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Article in *Marine Ecology Progress Series* · August 2000

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Effects of changes in sandeel availability on the reproductive output of seabirds

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ABSTRACT: The lesser sandeel *Ammodytes marinus* is a key prey species for many marine birds in the North Sea. This fish is currently the target of the largest single species fishery in the area, and this has led to concern about the potential impact of the fishery on seabirds. There are 2 critical issues: does the breeding success of seabirds depend on sandeel availability and does the fishery reduce sandeel availability to a level at which avian reproductive output is affected? This paper investigates the first question in detail and briefly touches on the second by testing for correlations between productivity, breeding effort and diet in 3 species of seabird with contrasting foraging and dietary characteristics (common guillemot *Uria aalge*, black-legged kittiwake *Rissa tridactyla*, and European shag *Phalacrocorax aristotelis*) and an index of availability of 1 group and older sandeels derived from catch per unit effort statistics from the Danish sandeel fishery. Breeding success in all 3 species was significantly reduced when sandeel availability to the fishery in June was low. There was also evidence that the timing of peak sandeel availability influenced reproductive output such that success was lower when availability peaked early. We speculate that these effects are linked to annual variations in sandeel life history events and, in particular, to the onset of burying behaviour of 1+ group fish and the arrival of 0 group sandeels on the seabirds' feeding grounds. Although the timing of these events is unlikely to be directly influenced by the sandeel fishery, since most catches are taken in June, it is possible that the fishery could exacerbate a difficult situation for seabirds by further reducing the biomass of available 1+ group fish. We suggest that this may have occurred in one of the years of the study.

KEY WORDS: *Ammodytes marinus* · Black-legged kittiwake · Common guillemot · European shag · Industrial fisheries · North Sea · Predator performance

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INTRODUCTION

Evaluating the potential consequences of competition between natural predators and man for common resources represents one of the major challenges for applied ecology. Central to understanding such situations is the need for knowledge of relationships between prey availability and predator performance. The lesser sandeel *Ammodytes marinus* is one of the commonest fish species on the continental shelf of north-west Europe and comprises 10 to 15% of the total fish biomass in the North Sea (Sherman et al. 1981, Sparholt 1990). It is eaten by many seabirds, marine

mammals and fish (Harwood & Croxall 1988, Daan 1989, Hammond et al. 1994, Furness & Tasker 1997) and is currently the target of the largest single species fishery in the North Sea (Gislason & Kirkegaard 1998). The magnitude of the fishery and the importance of the species for marine predators has led to concern over the potential impact of sandeel harvesting on the North Sea ecosystem (Monaghan 1992, ICES 1998b). One of the areas of greatest concern is centred around the fishing grounds on the Wee Bankie, Marr Bank and Scalp Bank (for convenience subsequently referred to as the Wee Bankie) off the southeast coast of Scotland (Dunn 1998). This area was first exploited by the industrial fishery in 1990. Since 1993, the annual catch has varied between 20 000 and 100 000 t (ICES 1995, 1996,

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1997, 1998a, 1999). The Wee Bankie is also known to be used as a feeding area by many of the 154 000 pairs of seabirds which breed at colonies in and around the Firth of Forth (Wanless et al. 1998). Recent analyses have shown that breeding success of some species in the area has declined (Harris & Wanless 1997, Thompson et al. 1999). The evidence suggests that this decline has been associated with changes in sandeel availability although the causal factors involved remain obscure. Thus 1 study concluded that poor breeding success in black-legged kittiwakes *Rissa tridactyla* was correlated with a reduced proportion of 0 group sandeel in the diet (Harris & Wanless 1997), while another found a significant positive correlation with the abundance of the North Sea 1+ group sandeel stock (Furness 1999b). However, neither of these studies were ideal for assessing predator/prey relationships since, in the first, data on prey availability were not collected independently of data on predator diet, and, in the second, information on prey availability was collected at a much greater spatial scale than data for the predator.

