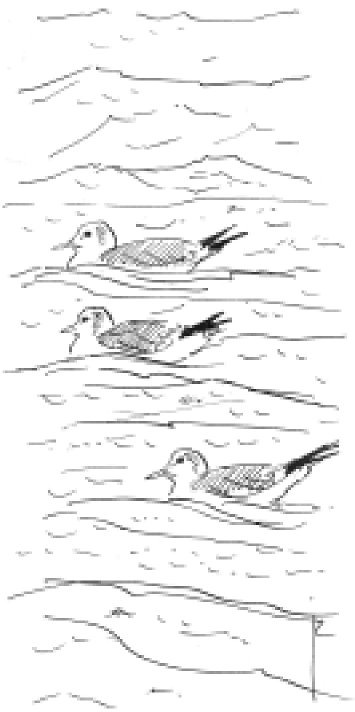
LOCAL-SCALE VARIABILITY IN THE DIET OF BLACK-LEGGED KITTIWAKES *RISSA TRIDACTYLA*

J. BULL[1], S. WANLESS[1*], D.A. ELSTON[2], F. DAUNT[1], S. LEWIS[1] & M.P. HARRIS[1]



Bull J., S. Wanless, D.A. Elston, F. Daunt, S. Lewis & M.P. Harris 2004. Local-scale variability in the diet of Black-legged Kittiwakes *Rissa tridactyla*. Ardea 92(1): 43-52.

The Black-legged Kittiwake *Rissa tridactyla* is a small gull that is widely distributed in the North Atlantic and Pacific. During the breeding season it feeds mainly on fish and, in the North Sea, the Lesser Sandeel *Ammodytes marinus* typically forms the main species in the diet. We compared the diet and breeding performance of Kittiwakes at four colonies in east Britain with potentially overlapping foraging ranges where both Lesser Sandeels and alternative prey (clupeids: Sprat *Sprattus sprattus* and Herring *Clupea harengus*) were potentially available. During the four years of the study Kittiwakes at all four colonies showed similar within-season shifts in the age class of sandeel taken with older (1+ group) fish being replaced by young of the year (0 group). However, in every year the predominant prey differed between the two marine colonies, where birds fed mainly on sandeels, and the two estuarine colonies, where clupeids were the most important prey. We suggest that these dietary differences reflect differences in foraging areas such that Kittiwakes from marine colonies feed offshore in areas with a sandy seabed, habitat favoured by sandeels, and birds from estuarine colonies feed closer inshore in areas with a more rocky seabed, habitat favoured by clupeids. Breeding success of Kittiwakes at the four colonies followed a similar trend over the first three years but the marked increase recorded at the marine colonies in 2000 was not apparent at the estuarine colonies.

Keywords: *Rissa tridactyla* - *Ammodytes marinus* – sandeels – foraging ranges – feeding overlap – clupeids – hinterland

[1]NERC Centre for Ecology and Hydrology, Hill of Brathens, Banchory AB31 4BW, U.K., **Corresponding author:* E-mail swanl@ceh.ac.uk; [2]Biomathematics and Statistics Scotland, Macaulay Institute, Craigiebuckler, Aberdeen AB15 8QH, U.K.

INTRODUCTION

Many species of seabird are colonial breeders and, during the breeding season, adults typically fly tens, hundreds or even thousands of kilometers to feed (Lack 1968). Thus, where colonies are close together, birds from neighbouring colonies can potentially have overlapping foraging ranges (Furness & Birkhead 1984; Cairns 1989; Hamer *et al.* 2001; Ainley *et al.* 2003). The few critical studies that have aimed to establish whether this is the case have found mutually exclusive rather than overlapping foraging areas (e.g. Wanless & Harris 1993; Brothers *et al.* 1998; Huin 2002; Gremillet *et al.* 2004). In areas where there is local-scale heterogeneity in foraging habitat, such colony-specific feeding areas could lead to differences in diet. The Black-legged Kittiwake *Rissa tridactyla* is widely distributed throughout the North Atlantic and North Pacific. During the breeding season it is typically piscivorous feeding on prey species including sandeels *Ammodytes* spp., Capelin *Mallotus villosus* and clupeids (Sprat *Sprattus sprattus* and small Herring *Clupea harengus*) (Cramp & Simmons 1983; Hamer *et al.* 1993; Suryan *et al.* 2000). A long-term study of the diet of Kittiwakes on the Isle of May, south-east Scotland, found that the Lesser Sandeel was the predominant prey taken even in years when availability was low (Rindorf *et al.* 2000). Birds fed on older sandeels (1+ group) early in the season before switching to young (0 group) during late incubation and chick rearing; clupeids formed only 15% of the diet (Harris & Wanless 1997; Lewis *et al.* 2001b). Here we use data from the Isle of May and three other nearby colonies (Fig. 1), collected over four years, to investigate the variation in dietary composition attributable to colonies and years. Two colonies were on islands well inside the Firth of Forth estuary (estuarine colonies) and two were on islands in predominantly marine conditions (marine colonies). Inter-colony distances varied from 10 to 115 km. Breeding Kittiwakes have a maximum foraging range of 80 – 120 km (Suryan *et al.* 2000; Daunt *et al.* 2002; Humphreys 2002). Thus birds from these four colonies potentially had largely overlapping foraging ranges. Suitable habitat for both Lesser Sandeels (predominantly sandy substrates: Reay 1986; Wanless *et al.* 1997) and Herring and Sprat (rock/sand mixed substrates: Parrish *et al.* 1959; Daan *et al.* 1990) occurs within 120 km of all the colonies. However, the fine-scale distribution of these habitats differs with the two estuarine colonies being surrounded mainly by rock/sand substrates while sandy substrates predominate in the vicinity of the two marine colonies. We use information from the four colonies to test the assumption that the populations had sufficiently overlapping foraging ranges that dietary patterns would be independent of colony.

