

Breeding success, diet, and brood neglect in the kittiwake (*Rissa tridactyla*) over an 11-year period

M. P. Harris and S. Wanless



Harris, M. P. and Wanless, S. 1997. Breeding success, diet, and brood neglect in the kittiwake (*Rissa tridactyla*) over an 11-year period. – ICES Journal of Marine Science, 54: 615–623.

Seabirds are frequently used as indicators of the state of the marine environment. The kittiwake (*Rissa tridactyla*) is a common and widespread surface-feeding seabird often used for such a purpose. Data were collected on the food of chicks, breeding success, and chick neglect at a colony in south-east Scotland every summer in the period 1986–1996. Breeding success declined significantly over the period and breeding became later. In one year, many adults failed to breed. A similar decline in breeding success was also recorded at colonies over a 250–300 km section of coast in south-east Scotland and north-east England. Sandeels (*Ammodytes marinus*), especially 0-group fish (young of the year), made up the bulk of the diet in all years; herring (*Clupea harengus*) and sprat (*Sprattus sprattus*), waste from trawlers, and planktonic Crustacea was of lesser importance. Nesting success increased significantly with the proportion of 0-group sandeels in the diet of chicks and with the average energy value of 0-group sandeels, variables which were significantly and positively correlated. Clupeids and trawler waste were probably taken only when sandeels were unavailable. Brood neglect was not a good indicator of annual total breeding success. The decline in nesting success appeared to commence before the development of a large local industrial fishery for sandeels.

© 1997 International Council for the Exploration of the Sea

Key words: *Ammodytes marinus*, kittiwake, monitoring, *Rissa tridactyla*, sandeels.

M. P. Harris and S. Wanless: Institute of Terrestrial Ecology, Hill of Brathens, Banchory AB31 4BY, Scotland, UK. Correspondence to M. P. Harris: tel: +441330823434; fax: +441330823303; email: m.p.harris@ite.ac.uk

Introduction

Seabirds are often used as cost-effective and convenient monitors of the marine environment (e.g. Monaghan *et al.*, 1989; Furness and Greenwood, 1993; Harris and Wanless, 1990). The kittiwake (*Rissa tridactyla*) is a common and widespread species which obtains its food from, or just below, the sea surface. Its biology has been intensively studied in both the North Atlantic and North Pacific (Coulson and Thomas, 1985; Hamer *et al.*, 1993; Murphy *et al.*, 1991; Roberts and Hatch, 1993) and it is now widely used as a monitoring species, e.g. in Britain and Ireland (Walsh *et al.*, 1992) and Alaska (Murphy *et al.*, 1991). In an earlier 3-year study of kittiwake food and breeding in Britain, we found evidence for possible links between annual breeding success at a colony and (a) the quantity of sandeels in the diet of chicks at that colony; (b) the availability of 0-group sandeels (i.e. those hatched in the current year) to the adults; and (c) the frequency of chick neglect (the extent to which adults leave their chicks unattended; Harris and Wanless, 1990; Wanless and Harris, 1989, 1992). Here, we use data

collected during an 11-year study on the Isle of May, Firth of Forth, Scotland, as part of the UK Joint Nature Conservation Committee (JNCC) Seabird Monitoring Programme to investigate further these aspects of kittiwake biology.

Materials and methods

Data were collected on the Isle of May, in a standardized manner, each summer from 1986 to 1996 unless otherwise stated. Breeding success was assessed by checks of nests in 16 study plots dispersed throughout the colony; one check was made when most pairs had laid, another was made 7–10 d later, and another two to four were made at weekly intervals commencing the day that the first young fledged (see Harris, 1987). These plots held 15–20% of the total population of 6500–7500 nests. Success is expressed as the number of young fledged per completed nest after averaging across plots. Except for 1987–1989, counts were also made of incomplete nests. First egg dates, which are a good

