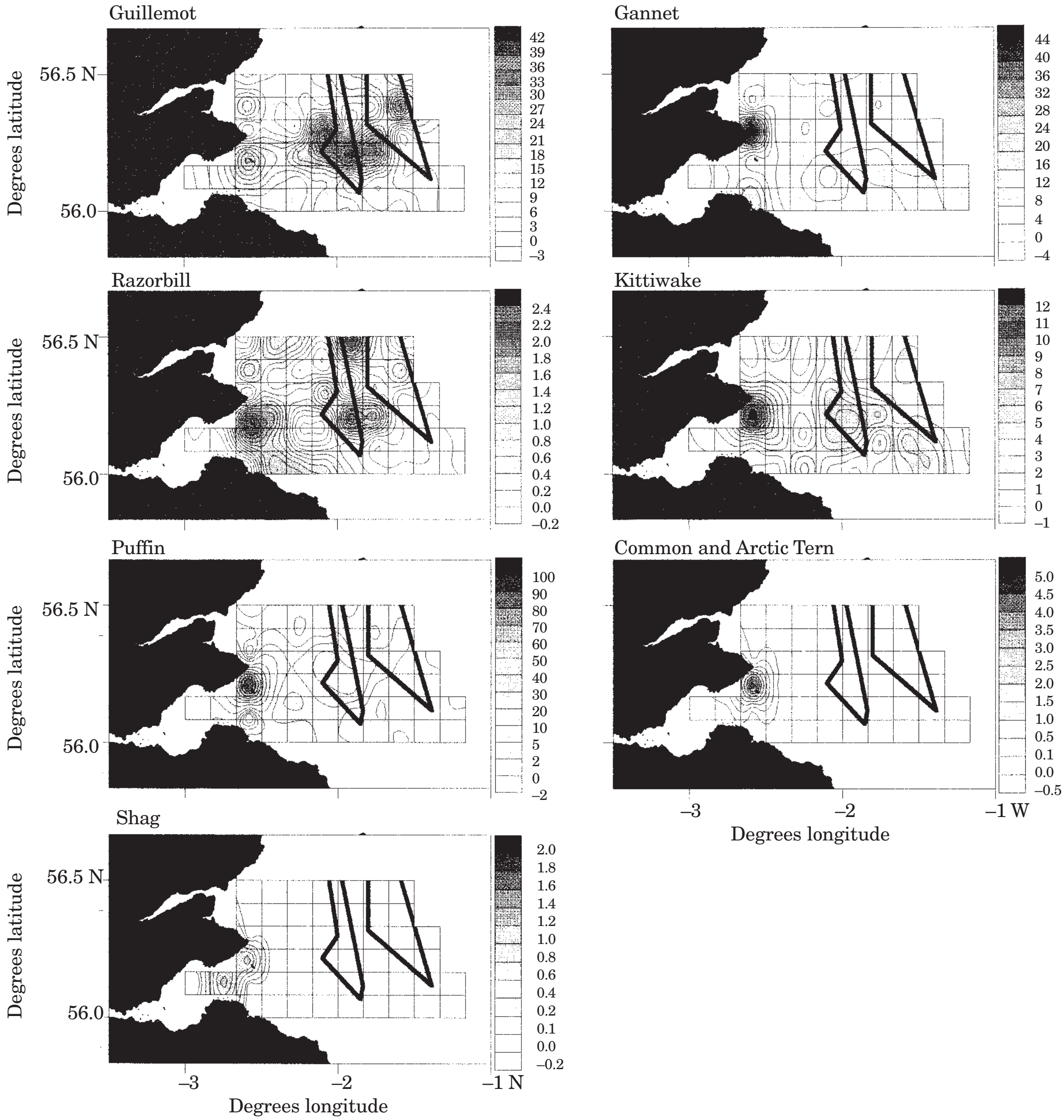

Figure 3. Spatial distribution plots of the sandeel specialist seabird species surveyed at sea. Density values are birds km^{-2}.

distributions and consequently, at a fine scale, exploitation of sandeels by these species and the fishery are spatially segregated. However, there is currently no information about how the removal of large quantities of sandeels from the Wee Bankie and Marr Bank would affect the distribution and density of sandeels in other parts of the region. Thus there is no way of knowing for certain whether or not inshore feeding seabirds are likely to be affected by the fishery.

During our survey the highest densities of gannets were recorded around the Bass Rock and off Fife Ness and there was no evidence that the Wee Bankie was a "hot spot" for gannets. This distribution was broadly similar to the pattern found by Tasker *et al.* (1985) during summers in the early 1980s. However, a survey carried out in July 1997, i.e. shortly after ours, found high densities of gannets feeding on the Wee Bankie, indicating that the area is sometimes used by this species during the summer and may at certain times be an important feeding location (Camphuysen *et al.*, unpubl. data).