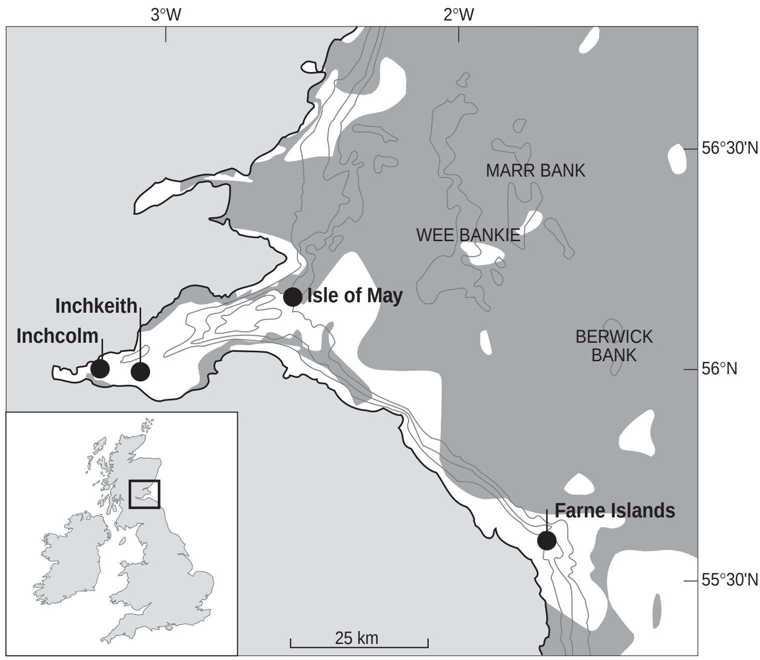


Fig. 1. Locations of the four colonies where Black-legged Kittiwake diet samples were collected. The 30m, 40m and 50m bathymetric contours are shown. The figure shows two sediment types: sandy substrates shown in dark grey (sand to mud ratio greater than 9:1, containing <30% gravel; British Geological Survey 1984), all other substrates shown in white (principally rocky-sandy mix sediments). The principal offshore sandbank complexes of Wee Bankie, Marr Bank and Berwick Bank, where the industrial fishery for Lesser Sandeels has been concentrated, are also shown.

METHODS

Diet samples were collected at two estuarine colonies, Inchcolm (56º02'N, 03º18'W) and Inchkeith (56º02'N, 03º08'W) and two marine colonies, Isle of May (56º11'N, 02º33'W) and Farne Islands (55º35'N, 01º39'W; Fig. 1). The number of Kittiwakes breeding at these colonies in 1999 was estimated at 116, 349, 4196 and 5492 pairs respectively (Fairlamb 1999; Hemsley 1999; Walton 2000). At each colony, food samples regurgitated by adults or chicks were obtained during routine ringing in at least three years between 1997 and 2000 (Table 1). The total number of sampling periods across years was six and seven for estuarine and marine colonies respectively. On the Isle of May, diet sampling was carried out throughout the breeding season so we selected the data for this colony that best matched the range of dates sampled at the other colonies (Table 1). A total of 543 diet samples were collected over the study period (Table 2).

After collection in the field, the food samples were stored frozen at –20ºC, in sealed bags. For analysis, samples were thawed, weighed, and the species composition and approximate size of any intact prey items assessed. Samples were then placed in a solution of biological washing powder (Biotex) at 40º C until all the flesh and soft material had been digested. The remaining hard items (mainly fish otoliths and bones) were identified to the lowest taxa possible using a binocular microscope (25x magnification), keys in Härkönen (1986) and Watt *et al.* (1997) and our own reference collection. The original mass of each fish was calculated using equations relating otolith length, fish length and fish mass given in Härkönen (1986) and Lewis *et al.* (2001b). For sandeels, the age class of the fish was also determined from otolith macrostructure using counts of annual growth rings (ICES 1995) with fish classified as either 0 group or 1+ group. The values derived above were combined to estimate 1) the frequency of occurrence and 2) the proportion by mass of each type of food in each regurgitate.