This paper reports on the first detailed investigation of the relationships between seabird breeding performance and the local availability of 1 yr and older (1+ group) sandeels in the northwestern North Sea. Analyses of other seabird communities have shown that, although there is often a coherent pattern, interspecific differences associated with feeding mode (in particular surface feeders vs diving species), and dietary breadth (generalist vs specialist feeders) are common (Montevocchi 1993, Monaghan 1996, Croxall et al. 1999). We therefore compared the responses of 3 species of marine birds with contrasting foraging and dietary characteristics: (1) the common guillemot *Uria aalge*, an offshore-feeding, wing-propelled, pursuit-diver known to take clupeids (small herring *Clupea harengus*, and sprat *Sprattus sprattus*) in addition to sandeels; (2) the European shag *Phalacrocorax aristotelis*, an inshore/coastal, foot-propelled, pursuit-diver with a high dependence on sandeels; and (3) the black-legged kittiwake *Rissa tridactyla*, an offshore, surface-feeder which also has a high dependence on sandeels. Information on sandeel availability was derived from monthly catch per unit effort (CPUE) statistics from the Danish sandeel fishery. The CPUE of a species is usually assumed to be proportional to the biomass in the area (Hilborn & Walters 1992). This proportionality factor is referred to as the catchability and is affected by both technical variables, such as fishing method and vessel size, and biotic effects, principally prey behaviour. Variations in catchability due to behaviour are likely to be particularly important in the case of the lesser sandeel because of the complexity of its life history (Winslade 1974a). Thus, as with other sandeel species, lesser sandeels are closely associated

with sandy substrates into which they burrow, following a planktonic larval phase (Macer 1966, Reay 1970). Both fisheries data and sediment sampling suggest that, except for spawning in December and January, this species rarely emerges from the seabed between September and March (Macer 1966, Gauld & Hutcheon 1990). Moreover, even during the active spring and summer periods, fish only emerge from the sediments to feed during daylight hours (Winslade 1974a). In general, the availability of sandeels to avian predators is likely to be less when they are in the sediment compared to when they are in the water column. However, little is known about how sandeel behaviour varies between years and the effect this has on predator performance.

Our approach fulfils 3 key criteria for predator/prey analyses, namely the data for predators and prey are independent and are at similar spatial and temporal scales. In combination they allowed us to explore the interactions between the performance of the seabirds and 2 components of sandeel availability: (1) abundance, and (2) behaviour, in particular annual variations in the timing of the sandeels' transition from a predominantly pelagic existence to spending the majority of their time buried in sandy sediments (Winslade 1974b).

METHODS

Sandeel availability. An index of sandeel availability on the Wee Bankie was derived using a model based on the commercial catch in tonnes per vessel per day (CPUE) obtained from information held in the Danish logbook data base. This data base contains the total catch in tonnes per vessel in each ICES (International Council for the Exploration of the Sea) square, the number of days fished by the vessel in the square and the size of the vessel in gross registered tonnes (GRT), all by fishing trip. The Wee Bankie is rarely fished outside May, June and July, so only these months were included in analyses. A total of 41 samples from the commercial sandeel catch in the area were taken in the period 1990 to 1998, distributed over the months April to August. The species and age distribution of these samples was determined, but due to large between-sample variation, the sample size was too small to allow calculation of the CPUE in terms of numbers at age. It was therefore not possible to separate the effects of changes in growth and age composition from the effects of changes in other parameters such as mortality and behaviour. In only 1 year (1996) did any of the samples taken contain 0 group sandeels, and so CPUE reflects 1+ group availability rather than the availability of all ages. CPUE was assumed to be a

potency function of vessel size, as suggested by ICES (1996). As preliminary inspection of the data indicated that the variance was an increasing function of the mean, CPUE was assumed to be gamma distributed. A generalised linear model of CPUE was constructed, using the log link function. The scale parameter was estimated by Pearson's statistic divided by the degrees of freedom. This procedure invalidates tests for model fit, but deviance residuals were examined for trends. Factors which did not have a significant effect at the 0.05 level were excluded (F -test). All statistical analyses were conducted using SASTM software for WindowsTM (Version 6.12).