Given the errors and assumptions inherent in both the at-sea and colony-based population estimates, any inferences drawn from comparisons of the two must be tentative. However, the approach further highlights the interspecific difference in at-sea distribution and dependence on the Wee Bankie. In the case of the guillemot, the at-sea distribution was strongly centred on the Wee Bankie and to a lesser extent, the Marr Bank, a feature previously noted by Wright and Begg (1997). This was the only species for which the at-sea population approximated to the number of birds predicted to be present in the area (Table 3). Since we were more likely to overlook birds rather than "imagine" their presence, the at-sea population was most probably an underestimate rather than an overestimate. These results therefore suggest that a high proportion of the Firth of Forth guillemot population was feeding within the study area, particularly on the Wee Bankie. For the remaining seven species the observed at-sea populations were all substantially lower than expected. In the case of the shag, razorbill and common/arctic terns these differences probably reflect the relatively poor coverage of the inshore waters in the study area (Fig. 2) since shags and terns forage exclusively or predominantly in the inshore zone and razorbills tend to have a more coastal distribution than guillemot or puffin (Wanless *et al.*, 1990, 1991; pers. obs.). For the shag the discrepancy may have been further compounded by the fact that much of the area inshore of the Isle of May was surveyed in the early morning (0415–0620 h GMT) before many of the adults would have started foraging (Wanless *et al.*, 1993). In addition, the distribution map for the razorbill (Fig. 3) indicates "hot spots" on the northern and southern boundaries suggesting that some important feeding areas were located outwith our survey area. Utilization of feeding areas beyond the bounds of the area surveyed probably also accounted for differences between the expected and observed population estimates for the gannet and possibly also for the kittiwake. In the case of the former, adults breeding on the Bass Rock have a theoretical range of 320–480 km (Nelson, 1978) and there is evidence that birds do indeed exploit areas at least 300 km from the colony, although most feeding areas appear to be within 150 km (Tasker *et al.*, 1985; Camphuysen *et al.*, 1995). The discrepancy between the two estimates was also large for puffins but the reason for this was not obvious. Neither the at-sea distribution pattern (Fig. 3) nor information on potential feeding ranges (Harris 1984, unpubl. data) indicated that birds were likely to be feeding outside the study area. The authors are also confident that the assumption that puffins spend less time at the colony than the other species considered here, was realistic. Some of this off-duty time is spent sitting in rafts very close to the breeding colony. However, since none of the survey transects passed within 500 m of the main puffin colony on the Isle of May, this category of birds was likely to be under recorded and thus may have contributed to the discrepancy. Figure 3 suggests that this explanation is quite likely since by far the highest densities of puffins were recorded in the sections of transect closest to the Isle of May.

Despite these potential sources of error in our calculations it is clear that during the breeding season the quantity of sandeels taken by the fishery in most recent years has far exceeded the amount consumed by seabirds associated with colonies in the Firth of Forth. The peak catch in 1993 of over 100 000 t is an order of magnitude higher than our "best" estimate of seabird sandeel consumption, and five times higher than our maximum. Even in 1997, when sandeel landings were the lowest since the initial year of the fishery, the catch was still double our "best" estimate, and exceeded our maximum. In all but the first year that the fishery operated, sandeel catches have been at least twice the level recorded in 1997 (Fig. 1). Thus the potential for the fishery to affect seabirds would appear to be much greater than the converse. It should, however, be noted that our comparison of the relative amounts of sandeels taken by marine birds and the industrial fishery refers only to the seabird breeding season, a period of 4–5 months depending on the species concerned. In the case of the seabirds some additional predation on sandeels will occur during other months, almost certainly involving individuals from colonies outwith the Firth of Forth. In contrast, the fishery only operates during spring and summer and so the landings reported here represent the total biomass of sandeels taken. However, Furness and Tasker (1997) in a much broader-scale comparison covering the North Sea over the whole year, also concluded that the fishery was more likely to affect seabirds than vice versa. Making further progress in assessing the level of any competition between the industrial fishery on the Wee Bankie and marine birds associated with the area is hampered by numerous uncertainties, the most important of which is the current lack of quantitative data on the size of this specific sandeel stock, or even any information as to whether it constitutes a discrete stock. In addition, we are largely ignorant of the form of the functional relationship between sandeel abundance and availability to seabird predators. Finally, in contrast to some other areas in the North Sea, e.g. Shetland, where sandeels are the only major prey item taken by most species (Furness, 1978), seabirds in the Firth of Forth have several potentially suitable alternative prey, e.g. herring (*Clupea harengus*) and sprat (*Sprattus sprattus*). Particularly in the case of the auks, and probably the gannet, the extent of any impact of the sandeel fishery will also depend on the availability of these alternative prey.

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