Breeding success, defined as the number of chicks fledged per apparently occupied nest, was recorded each year on the Isle of May and the Farne Islands (Lewis *et al.* 2001b; National Trust data in Joint Nature Conservation Committee data base) using standard protocols (Walsh *et al.* 1995). Breeding success was not recorded directly at Inchkeith and Inchcolm. However, data were available on brood size in early July (unpublished data). This measure can be used as an index of breeding success (Aebischer 1986). Using detailed data from 20-90 nests for 5 years on the Isle of May, mean breeding success (chicks fledged/active nest) and mean brood size in early July were calculated for each year. These values were used to derive a least squares regression equation for estimating mean breeding success from mean brood size: breeding success = 1.18 (brood size) – 1.28; $r^2 = 0.61$. This relationship was used to derive breeding success from brood size at the two estuarine colonies.

Table 1. Range of sampling dates at the four study colonies.

	Inchcolm	Inchkeith	Farne Islands	Isle of May
1997	8 July	29 June - 6 July	No data	29 June - 8 July
1998	21 June - 17 July	25 June - 11 July	14 July - 5 August	7 June - 14 July
1999	No data	5 July	24 - 26 May	24 May - 5 July
2000	27 June	No data	16 June - 25 July	16 June - 24 July

Statistical analysis

Preliminary inspection of the data indicated seven prey categories in the diet: 1+ sandeels, 0 group sandeels, clupeids, gadoids, crustacea, polychaetes and unknown (Table 2). For analyses the latter four categories were placed in a single cate-

Table 2. Frequency (%) of occurrence of different prey items in regurgitates from Black–legged Kittiwakes at four colonies between 1997 and 2000. * = no data collected.

Estuarine:	Inchcolm				Inchkeith			
	1997	1998	1999	2000	1997	1998	1999	2000
No. of regurgitates	11	6	*	14	17	21	16	*
% with sandeel (all)	18	67	*	50	6	57	25	*
Sandeel (0 group)	18	67	*	43	6	57	25	*
Sandeel (1+ group)	0	17	*	7	0	0	0	*
Clupeidae	91	83	*	71	94	67	75	*
Gadidae	9	0	*	14	12	19	0	*
Planktonic crustacea	18	0	*	0	6	0	0	*
Polychaete	0	0	*	0	0	0	0	*
Unknown	0	0	*	0	0	0	0	*
Marine:	Farne Islands				Isle of May			
	1997	1998	1999	2000	1997	1998	1999	2000
No. of regurgitates	*	31	26	43	54	69	144	91
% with sandeel (all)	*	100	100	95	100	92	88	100
Sandeel (0 – group)	*	94	0	95	87	91	72	99
Sandeel (1+ group)	*	6	100	16	37	17	33	13
Clupeid	*	23	0	21	9	20	27	19
Gadidae	*	3	0	5	4	3	10	5
Planktonic crustacea	*	3	0	0	2	0	7	0
Polychaete	*	0	0	0	0	2	0	0
Unknown	*	0	0	0	2	2	0	0

gory 'other' as they were a minor component of the diet in all colonies and years (comprising <6 % of the diet by biomass). The effects of date (Julian day), year, colony type (marine vs estuarine) and colony on composition of Kittiwake diets were analysed by modelling the proportion of the biomass in the diet that belonged to food type j in regurgitate sample s. The fitted proportions (p_{sj}) were constrained to sum to 1 by using the multinomial logit link function:

$$p_{sj} = \exp(k_{sj}) / \sum_j \exp(k_{sj})$$

where k_{sj} is a linear predictor for each dietary component dependent on the fitted model. The models were fitted using an iteratively reweighted least squares procedure (Montgomery *et al.* 2001) minimising as an objective function the weighted sum of squares:

$$\mathrm{WSS} = \sum_{s,j} (p_{sj} - y_{sj})^2 / [p_{sj}(1 - p_{sj})]^b$$

where y_{sj} is the observed proportion of component j in diet s and p_{sj} is the corresponding fitted proportion. The parameter b defining the variance-mean relationship was estimated by calculating sample mean (m_{ij}) and variance (v_{ij}) of prey type j for each combination, i, of colony, year and four periods of Julian days (≤162, 163-182, 183-202, ≥203), and thereafter modelling the variances (v_{ij}) using a generalised linear model with gamma errors and a log link function (McCullagh & Nelder 1989) treating $x_{ij}=\log[(m_{ij})(1-m_{ij})]$ as a covariate with estimated slope b. The regression used weights to allow for the unequal degrees of freedom in estimating the variances, and excluded variances with corresponding means of 0 or 1 as both observed and fitted variances were necessarily zero.

Candidate models investigated are summarised in Table 3. The importance of different effects in the model for diet composition was assessed by observing the reduction in WSS obtained on the addition of the corresponding parameters to the model. Predicted diet compositions were estimated by modelling the data from the two colony types separately after pooling across years and colony within colony type. For the marine colony type, the trend across dates was modelled by a quadratic regression, whereas for the estuarine colony type spanning a shorter range, a linear regression was used. Confidence intervals for these predicted compositions were derived by bootstrapping (Manly 1997), in which the process of sampling with replacement took place within combinations of colony type and period. This restriction ensured the bootstrap resamples had a similar balance over dates within colony type to the original data without being overly restrictive. The confidence intervals are thus somewhat conservative, as imbalance in the bootstrap resamples either between colonies within colony types or between years may inflate the confidence intervals.