The model analysed was:

$$\ln(\text{CPUE}) = \alpha_{\text{sq},y,m} + \beta_{y,m} \times \ln(\text{GRT})$$

where sq = ICES-square, y = year, m = month, GRT = gross registered tonnes and α , β = constants within indices. The model was constructed using data for ICES squares 40E8, 41E7 and 41E8, the squares closest to the seabird colony on the Isle of May where the data on predator performance were collected (Fig. 1). In addition, the mean monthly CPUE of a vessel of 325 GRT in the area of the North Sea between 55° 30' N and 57° 30' N, excluding the ICES squares 40E8, 41E7 and 41E8, was also calculated (Fig. 1). This value was used to compare monthly variations in CPUE in the 2 areas. The predicted mean CPUE in square 41E8 in each month and year for a vessel of 325 GRT was calculated as:

$$\widehat{\text{CPUE}}_{\text{sq}=41\text{E8},y,m} = \exp[\hat{\alpha}_{\text{sq}=41\text{E8},y,m} + \hat{\beta}_{y,m} \times \ln(325)]$$

where α and β are the parameters estimated from the generalised linear model. This CPUE was assumed to be an index of sandeel availability to the fishery at that time. This square was chosen since the majority of the catch was taken there in all years; moreover, it was the only square fished in all years.

In addition to catches by Danish vessels, some fishing was also carried out in the area by Scottish and Norwegian boats. To allow for this the total fishing-effort in the area was standardised to fishing days of a Danish vessel of 325 GRT by the equation:

$$\text{standardised total international effort} = \frac{\text{total international catch}}{\text{standardised CPUE}}$$

Predator performance. Data came from guillemots, kittiwakes and shags breeding on the Isle of May (56° 11' N, 02° 23' W), approximately 30 km from the western edge of the Wee Bankie (Fig. 1). Data on breeding success (chicks fledged per pair breeding) and population size (breeding pairs) were collected between 1986 and 1998. Information on the diet of these species was obtained during the chick-rearing period (predominantly June and early July) over the same time period. Diet was assessed in terms of prey species and, for sandeels, 2 age categories: 0 group and 1+ group. These assessments were based on visual observations of prey brought in for chicks and fish collected from the breeding ledges to check identifications and size estimates (guillemots), and examination of intact prey or otoliths extracted from regurgitated food samples (kittiwakes and shags). In addition, an annual index of guillemot chick quality was estimated

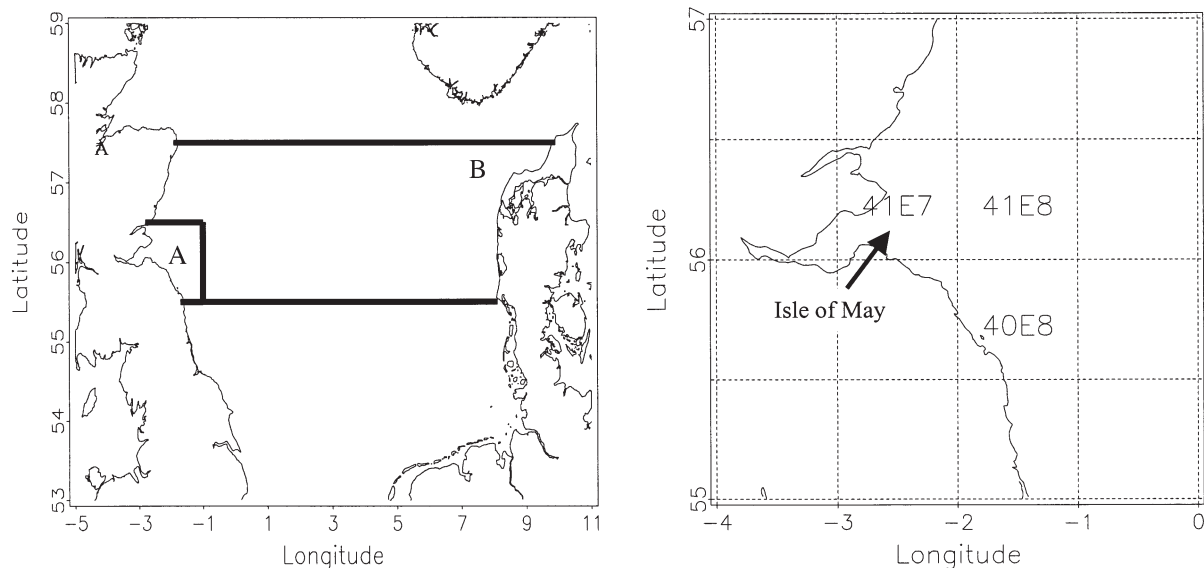


Fig. 1. Left panel: study area indicating the focal area in the Firth of Forth (A) and the limits of the larger North Sea area used for comparisons (B). Right panel: positions of the seabird breeding colony on the Isle of May and the ICES squares used in the analyses

as the mean mass of a sample of chicks weighed just prior to fledging. Indices of breeding effort for guillemots were derived from the proportion of chicks for which only 1 adult was present at midday and for kittiwakes from the proportion of 2-chick broods that were unattended at midday. High values of these indices were assumed to represent increased breeding effort (Burger & Piatt 1990).