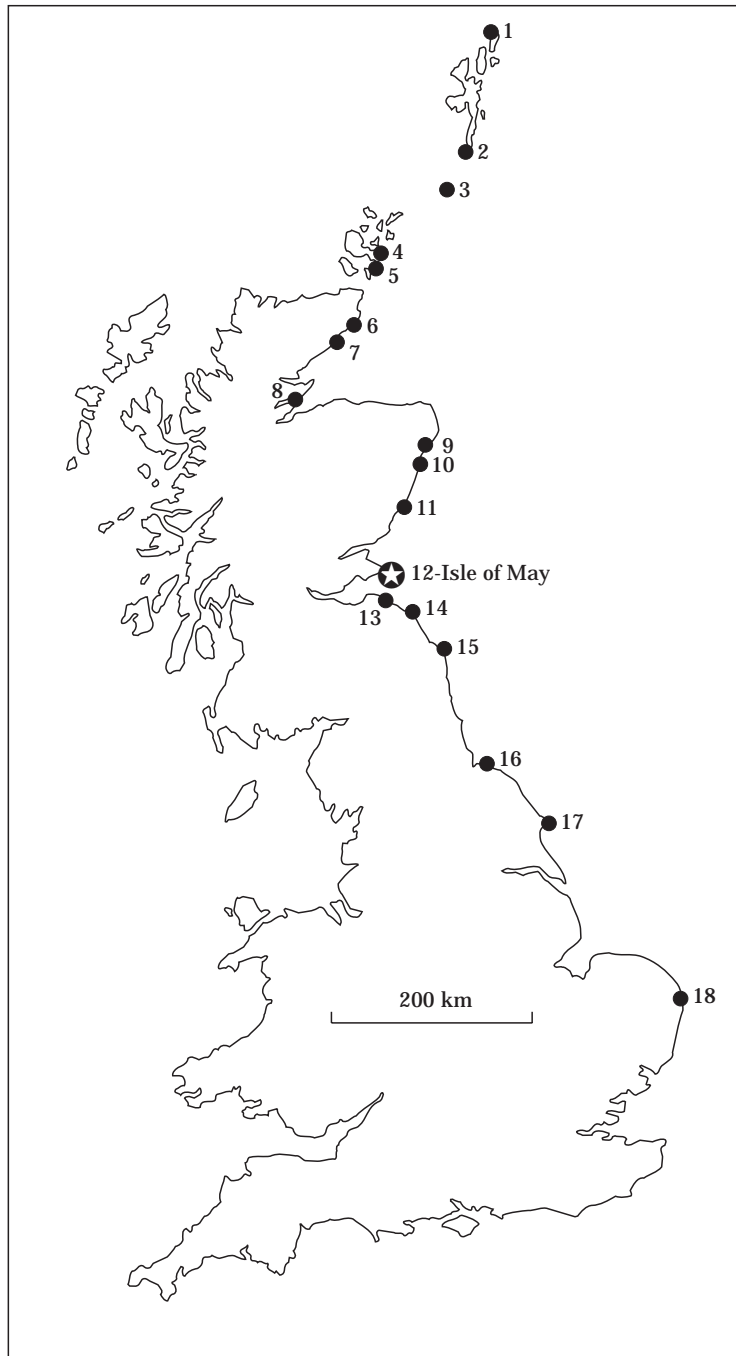


Figure 1. Colonies of kittiwakes where breeding success was monitored between 1986 and 1995. The colonies are listed in [Table 1](#).

indicator of median laying date (Murphy *et al.*, 1991), were determined by daily checks. The mean clutch-size (which included empty, but fully-lined nests) was based on checks of 50–200 nests after laying had finished. Breeding success at 17 other colonies distributed along the east coast of Britain (Fig. 1) was

recorded using similar methods as part of JNCC's Seabird Monitoring Programme (Walsh *et al.*, 1992; Thompson *et al.*, 1996). Where several colonies were monitored within a relatively small area, e.g. Shetland, only the most northern and southern sites were included.

Regurgitations from small to medium-sized chicks and adult kittiwakes that were brooding chicks were collected annually from 1986 to 1996. Sampling was carried out over approximately the same 3 to 4-week period each year from 1986 to 1993, with the mid-date varying from 21 to 26 June. However, in 1994, 1995, and 1996, when breeding was later, the mid-dates for sampling were 14, 5, and 10 July, respectively. Few samples were collected in 1990 and 1991 because: (1) there were very few chicks present; and (2) we were reluctant to make starving chicks regurgitate what little food they were receiving. Each regurgitate was weighed and the approximate percentages (by weight) in each load of: (a) sandeels (all individuals specifically identified were *Ammodytes marinus*); (b) clupeids (sprat (*Sprattus sprattus*) and herring (*Clupea harengus*)); (c) planktonic crustaceans; and (d) trawler waste (offal, large or demersal fish, and Crustacea unlikely to be caught directly by surface-feeding birds) were estimated. Intact fish were measured or assigned to 2 cm length classes using reference material.

Otoliths were extracted from the residual material, identified and the lengths of fish from which they came calculated using keys and formulae in Härkönen (1986), except for sandeels, where fish length (FL; mm) was calculated from otolith length (OL; mm) using the relationship: $FL = 50 \cdot OL + 28.1$ ($r^2 = 95\%$) obtained from 150 intact sandeels collected from seabirds on the Isle of May. Microscopic examinations showed that otoliths from fish 11 cm or less in length lacked annual growth rings, indicating that the fish were 0-group (i.e. young of the year), and we assume that this was also the case for intact fish. Diet is expressed as: (a) the percentage of regurgitates that contained sandeels (total and 0-group only), clupeids, crustaceans and trawler waste; and (b) the proportion (by biomass) of sandeels in the total mass of material examined in that year. As the energy value (EV) of a 0-group sandeel increases very rapidly as the fish grows, we converted the annual mean length (FL, cm) of a 0-group sandeel to EV (in kJ) using the relationship:

$$EV = 0.0021 FL^{3.92} \text{ (Hislop et al., 1991)}$$

Linear regression analysis was used to assess temporal changes and the effect of EV of 0-group sandeels on breeding success. Relationships between annual breeding success (and brood neglect) and the composition of the regurgitations were tested using Spearman rank correlation coefficients (1-tailed tests).

In each year except 1987, the incidence of broods with no adult in attendance (neglected broods) was recorded in samples of 50–200 nests that were checked around midday, from the day the first neglected brood was seen until the first young fledged (details in Wanless and Harris, 1989). There was a highly significant correlation

between the mean annual incidence of neglect in broods of one and two young ($r = 0.98$, $n = 10$ years, $p < 0.001$) and we use the latter (which was always the higher) as an annual index of neglect.

Results

Breeding success

Breeding success of kittiwakes on the Isle of May declined significantly over the period (Fig. 2; $n = 11$, $r^2 = 49\%$, $p < 0.02$). Success in 1993 was even lower than the 0.07 young per pair recorded, since many young died at, or very soon after, fledging, and the population of 7000 pairs was thought to have reared only 200 young. The monitoring scheme was not designed to collect data on nests that failed, but general observations showed that between 1986 and 1989, and in 1992, breeding failure occurred predominantly during the chick-rearing period. In the remaining years, failures occurred throughout the season, with some adults appearing to discontinue incubation even though they still attended the nests. The Isle of May has 1500–2500 pairs of herring gulls (*Larus argentatus*) that are well known as predators of young kittiwakes (Galbraith, 1983; Barrett and Runde, 1980; Cadiou and Monnat, 1996). However, only when a few individual gulls actually specialized in such predation, and only in small areas apparently within their nesting territories, did predation have any serious effect on kittiwake breeding success (Galbraith, 1983; personal observations). Eggs and dead or dying chicks left unattended often remained uneaten for days or weeks.