Table 3. Candidate models for linear predictor in dietary composition analysis

Name	Model
M1	constant across date
M2	linear regression with date
M3	quadratic regression with date
M4	quadratic regression with date and additive colony type effect
M5	quadratic regression with date and additive colony effect
M6	quadratic regression with date and additive year effect
M7	quadratic regression with date and additive colony and year effect

Taken as a whole, this approach allows modelling of the compositional data on the logratio scale, as proposed by Aitchison (1986), but without recourse to taking logratio transformations of the data. All analyses were carried out using the statistics package GenStat 6.2 (VSN International Ltd).

RESULTS

At all the colonies, Kittiwakes fed mainly on Lesser Sandeels and Clupeidae (probably mostly small Sprats although many remains could not be identified to species). Small Gadidae (mostly Whiting *Merlangius merlangus*), small planktonic crustacea and polychaetes were also recorded but made up only a minor part of the diet (Table 2). There were, however, marked differences in diet composition of Kittiwakes from marine and estuarine colonies and these differences were apparent across all years. Thus, at marine colonies the diet was dominated by Lesser Sandeels (present in 88%–100% of regurgitates) while clupeids were more important at estuarine colonies (present in 67%-94% of regurgitates). Clupeids ranked second in the diet of birds from marine colonies, occurring in six out of the seven sampling periods (range 9%-27%) while sandeels ranked second at estuarine colonies (present on all six sampling occasions, range 6%-67%). Gadoids were uncommon overall but occurred more frequently at estuarine colonies (estuarine range 0%-19%, marine range 0%-10%). Results from the candidate models for differences in diet composition by biomass are shown in Table 4. A change mean square of 85.27 on addition of linear regressions with date, indicated that there was clear evidence of within-season changes in dietary composition. The evidence for a quadratic trends with date (M3) was not very strong (change mean square 10.81) but this term was kept in the model to guard against non-linearity in the response to date. The most important change in the model consisted of the addition of a colony type effect to the quadratic regression with date (M4). The addition of a colony type effect to a common quadratic regression with date resulted in a change mean square of 79.88, whereas the subsequent addition of colony within colony type had a change mean square 3.05. This indicates the colony type effect was highly significant ($F_{3,6}$=26.2, P = 0.001) despite the limited degrees of freedom. Compared to the colony type effect, there was relatively little variation in the diet of Kittiwakes between colonies within colony types or between years (change mean squares of 3.05, 9.14 and 6.39 for models

Table 4. Changes in weighted sum of squares (WSS) on adding parameters to models M1 – M7 for diet composition. Change in sum of squares (CSS) is calculated from the preceding model except, * CSS calculated from M3; # CSS calculated from M4; + CSS calculated from M5. Residual mean square = 1618.06 / 1599 = 1.01

Model fitted	Number of parameters	Residual sum of squares	Change in sum of squares	Change in df	Mean square
M1	3	2240.87			
M2	6	1985.07	255.80	3	85.27
M3	9	1952.64	32.43	3	10.81
M4	12	1713.01	239.63	3	79.88
M5*	18	1694.70	257.94	9	28.66
M5a#			18.31	6	3.05
M6*	18	1870.34	82.30	9	9.14
M7+	30	1618.06	76.64	12	6.39

M5, M6 and M7 respectively). Similarly, the additional variation explained by allowing trends over date to differ between colony types was small (change mean square 1.49 on augmenting M4 by an independently estimated, linear, trend for the estuarine colony type).

Figure 2 shows the predicted percentages by biomass of each of the four dietary components of Kittiwakes at marine and estuarine colonies over the sampling period, with associated confidence intervals. The estimates demonstrate the major effect of colony type upon dietary composition, with clupeids forming on average about 50% of the diet at the estuarine colonies compared to less than 20% at marine colonies. Conversely, sandeels formed over 50% of the diet at the marine colonies, the proportions for both 0 group and 1+ group being at least double the corresponding values at the estuarine colonies. The intra-annual trends were broadly similar for the two colony types, with a marked increase in 0 group sandeels mirrored by a decline in 1+ group sandeels. By contrast, the proportion of diet comprising clupeids and other peaked mid-season for the marine colony type, but were relatively stable for the estuarine colony type.

Breeding success varied considerably among years at all colonies (Fig. 3). Trends at the two marine colonies were broadly similar with output being lowest in 1998 and highest in 2000, although success was consistently higher on the Farne Islands than the Isle of May. The two estuarine colonies followed a similar pattern to the marine colonies over the first three years but did not show a marked improvement in 2000.