Predator performance in relation to sandeel availability. Correlations between breeding success of each of the seabird species and CPUE in May, June and July and the ratio between CPUE in May and June (see the 'Results' section for the reasons for this) were calculated to assess the effect of sandeel availability on these parameters. The ability of the 3 predators to compensate for changes in sandeel availability is likely to depend on (1) their ability to switch to other prey and (2) their potential to increase breeding effort. If compensation is incomplete, both chick survival and chick quality may be affected. To investigate these aspects, the correlation between dietary composition of the birds in terms of the percentage of 1+ group sandeels in the diet, guillemot chick quality and indices of breeding effort in guillemots and kittiwakes and CPUE parameters were calculated. Significance level in correlation analyses was set at 5%.

RESULTS

1+ group sandeel availability

Results from the CPUE model indicated that variation between years and months was much greater than the variation between squares and vessel size, emphasising the importance of considering sandeel CPUE at the lowest possible temporal scale (Table 1). Predicted mean monthly CPUEs in the ICES square 41E8 are shown in Fig. 2. The highest June CPUE occurred in 1992 and was approximately 3 times greater than the lowest CPUE in 1990. CPUE in May showed a 2-fold variation over the years.

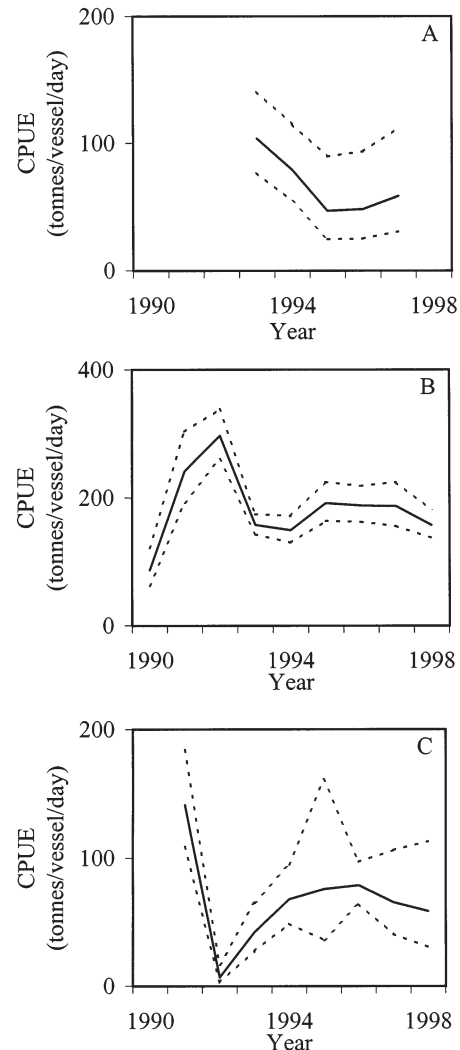


Fig. 2. Predicted catch per unit effort (CPUE, solid line) and 95% confidence limits of the predicted mean (dashed lines) on the Wee Bankie in (A) May, (B) June and (C) July. Note that y-axes are not to the same scale

The Wee Bankie was only fished in May in 5 of the 8 years the fishery operated. In these years, CPUEs in May and June were significantly and negatively corre-

Table 1. Summary of results of the generalised linear model of CPUE

Factor	Deviance	df	F	p	r ²	Cumulative r ²
Total	598.8					
Ln(GRT)	7.5	1	20.6	0.0001	0.013	0.013
Year	63.2	8	21.7	0.0001	0.106	0.118
Month	44.3	2	61	0.0001	0.074	0.192
Year × Month	16.7	11	4.2	0.0001	0.028	0.220
Square	1.8	2	2.5	0.0810	0.003	0.223
Square × Month	7.4	4	5.1	0.0004	0.012	0.235
Residual	457.9					