The variable timing of breeding failure suggests that a range of different factors might be acting on Isle of May kittiwakes. In some parts of the range, non-breeding by kittiwakes is a regular occurrence (Murphy et al., 1991) but, prior to 1994, large-scale non-breeding had apparently not been recorded on the Isle of May. In that year breeding was severely disrupted, apparently by a food shortage in the spring that also caused a high mortality of adult shags (*Phalacrocorax aristotelis*) and delayed the breeding of both this species and common guillemots (*Uria aalge*) (Harris and Wanless, 1996). Of the kittiwakes holding sites in the study plots, 32% did not even build nests in 1994, compared with the usual $5.1\% \pm \text{S.E. } 1\%$ ($n = 6$ years). In contrast to the incidence of birds failing to build nests, date of laying of the first egg was significantly later towards the end of the period (Fig. 2b; $r^2 = 39\%$, $n = 11$, $p < 0.05$). Also, mean clutch-size declined significantly during the study (Fig. 2c; $r^2 = 56\%$, $n = 8$, $p < 0.05$), and clutch-size was significantly larger in years when breeding was early ($r = -0.856$, $p < 0.01$, $n = 8$ years).

In five of the eight years there was a suggestion that breeding success was, as might be expected, positively

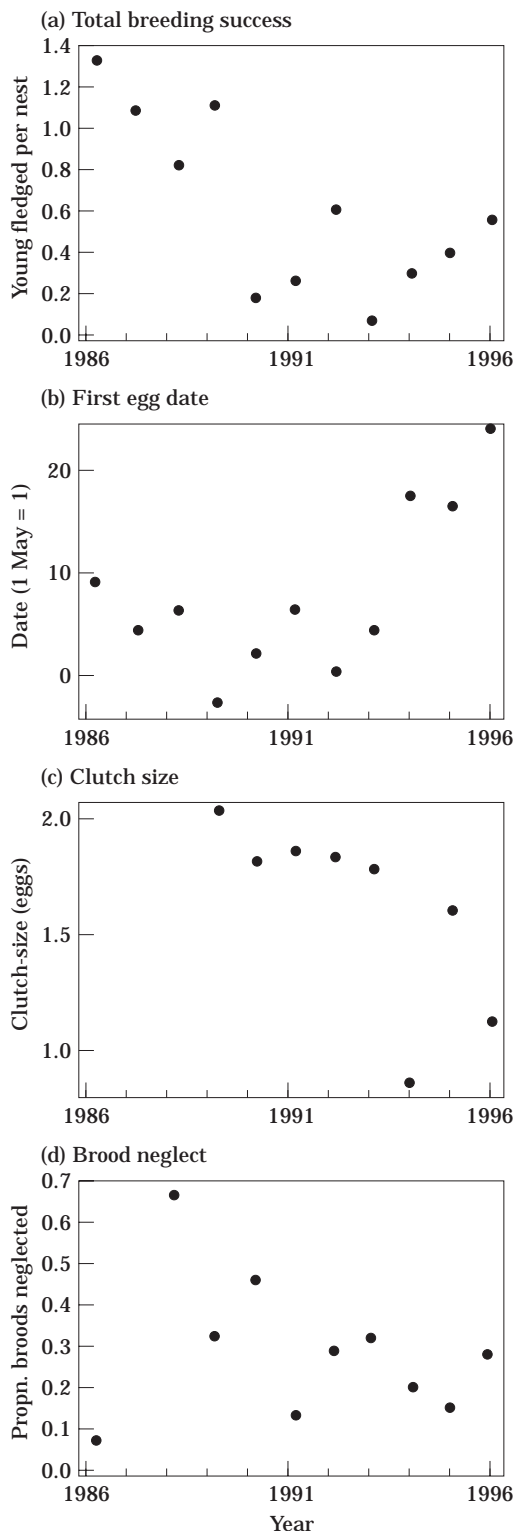


Figure 2. Annual estimates of (a) total breeding success; (b) first egg dates (1=1 May); (c) clutch size, and (d) brood neglect of kittiwakes on the Isle of May, 1986–1996.

related to clutch-size, whereas in 1990, 1991, and 1993 breeding success was considerably lower than might have been anticipated from the observed clutch size (Fig. 3). Such a pattern suggests that in these three years conditions were initially favourable but subsequently deteriorated until some birds were forced to abandon their eggs or chicks. There was no significant correlation between breeding success and first egg date ($r = -0.10$, $n=11$, n.s.), as has been recorded in Alaska (Murphy *et al.*, 1991).

Between 1986 and 1995 breeding output at 17 other colonies in east Britain was higher than that on the Isle of May (Table 1). (Although the annual average for the colony at Forvie was 0.48, this was measured over seven seasons during which the average for the Isle of May was 0.42.) The pattern of breeding success noted on the Isle of May also occurred at the three nearest monitored colonies to the north (all within 100 km) and the three to the south (all within 130 km) but not at 10 of the 11 more distant colonies (Table 1). The importance, if any, of the significant correlation between the Isle of May data and those for Lowestoft (500 km away) is unclear.