DISCUSSION

In accordance with previous results from the Isle of May (Lewis *et al.* 2001b) we found that Kittiwakes at other colonies in eastern Britain also showed a consistent within-season shift in the age class of sandeel in their diet with the importance of 0 group increasing as the season progressed (Fig 2). However in every year the predominant prey taken by Kittiwakes differed between the marine and estuarine colonies. In line with studies at other North Sea colonies (Pearson 1968; Hamer *et al.* 1993), Lesser Sandeels were the main prey (both by frequency of occurrence and biomass) at the two marine colonies. In contrast, in all four years clupeids were the main prey at estuarine colonies and less complete data indicate that these inter-colony differences persisted in 2001 and 2002 (unpublished data). To the best of our knowledge, the diet of Kittiwakes at estuarine colonies has not previously been quantified. However, similar local scale differences have been recorded at colonies of Kittiwakes in the Gulf of Alaska (Suryan *et al.* 2000).

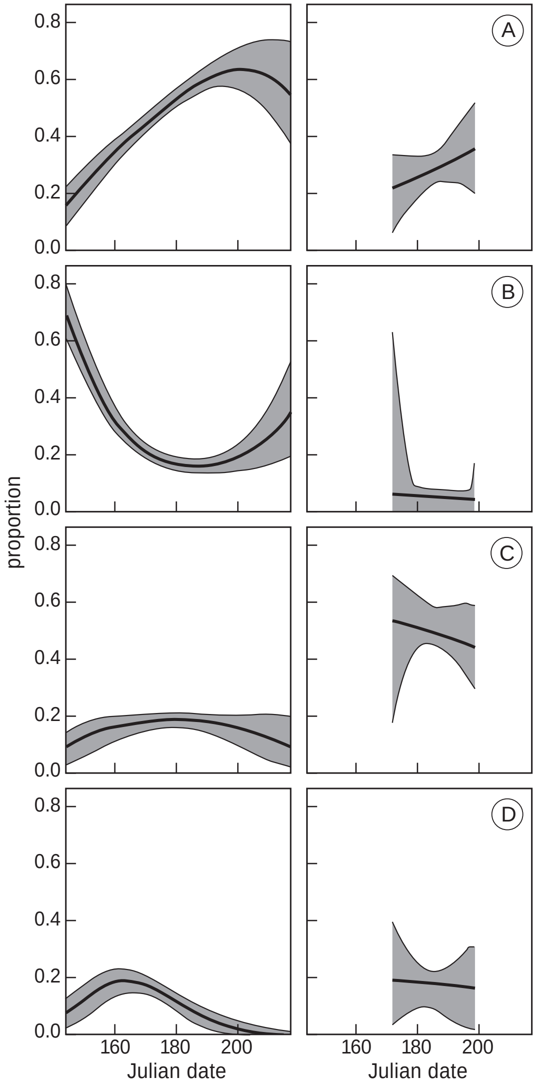


Fig.2. Fitted proportions (thick lines) and 95% confidence intervals (thin lines) for the four dietary components, (A) 0 group sandeel; (B) 1+ group sandeel; (C) clupeids; (D) other prey of Black-legged Kittiwakes after pooling across years and colonies within each colony type. For the marine (left hand column) and estuarine (right hand column) colony types, the linear predictors were quadratic and linear in Julian date respectively. Lines are drawn to indicate the range of dates sampled.

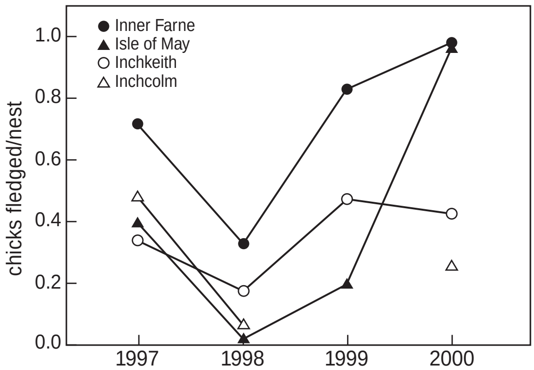


Fig. 3. Black-legged Kittiwake breeding success (chicks fledged per nest) from the Isle of May, the Farne Islands, Inchkeith and Inchcolm, 1997-2000.

The between colony differences that we found suggest that birds from the estuarine colonies were feeding relatively close inshore. The seabed in this area is dominated by rock/sand substrate (Fig. 1), a habitat favoured by Sprat and Herring (Daan *et al*. 1990; Marshall & Elliot 1998; Greenstreet *et al.* 1998; Power *et al.* 2000) and largely avoided by sandeels. In contrast, the predominance of sandeels in the diet of Kittiwakes at marine colonies suggests that they were foraging further offshore over sandy substrates. Data from VHF radio tracking and activity loggers deployed on Kittiwakes from the Isle of May provide direct support for this with most birds feeding within 80 km between northeast and southeast of the island (Humphreys 2002; Daunt *et al.* 2002). Much of this area is dominated by sand (Fig. 1) and includes the important sandeel fishing grounds of the Wee Bankie, Marr Bank and associated sandbanks (ICES 1994; Wright & Begg 1997). The seabed around the Farne Islands is also dominated by sandy substrates (Fig. 1). Indirect estimates of the foraging range of Kittiwakes from this colony in the 1960s, based on feeding trip durations and average flight speed, suggested a maximum distance of 55 km (Pearson 1968) and an important sandbank complex, the Berwick Bank, occurs within this range.