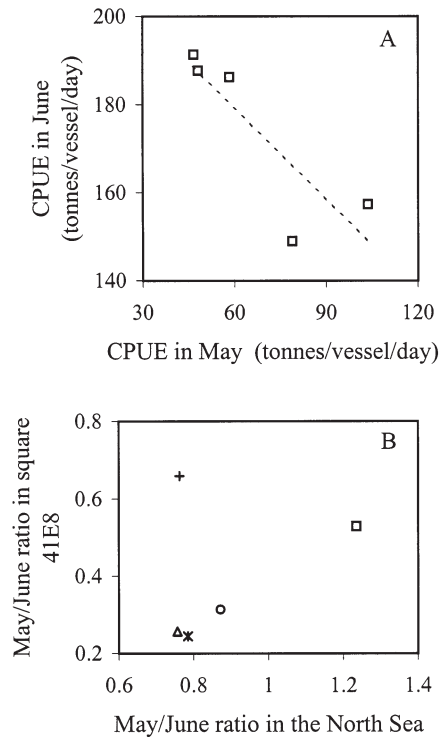


Fig. 3. (A) CPUE in June as a function of CPUE in May on the Wee Bankie and (B) comparisons of May/June CPUE ratios on the Wee Bankie and in the northern North Sea. Values for the various years are indicated by: 1993 (+), 1994 (□), 1995 (✱), 1996 (Δ) and 1997 (○)

lated ($r = -0.86$, $p < 0.01$; Fig. 3A). The direction of the relationship was of particular interest because intuitively CPUE in 2 mo in any year would be expected to be positively correlated. The negative trend could potentially be due to annual differences in the seasonal pattern of sandeel availability to the fishery, in particular to the timing of peak availability. An index of the annual timing of this peak was estimated from the ratio between May and June CPUE. Thus an early peak in availability gives a high CPUE in May compared to that in June, resulting in a high CPUE index. Conversely a late peak gives a high June CPUE relative to that in May, resulting in a low CPUE index.

To investigate if the pattern found on the Wee Bankie was also present over a wider area, May/June CPUE ratios for the Wee Bankie were compared with those for the northern North Sea (Fig. 3B). Ratios for the Wee Bankie were lower than for the North Sea as a whole, indicating that, in general, sandeel availability in this localised area peaked later. CPUE ratios in the 2 areas were not significantly correlated, but inspection of the scatter plot indicated that while values for the years 1994 to 1997 showed a clear positive trend, the point for 1993 was a conspicuous outlier. Thus the 1993

CPUE ratio on the Wee Bankie was disproportionately higher than elsewhere in the northern North Sea, suggesting that in this year availability peaked relatively earlier on the Wee Bankie.

An alternative explanation for the negative correlation between June and May CPUE is that it was caused by variations in fishing effort. Annual estimates of fishing effort and total catch in ICES square 41E8 for each of the 3 months are shown in Fig. 4. Both catch and effort in May were always low relative to values in June and July. The highest May catch was taken in 1994. However, even in this year the catch was low compared to the June catch. Effort in June peaked in 1993, with the value being 3 times higher than in any other year. Subsequently, effort in June declined, apart from a slight increase in 1998. Effort in July fluctuated without any particular trend.