Diet of chicks

In all years, sandeels made up the bulk of the diet both in frequency of occurrence (67–100%) of regurgitations and in terms of biomass (50–98%; Table 2). The lengths of sandeels ranged from 5 to 20 cm, but most measured 11 cm or less, indicating that the majority were 0-group fish. The highest percentage of loads containing 0-group sandeels occurred in 1986 (97%), the lowest in 1991 (33%). The mean length and EV of 0-group sandeels was greatest in 1987 and 1988 (both 10.0 cm, 17 kJ) and least in 1991 (4.7 cm, 0.9 kJ). The annual proportion of loads with 0-group sandeels and the mean lengths of the fish were highly correlated ($r=0.82$, $n=11$, $p<0.01$).

The proportion of loads containing clupeids varied from 0 to 40%; specific determinations of clupeids were 13 herring (lengths 6–17 cm) and 83 sprat (4–10 cm). Trawler waste was composed mainly of whiting (*Merlangius merlangus*) 13–23 cm long ($n=14$) with some fish guts. Bottom-living Crustacea such as *Nephrops norvegicus* and polychaetes were also recorded and these items were assumed to have come from the many trawlers fishing for *Nephrops* within sight of the island.

Pelagic crustaceans were recorded in three years. However, only in 1993, when one sample comprised the copepod *Calanus finmarchicus*, and another was made up mainly of unidentifiable juvenile euphausiids and some adult *Thysanoessa inermis* (J. R. G. Hislop pers. comm.), and 1995, when one sample was composed of small euphausiids, did they form the bulk of any

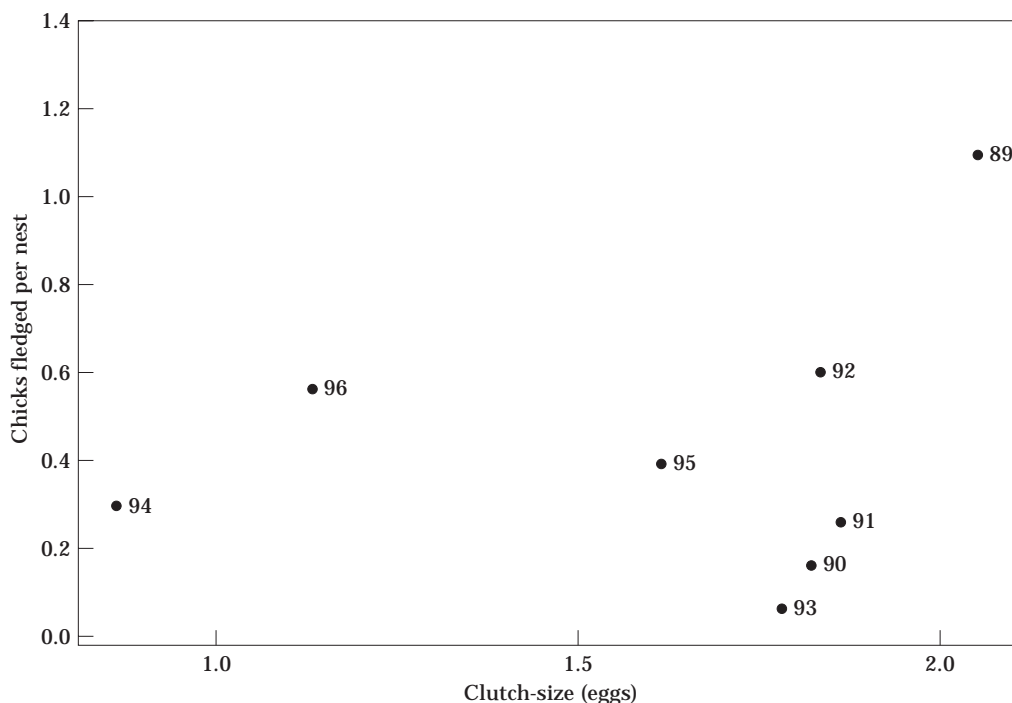


Figure 3. The relationship between breeding success and clutch-size of kittiwakes on the Isle of May, 1989–1996. The numbers indicate the year.

regurgitate. Additional items included some beetle remains and a moth larva.

Breeding success increased significantly with the percentage of sandeels in the total biomass (Fig. 4a;

Table 1. Breeding success (young fledged per completed nest) at 18 colonies in east Britain in 1986–1995. The locations of the colonies are shown in Fig. 1.

Colony	No. of years	Mean breeding success	Correlation with Isle of May	
1 Hermaness	5	0.75	-0.02	n.s.
2 Sumburgh	9	0.65	-0.31	n.s.
3 Fair Isle	10	0.79	-0.03	n.s.
4 Mull	8	1.01	-0.16	n.s.
5 Gultak	8	0.89	0.17	n.s.
6 Skirza	8	1.02	0.51	n.s.
7 An Dun	8	1.18	0.55	n.s.
8 North Sutor	6	0.91	-0.32	n.s.
9 Bullers of Buchan	6	0.72	0.91	p<0.02
10 Forvie	7	0.48	0.77	p<0.05
11 Fowlshough	8	0.87	0.94	p<0.001
12 Isle of May	10	0.62	—	
13 Dunbar	9	1.01	0.84	p<0.01
14 St Abb's Head	8	0.78	0.92	p<0.01
15 Farne Islands	9	1.00	0.90	p<0.001
16 Saltburn	9	1.12	0.28	n.s.
17 Bempton	9	1.11	0.07	n.s.
18 Lowestoft	9	1.27	0.74	p<0.05

$r_s=0.72$, $n=11$, $p<0.05$), the percentage of regurgitates that contained 0-group sandeels (Fig. 4b; $r_s=0.66$, $p<0.05$), and the EV of 0-group sandeels (Fig. 4c; $r^2=40\%$, $p<0.05$). It also declined with the frequency of both clupeids and trawler waste ($r_s=0.65$ and 0.78 , $p<0.05$).