While our results provide circumstantial evidence that the foraging areas of Kittiwakes from the marine and estuarine colonies were segregated, the mechanism bringing this about is unclear. A confounding problem is that the estuarine colonies were much smaller than the marine ones (116 and 349 nests compared to 4196 and 5492 nests respectively). In the Northern Gannet *Morus bassanus*, mean foraging range is positively correlated with colony size (Lewis *et al.* 2001a). Kittiwakes on the Isle of May differ from Gannets and have an upper limit to the distance traveled from the colony rather than showing a linear relationship between foraging range and trip duration (Daunt *et al.* 2002; Humphreys 2002). However, the possibility remains that mean foraging ranges at small colonies are also smaller in Kittiwakes although if this is the case, it is unclear why Kittiwakes from the Isle of May do not fly west up the Firth of Forth to the estuarine waters that are closer than the sandbanks. Kittiwakes are highly visual feeders and large feeding flocks develop rapidly after a food source is located (Camphuysen & Webb 1999). It is therefore possible that estuarine clupeids are a more ephemeral food source than sandeels and are only profitable to exploit when travel distances are small. Perhaps Kittiwakes from the Isle of May operate a general rule of heading east to foraging areas that, although more distant, have higher probabilities of foraging success.

Data from the Isle of May and the Farne Islands indicate that although breeding success at the latter was generally higher, the two colonies showed similar trends over the period. Long-term studies on the Isle of May have shown a significant and positive association between sandeel availability and breeding success (Rindorf *et al.* 2000). The two estuarine colonies followed a broadly similar pattern to the marine ones between 1997 and 1999 with a decrease in success in 1998, but did not show a marked increase in 2000. During this season 0 group sandeels appeared earlier and were larger than average, characteristics that are typically associated with good breeding conditions for Kittiwakes (Wright 1996; Harris & Wanless 1997; Lewis *et al.* 2001b). There was no evidence from the birds at the estuarine colonies that they had altered their diet in response to this since clupeids remained the main item in the diet. Nor, to judge from their breeding success, was there any evidence that availability of clupeids increased in 2000.

The most parsimonious explanation for our finding of a consistent difference in the diet of Kittiwakes at estuarine and marine colonies is that the birds were exploiting different foraging areas. Studies have shown that Isle of May Kittiwakes do forage offshore (Humphreys 2002; Daunt *et al.* 2002) but equivalent data are needed for birds from the estuarine colonies. Our results also highlight the fact that some Kittiwakes in parts of the North Sea where sandeels are present (Daan *et al.* 1990) are not sandeel specialists and do consistently feed on other prey during the chick rearing periods. Such findings have important implications for monitoring schemes proposing to use Kittiwake breeding success as an indicator of the state of sandeel stocks (ICES 1994).

ACKNOWLEDGEMENTS

We are grateful to Bernadette Clarke, David Hammond and Robin Cox for help with collecting diet samples on the Isle of May, to John Davies, Alan Leitch, Martin Moss and other members of the Lothian Ringing Group for samples from Inchkeith, to Brian and Stephanie Little and other members of the Fife Ringing Group for samples from Inchcolm, and to John Walton and the National Trust wardens for samples from the Farne Islands. We thank Audun Stien, Laurent Crespin, Sarah Brocklehurst and Morten Frederiksen for statistical suggestions and Iain Gibb for help with otolith identification.

Scottish Natural Heritage allowed us to work on the Isle of May. British Geological Survey allowed us to use a GIS version of their substrate data (©NERC, see http://www.bgs.ac.uk/GeoData/home/html where further information relating to offshore digital data holdings may be found).

Data on bathymetry are reproduced by permission of the Controller of Her Majesty's Stationery Office and the UK Hydrographic Office. Part of the field work was supported by the Joint Nature Conservation Committees's integrated seabird monitoring scheme and by the European Commision Study Contract 95/C76/15 'Effects of large-scale industrial fisheries on non-target species'.

REFERENCES

Aebischer N.J. 1986. Retrospective investigation of an ecological disaster in the shag, *Phalacrocorax aristotelis*: a general method based on long-term marking. J Anim Ecol 55: 613-629.

Ainley D.G., G. Ballard, K.J. Barton, B.J. Karl, G.H. Rau, C.A. Ribic & P.R. Wilson 2003. Spatial and temporal variation of diet within a presumed metapopulation of Adélie Penguins. Condor 105: 95-106.

Aitchison J. 1986. The statistical analysis of compositional data. Chapman and Hall, London.

British Geological Survey 1984. 1:250 000 series, sea bed sediments and quarternary geology. British Geological Survey, Keyworth, UK.

Brothers N., R. Gales, A. Hedd & G. Robertson 1998. Foraging movements of the Shy Albatross *Diomedea cauta* breeding in Australia; implications for interactions with longline fisheries. Ibis 140: 446-457.

Cairns D.K. 1989. The regulation of seabird colony size: a hinterland model. Amer. Nat. 134: 141-146.

Camphuysen C.J. & A. Webb 1999. Multi-species feeding associations in North Sea seabirds: jointly exploiting a patchy environment. Ardea 87: 177-198.

Cramp S. & K.E.L. Simmons (eds) 1983. Handbook of the Birds of Europe the Middle East and North Africa. The birds of the Western Palearctic. Volume III. Oxford University Press, Oxford.

Daan N., P.J. Bromley, J.R.G. Hislop & N.A. Nielsen 1990. Ecology of North Sea Fish. Neth. J. Sea Res. 26: 343-386.

Daunt F., S. Benvenuti, M.P. Harris, L. Dall'Antonia, D.A. Elston & S. Wanless 2002. Foraging strategies of the Black-legged Kittiwake *Rissa tridactyla* at a North Sea colony: evidence for a maximum foraging range. Mar. Ecol. Prog. Ser. 245: 239-247.

Fairlamb D. 1999. Forth Islands Bird Report 1999. Forth Seabird Group Annual Report.

Furness R.W. & T.R. Birkhead 1984. Seabird colony distributions suggest competition for food supplies during the breeding season. Nature 311: 655-656.

Greenstreet S.P.R., J.A. McMillan & E. Armstrong 1998. Seasonal variation in the importance of pelagic fish in the diet of piscivorous fish in the Moray Firth, N E Scotland: a response to variation in prey abundance? ICES J. Mar. Sc. 55: 121-133.

Gremillet D., G. Dell'Omo, P.G. Ryan, G. Peters, Y. Ropert-Coudert & S.J. Weeks. 2004. Offshore diplomacy, or how seabirds mitigate intra-specific competition : a case study based on GPS tracking of Cape Gannets from neighbouring colonies. Mar. Ecol. Prog. Ser. 268 : 265-279.

Hamer K.C., P. Monaghan, J.D. Uttley, P. Walton & M.D. Burns 1993. The influence on food supply on the breeding ecology of Kittiwakes *Rissa tridactyla* in Shetland. Ibis 135: 255-263.

Hamer K.C., R.A. Phillips, J.K. Hill, S. Wanless & A.G. Woods 2001. Contrasting foraging strategies of Gannets *Morus bassanus* at two North Atlantic colonies: foraging trip duration and foraging area fidelity. Mar. Ecol. Prog. Ser. 224: 283-290.

Harris M.P. & S. Wanless 1997. Breeding success, diet and brood neglect in the Kittiwake (*Rissa tridactyla*) over an 11-year period ICES J. Mar. Sci. 54: 615-623.

Härkönen T. 1986. Otoliths: guide to the otoliths of the bony fishes on the north east Atlantic. Danibu ApS, Hellerup, Denmark.

Hemsley D. 1999. Studies of breeding birds and other biological recording on the Isle of May in 1999. Scottish Natural Heritage Report, Edinburgh.

Huin N. 2002. Foraging distribution of the Black-browed Albatross, *Thalassarche melanophris*, breeding in the Falkland Islands. Aquat. Conserv. 12: 89-99.

Humphreys E.M. 2002. Energetics of spatial exploitation of the North Sea by kittiwakes breeding on the Isle of May, Scotland. Ph.D-thesis, University of Stirling, Stirling.

ICES 1994. Reports of the ICES Advisory Committee on the Fisheries Management 1993. Parts 1 and 2. ICES Co-operative Research Report 196, Copenhagen

ICES 1995. Report of the ICES workshop on sandeel otolith analysis: review of sandeel biology. ICES CM 1995/G:4

Lack D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

Lewis S., T.N. Sherratt, K.C. Hamer & S. Wanless 2001a. Direct evidence for intraspecific competition for food in a pelagic seabird. Nature 412: 816-819.

Lewis S., S. Wanless, P.J. Wright, M.P. Harris, J. Bull, & D.A. Elston 2001b. Diet and breeding performance of Black-legged Kittiwakes *Rissa tridactyla* at a North Sea colony. Mar. Ecol. Prog. Ser. 221: 277-284.

Manly B.F.J. 1997. Randomization, bootstrap and Monte Carlo methods in biology, 2nd edition. Chapman and Hall, London.

Marshall S. & M. Elliott 1998. Environmental influences on the fish assemblage of the Humber Estuary, U.K. Estuar. Coast. Shelf 46: 175-184.

McCullagh P. & J.A. Nelder 1989. Generalized linear models, 2nd edition. Chapman and Hall/CRC, London.

Montgomery D.C., E.A. Peck & G. Vining 2001. Introduction to linear regression analysis, 3rd edition. Wiley, New York.

Parrish B.B., A. Saville, R.E. Craig, G. Baxter & R. Priestley 1959. Observations on herring spawning and larval distribution in the Firth of Clyde in 1958. J. Mar. Biol. Assoc. U.K. 38: 445-453.