Diet before laying

We collected 13 food samples during the pre-breeding period in May 1994. Of these, seven (54%) were composed of small planktonic crustaceans, three (23%) contained large sandeels, two (15%) contained clupeids, two (15%) contained fish discards, and single samples (8%) contained a few 4–5 cm long 0-group sandeels and a moth larva. In every April since 1973, kittiwake droppings on the Isle of May have been stained pink, apparently as a result of eating crustaceans, suggesting that these are an important prey item at this time of year.

Brood neglect

Brood neglect was lowest in 1986 and highest in 1988 (Fig. 2d). Neglect always occurred in the latter part of the chick-rearing period and the average interval between the onset of neglect and the start of fledging was $16 \pm \text{S.E. } 1$ days ($n=8$ years). Brood neglect has been

Table 2. Frequency of occurrence of types of food, the percentage (by weight) of sandeels in the diet, and length of 0-group sandeels from kittiwake regurgitations on the Isle of May 1986–1996.

Year	Frequency of occurrence					% (weight) of sandeels in diet	0-group sandeels	
	Samples (n)	Sandeels (%)	Fish discards (%)	Clupeidae (%)	Crustacea		No.	Mean length (mm)
1986	35	97 (97)	0	0	9	98	95	93
1987	17	94 (94)	0	6	9	95	40	100
1988	32	94 (79)	0	11	0	94	44	100
1989	25	100 (88)	8	0	0	95	4	80
1990	9	100 (79)	11	11	0	86	199	84
1991	9	67 (33)	44	11	0	50	22	47
1992	26	81 (50)	0	12	0	61	22	62
1993	56	73 (59)	30	16	4	63	274	63
1994	63	89 (81)	10	40	0	84	61	83
1995	47	91 (87)	4	13	4	86	97	74
1996	43	91 (91)	7	28	0	81	365	75

The percentage of regurgitations containing 0-group sandeels is given in parentheses.

regarded as a response to poor feeding conditions (e.g. Wanless and Harris, 1992). However, on the Isle of May brood neglect was not correlated significantly with any diet variable (all $r_s < 0.5$, $n = 11$, n.s.), nor with breeding success ($r_s = -0.094$, $n = 11$, n.s.).

Discussion

The JNCC Seabird Monitoring Programme collects long-term basic data on seabird productivity over a wide geographic area. This approach allows the rapid identification of colonies, or areas where changes, usually of an adverse nature, are occurring. Monitoring proved extremely effective in Shetland, where a scheme organized by the Shetland Oil Terminal Environmental Advisory Group highlighted problems among many marine birds in the 1980s (Heubeck, 1989) and provided the justification for an in-depth, but short-term, investigation of the interactions between seabirds and sandeels (Monaghan, *et al.*, 1989; Hamer *et al.*, 1993; Wright and Bailey, 1993). The results reported in this paper come purely from a monitoring study. However, the decline in breeding success of the kittiwake and the start of an industrial fishery for sandeels on the Wee Bankie, near the Isle of May, have prompted more detailed work in the area under the auspices of an EC-funded study, "Effects of Large-scale Industrial Fisheries on Non-Target Species" (ELIFONTS), in support of the Commission's programme supporting the Common Fisheries Policy which will commence during the 1997 field season.

Kittiwakes nesting at most colonies along the east coast of England and mainland Scotland have had generally good breeding success for many years

(Coulson and Thomas, 1985; Harris and Wanless, 1990). This contrasts with the situation in west Britain (Harris and Wanless, 1990) and Shetland, where the species experienced severe breeding failures during the late 1980s coincident with a decline in stocks, and very low recruitment, of sandeels (Heubeck, 1989; Wright and Bailey, 1993), and in Alaska, where breeding success is highly variable but generally very low by Atlantic standards (Murphy *et al.*, 1991; Roberts and Hatch, 1993). During the period 1986–1996, the breeding success of kittiwakes breeding on the Isle of May declined by an average of 0.09 chicks per pair per year. This, and the high proportion of adults failing to breed in one year, suggests that, as in Shetland in the late 1980s, adults were having difficulty in finding sufficient food to breed successfully. This was not a purely local phenomenon as monitoring at other colonies showed that breeding success of kittiwakes over a 250–300 km stretch of coast in south-east Scotland and north-east England was depressed. Few studies have investigated the relationship between kittiwake feeding distribution and breeding success. In Shetland, in a season when 81% of young fledged, almost all adults fed within 5 km of the colony (Hamer *et al.*, 1993). In contrast, in a year when no young survived, feeding areas were located at least 40 km away (Wanless *et al.*, 1992). Adults at colonies with depressed breeding output probably fed in different areas.