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

Power M., M.J. Attrill & R.M. Thomas 2000. Temporal abundance patterns and growth of juvenile herring and sprat from the Thames estuary 1977-1992. J. Fish Biol. 56: 1408–1426.

Reay P.J. 1986. Ammodytidae. In: Whitehead P.J.P., M.L. Bauchot, J.C. Hureau, J. Nielsen & E. Tortonese (eds) Fishes of the north-eastern Atlantic and the Mediterranean Vol 2, 945-950. UNESCO.

Rindorf A., S. Wanless & M.P. Harris 2000. Effects of changes of sandeel availability on the reproductive output of seabirds. Mar. Ecol. Prog. Ser. 202: 241-252.

Suryan R.M., D.B. Irons, & J. Benson 2000. Prey switching and variable foraging strategies of Black-legged Kittiwakes and the effect of reproductive success. Condor 102: 374–384.

Walsh P.M., D.J. Halley, M.P. Harris, A. del Nevo, I.M.W. Sim & M.L. Tasker 1995. Seabird monitoring handbook for Britain and Ireland. JNCC/RSPB/ITE/Seabird Group, Peterborough.

Walton J. 2000. Birds of the Farne Islands in 1999. Trans. Nat. Hist. Soc. Northumbria 60: 37-58.

Wanless S., P.J. Bacon, M.P. Harris, A.D. Webb, S.P.R. Greenstreet & A. Webb 1997. Modelling environmental and energetic effects on feeding performance and distribution of shags (*Phalacrocorax aristotelis*): integrating telemetry. Geographical information systems and modeling techniques. ICES J Mar Sci. 54: 524-544.

Wanless S., & M.P. Harris 1993. Use of mutually exclusive feeding areas by adjacent colonies of Blue-eyed Shags (*Phalacrocorax atriceps*) at South Georgia. Colon. Wat. 16: 176-182.

Watt J., G.J. Pierce & P.R. Boyle 1997. Guide to the identification of North Sea fish using premaxillae and vertebrae. ICES Cooperative Research Report No 220.

Wright P.J. 1996. Is there a conflict between sandeel fisheries and seabirds? A case study at Shetland. In: Greenstreet S.P.R. & M.L. Tasker (eds) Aquatic predators and their prey, 154-165. Fishing News Books, Blackwell, Oxford.

Wright P.J. & G.S. Begg 1997. A spatial comparison of Common Guillemots and sandeels in Scottish waters. ICES. J. Mar. Sci. 54: 578-592.

SAMENVATTING

De Drieteenmeeuw *Rissa tridactyla* komt in grote delen van de Noord-Atlantische Oceaan voor. In de broedtijd leven Drieteenmeeuwen hoofdzakelijk van vis. In de Noordzee is de Kleine Zandspiering *Ammodytes marinus* een van de belangrijkste prooidieren. In dit artikel worden voedselkeuze en broedsucces in vier verschillende kolonies Drieteenmeeuwen aan de Schotse oostkust met elkaar vergeleken: twee kolonies in de monding van de Firth of Forth (Inchcolm en Inckeith; aangeduid als 'estuariene kolonies') en twee kolonies aan de Schotse oostkust (Farne Islands en Isle of May; aangeduid als 'mariene kolonies'). In elk van deze kolonies foerageren de meeuwen in gebieden waar zowel zandspiering als alternatieve prooidieren (haringachtigen: Sprot en Haring) in ruime mate beschikbaar zouden moeten zijn geweest. In elk van de vier onderzoeksjaren vertoonden de meeuwen in alle vier kolonies een vergelijkbare verschuiving in prooikeuze in de loop van het seizoen (al dan niet door het aanbod veroorzaakt), waarbij oudere jaarklassen zandspiering (1+ groep) werden vervangen door jonge vis van dat jaar (0-groep). In elk van de jaren was er een verschil in prooikeuze tussen de mariene en estuariene kolonies. Zandspiering was veruit de belangrijkste prooi op de Isle of May en op de Farne Islands, terwijl haringachtigen het beeld domineerden in de beide estuariene kolonies. Verondersteld wordt dat deze verschillen worden veroorzaakt door verschillen in de structuur en bodemsoort van de foerageergebieden. Zandige bodems, geprefereerd door zandspieringen, zijn in ruimere mate voorhanden voor de meeuwen van de mariene kolonies, terwijl de broedvogels van de estuariene kolonies niet ver van de kolonie in gebieden met een meer rotsige bodem foerageerden: habitats waar haringachtigen het beter naar de zin hebben dan zandspieringen. Het broedsucces in de vier kolonies had in de eerste drie jaren van het onderzoek een vergelijkbaar verloop, maar de sterke toename in broedsucces in de mariene kolonies in het vierde onderzoeksjaar werd niet gevonden in de twee kolonies dichter onder de kust. (CJC)

Corresponding editor: Kees (C.J.) Camphuysen
Received 20 November 2003, accepted 1 June 2004