Kittiwakes eat a wide variety of fish, planktonic crustaceans, and polychaetes, and commonly take discards, waste fish, and invertebrates from trawlers (Cramp and Simmons, 1983). In the North-east Atlantic, young are known to be fed mainly on 0-group sandeels (Cramp and Simmons, 1983; Harris and Wanless, 1990; Wright and Bailey, 1993). Our study

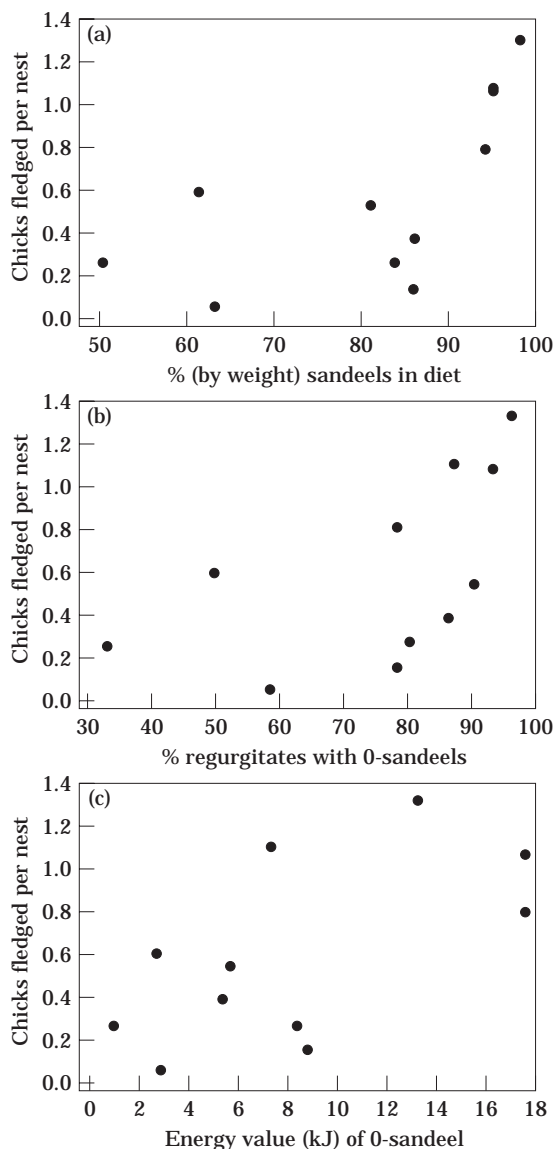


Figure 4. The relationship between annual measures of breeding success of kittiwakes on the Isle of May and (a) percentage (by weight) of sandeels in the diet of chicks; (b) percentage of loads which had 0-group sandeels; and (c) energy value of 0-group sandeel.

confirmed this. However, as *Ammodytes marinus* eggs do not hatch until late winter and the larvae metamorphose, at a length of 40–55 mm, only in late May or June, 0-group sandeels are unlikely to be available to kittiwakes during the pre-laying period (Wright and Bailey, 1993). Little is known of the diet of kittiwakes in the spring. Coulson and Thomas (1985) examined 13 samples collected from north-east England in February–April; 75% (by total weight) was clupeids, 13% sandeels (ages/sizes not given), 10% Gadidae and the remainder

Crustacea. Together with our data this suggests that the species is not then dependent on sandeels. More data are needed before we can look for links between pre-breeding food supply, laying date, and subsequent availability of 0-group sandeels.

Harris and Wanless (1990) speculated that there might be a positive relationship between the reduced proportion of 0-group sandeels in the diet of young and lower breeding success. The present study supports this hypothesis, and further suggests that clupeids and waste from trawlers are only fed to chicks when, to judge from low breeding success, feeding conditions are poor. Hamer *et al.* (1993) demonstrated a marked improvement in kittiwake breeding success between a year when sandeels were known to be scarce and a year when they were abundant, but, as kittiwakes obtain all their food at, or down to 30 cm below, the surface of the sea, they depend, to a certain extent, on external factors, such as upwelling or predatory fish making sandeels available. The puffin (*Fratercula arctica*) also specializes on feeding its young on 0-group sandeels but it catches them by underwater pursuit and forages to at least 68 m below the surface (Piatt and Nettleship, 1985). Between 1986 and 1996 the breeding success of puffins and kittiwakes on the Isle of May was significantly correlated ($r=0.64$, $n=11$, $p<0.05$). Thus, it is probable that breeding success of kittiwakes is a reasonable indicator of the abundance of sandeels within the whole water column.

Breeding success was also highest in years when the energy value of the 0-group sandeels fed to young was highest, i.e. the birds appeared to benefit from early hatching of sandeels. However, the size of 0-group sandeels and the frequency of occurrence of these in regurgitations were highly correlated, so it is not possible to determine which of the two factors is the more important. The limited evidence suggests the former. Thus, in Shetland, the late appearance of 0-group sandeels near the seabird colonies appeared to have a far greater adverse effect on the foraging and breeding of kittiwakes than did the reduced numbers of sandeels of this age that resulted from poor recruitment in the same year (Wright and Bailey, 1993). There are no estimates of sandeel stocks near the Isle of May. There is, however, a significant correlation between the breeding success of Isle of May kittiwakes and estimates of the number of 0-group sandeels in the southern North Sea in July (S. Reeves, Scottish Office Agriculture, Environment and Fisheries Department), but the relationship is negative ($r=-0.75$, $n=8$, $p<0.05$). The biological meaning, if any, of this result is again unclear, but it may well be that these stock assessments, made over thousands of km^2 , have little relevance to kittiwakes, which need to feed within a few tens of kilometres of the colony to rear young successfully (Hamer *et al.*, 1993).

On the Isle of May, kittiwake breeding was severely delayed in 1996 and clutch sizes were markedly lower

than normal, yet breeding success was higher than in most recent years. Measurements of sandeels being fed to puffin chicks on the Isle of May in May and June 1996 suggested that metamorphosis of sandeels was later than normal, but that towards the end of the season small sandeels became abundant. Fishery surveys in the western North Sea supported the suggestion that 1996 was a late season for sandeel recruitment (P. Wright, Scottish Office Agriculture, Environment and Fisheries Department unpublished data). It might be advantageous for kittiwakes to delay laying in order to increase the likelihood of there being larger sandeels to feed to the chicks. However, there could well be conflicting pressures against late breeding since earlier breeders tend to be more productive than late breeders in most species of birds (Lack, 1954). At least in some years, there is a large mortality of kittiwake chicks just at or after fledging, which suggests that food may become difficult to obtain then (Harris and Wanless, 1990).

Kittiwake chicks are normally attended by one adult, although older chicks are sometimes deserted temporarily even when food appears to be plentiful (Coulson and Johnson, 1993). It seems likely that as feeding conditions deteriorate adults will ultimately switch from an attendance pattern where one or other of the pair is always present at the nest to one where, at least for some of the time, both parents are foraging simultaneously (Barrett and Runde, 1980; Hamer *et al.*, 1993). Consequently, Wanless and Harris (1989, 1992) suggested that the frequency of neglect might be a useful indication of feeding conditions and, hence, breeding success. However, further investigation, as reported here, revealed no significant correlation between overall success and chick neglect. Breeding success is influenced by several factors besides the ease with which adults can obtain food for the chicks. Some of these will act before the chicks hatch and have little influence on whether or not adults attend their young. Predation pressure on kittiwakes on the Isle of May appears to be low and, although neglected chicks became wet and soiled with droppings from nearby nests and were sometimes attacked by prospecting immature birds (Danchin, 1987), the risks of being left alone would appear to be lower than those of starvation if one adult always remained at the nest even when food could only be obtained after a long foraging trip. As stressed by Cadiou and Monnat (1996), parental neglect can result from a variety of causes; low adult attendance cannot be taken alone as evidence of food shortage.

Our study has demonstrated that sandeels, especially those hatched during the current year, are of key importance to the breeding success of kittiwakes. Radio-tracking and observational data indicate that during the breeding season, many seabirds from the Isle of May feed over the Wee Bankie, a rich fishing ground located about 30 km away from the colony (Wanless *et al.*, 1990). An industrial sandeel fishery started at the Wee

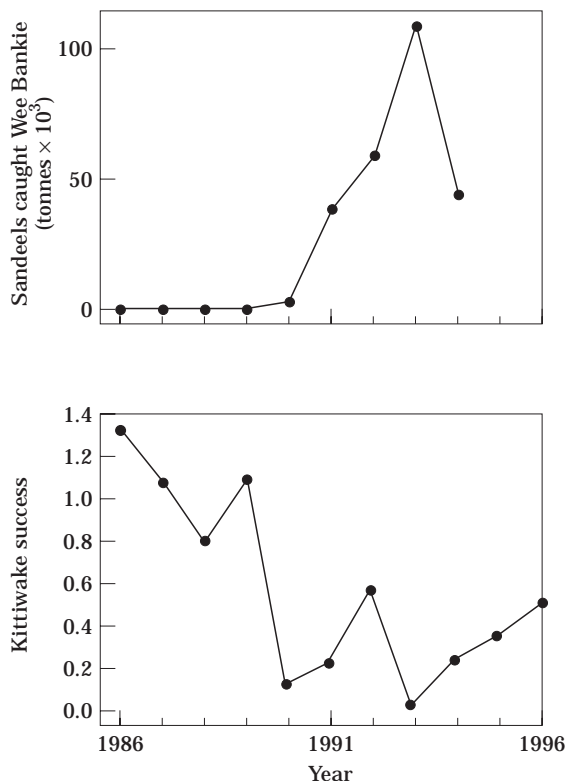


Figure 5. The annual reported landings of sandeels from the Wee Bankie (near the Isle of May) and nearby areas (ICES, 1995) and the breeding success of kittiwakes on the Isle of May.

Bankie in 1990, when the reported landing was 3000 t. Annual catches increased rapidly and, in 1993, 109 000 t were landed (Fig. 5). The rapid expansion of the fishery resulted in justifiable concern for seabirds in the area being forcefully expressed by conservation bodies, notably Greenpeace and the Royal Society for the Protection of Birds, as the nesting success of the kittiwakes on the Isle of May declined. The decline in breeding success appears to have commenced before the development of the fishery and to have extended to populations whose adults are unlikely to be foraging for their chicks at the Wee Bankie. In addition, the fishery operates in June and catches negligible numbers of 0-group sandeels (ICES, 1995; S. Reeves, pers. comm.). Thus, although there is no evidence that this fishery is the primary cause of kittiwake breeding failure, there is an obvious and urgent need to investigate interactions between marine birds and mammals and the sandeel fishery in the area. ELIFONTS will be carrying out such an investigation during the summers of 1997 and 1998.

Acknowledgements

We thank the many people who helped collect the field data, both on the Isle of May and elsewhere under

JNCC's Seabird Monitoring Programme. J. R. G. Hislop, P. J. Wright, and S. Reeves of SOAEFD Marine Laboratory gave much useful help, and R. Barrett, M. Heubeck, and K. Thompson improved the manuscript with their critical comments. Much of the work was carried out under a contract placed by JNCC with the Institute of Terrestrial Ecology (Natural Environment Research Council). The project also received financial support under EC study contract 95/C 76/IS-ELIFONTS.

References

- Barrett, R. T. and Runde, O. J. 1980. Growth and survival of nestling kittiwake *Rissa tridactyla* in Norway. *Ornis Scandinavica*, 11: 228–235.
- Cadiou, B. and Monnat, Y. J. 1996. Parental attendance and squatting in the kittiwake *Rissa tridactyla* during the rearing period. *Bird Study*, 43: 164–171.
- Coulson, J. C. and Johnson, M. P. 1993. The attendance and absence of adult kittiwakes *Rissa tridactyla* from the nest site during the chick stage. *Ibis*, 135: 372–378.
- Coulson, J. C. and Thomas, C. J. 1985. Changes in the biology of the kittiwake *Rissa tridactyla*: a 31-year study of a breeding colony. *Journal of Animal Ecology*, 54: 9–26.
- Cramp, S. and Simmons, K. E. L. (Eds). 1983. The birds of the western Palearctic, Vol. 3. Waders to gulls. Oxford University Press, Oxford. 913 pp.
- Danchin, E. 1987. The behaviour associated with the occupation of breeding site in the kittiwake gull *Rissa tridactyla*: the social status of landing birds. *Animal Behaviour*, 35: 81–93.
- Furness, R. W. and Greenwood, J. J. D. 1993. Birds as monitors of environmental change. Chapman and Hall, London. 368 pp.
- Galbraith, H. 1983. The diet and feeding ecology of breeding kittiwakes *Rissa tridactyla*. *Bird Study*, 30: 109–120.
- Hamer, K. C., Monaghan, P., Uttley, J. D., Walton, P., and Burns, M. D. 1993. The influence of food supply on the breeding ecology of kittiwakes *Rissa tridactyla* in Shetland. *Ibis*, 135: 255–263.
- Härkönen, T. 1986. Guide to the otoliths of the bony fishes of the Northeast Atlantic. Danbiu Aps, Hellerup. 256 pp.
- Harris, M. P. 1987. A low-input method of monitoring kittiwake *Rissa tridactyla* breeding success. *Biological Conservation*, 41: 1–10.
- Harris, M. P. and Wanless, S. 1990. Breeding success of British kittiwakes *Rissa tridactyla* in 1986–88: evidence of changing conditions in the northern North Sea. *Journal of Applied Ecology*, 27: 172–187.
- Harris, M. P. and Wanless, S. 1996. Differential responses of guillemot *Uria aalge* and shag *Phalacrocorax aristotelis* to a late winter wreck. *Bird Study*, 43: 220–230.
- Heubeck, M. 1989. Breeding success of Shetland's seabirds. *In* Seabirds and sandeels: proceedings of a seminar held in Lerwick, Shetland, 15–16th October 1988, pp. 34–44. Ed. by M. Heubeck. Shetland Bird Club, Lerwick. 76 pp.
- Hislop, J. R. G., Harris, M. P., and Smith, J. G. M. 1991. Variation in the calorific value and total energy content of the lesser sandeel (*Ammodytes marinus*) and other fish preyed on by seabirds. *Journal of Zoology* (London), 224: 501–517.
- ICES. 1995. Report of the Working Group on the Assessment of Norway Pout and Sandeel. ICES CM 1995/Assess: 5.
- Lack, D. 1954. The natural regulation of animal numbers. Oxford University Press, London. 343 pp.
- Monaghan, P., Uttley, J. D., Burns, M. D., Thaine, C., and Blackwood, J. 1989. The relationship between food supply, reproductive effort and breeding success in Arctic Terns, *Sterna paradisaea*. *Journal of Applied Ecology*, 58: 261–274.
- Murphy, E. C., Springer, A. M., and Roseneau, D. G. 1991. High annual variability in reproductive success of kittiwakes (*Rissa tridactyla* L.) at a colony in western Alaska. *Journal of Animal Ecology*, 60: 515–534.
- Piatt, J. F. and Nettleship, D. N. 1985. Diving depth of four alcids. *Auk*, 102: 292–297.
- Roberts, B. D. and Hatch, S. A. 1993. Behavioral ecology of black-legged kittiwakes during chick rearing in a failing colony. *Condor*, 95: 330–342.
- Thompson, K. R., Brindley, E., and Heubeck, M. 1996. Seabird numbers and breeding success in Britain and Ireland, 1995. UK Nature Conservation No. 20. Joint Nature Conservation Committee, Peterborough.
- Walsh, P. M., Sim, I., and Heubeck, M. 1992. Seabird numbers and breeding success in Britain and Ireland, 1991. UK Nature Conservation No. 6. Joint Nature Conservation Committee, Peterborough.
- Wanless, S. and Harris, M. P. 1989. Kittiwake attendance patterns during chick rearing on the Isle of May. *Scottish Birds*, 15: 156–161.
- Wanless, S. and Harris, M. P. 1992. Activity budgets, diet and breeding success of Kittiwakes *Rissa tridactyla* on the Isle of May. *Bird Study*, 39: 145–154.
- Wanless, S., Harris, M. P., and Morris, J. A. 1990. A comparison of feeding areas used by individual common murrens (*Uria aalge*), razorbills (*Alca torda*) and an Atlantic puffin (*Fratercula arctica*) during the breeding season. *Colonial Waterbirds*, 13: 16–24.
- Wanless, S., Monaghan, P., Uttley, J. D., Walton, P., and Morris, J. A. 1992. A radio-tracking study of kittiwakes (*Rissa tridactyla*) foraging under suboptimal conditions. *In* Wildlife telemetry, pp. 580–590. Ed. by I. G. Priede and S. M. Swift. Horwood, New York. 708 pp.
- Wright, P. J. and Bailey, M. C. 1993. Biology of sandeels in the vicinity of seabird colonies at Shetland. Scottish Office Agriculture and Fisheries Department, Aberdeen. 64 pp.