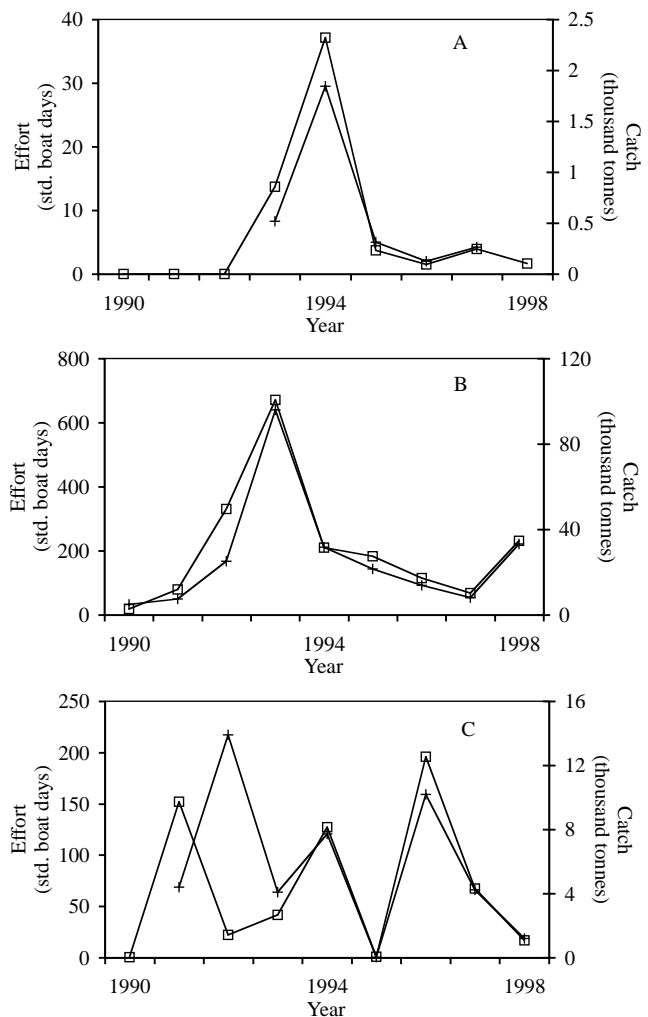


Fig. 4. Total catch of sandeels (□) and fishing effort (+) in ICES square 41E8 between 1990 and 1998 in (A) May, (B) June and (C) July

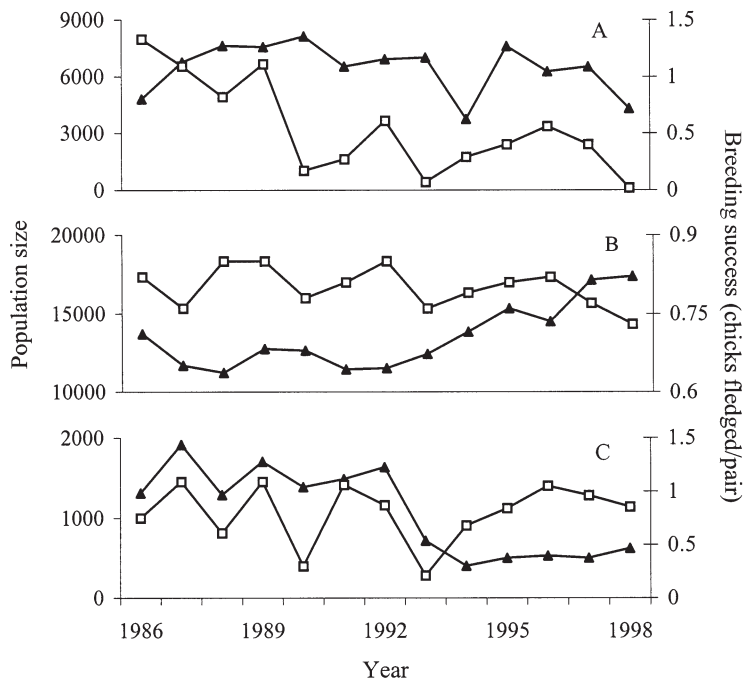


Fig. 5. Temporal changes in population size (\blacktriangle) and breeding success (\square) of (A) kittiwakes, (B) guillemots and (C) shags on the Isle of May between 1986 and 1998. Note that y-axes are not to the same scale

Seabird responses

Annual estimates of breeding success in the 3 seabird species are shown in Fig. 5. Guillemots only rear a single chick, whereas brood size in shags and kittiwakes varies between 1 and 3. It was therefore not surprising that the magnitude of annual changes in breeding success shown by guillemots was much less than that of the other 2 species. However, the main temporal effects were broadly similar, with success being low in all 3 species in 1990 and 1993 and also low for guillemots and kittiwakes in 1998. There was no evidence of any systematic temporal trend in reproductive output of guillemots or shags but output in kittiwakes declined significantly between 1986 and 1998 ($r = -0.86$, $p = 0.004$). The reduction in breeding success between 1989 and 1990 was particularly marked, and productivity since 1990 has generally remained low. There were no significant correlations between breeding success and population size for any of the species (all p -values > 0.08).

The time series data for seabird diets in June revealed clear interspecific differences, with kittiwakes and shags showing a consistently high dependence on sandeels but with the age

class taken varying between years (Fig. 6). In contrast, guillemots showed considerable annual variation in the proportion of sandeels taken (with the alternative prey being almost entirely small herring or sprat) but almost no variation in the age category taken, with $> 97\%$ of sandeels being 1+ group fish.

Indices of breeding effort in guillemots and kittiwakes showed broadly similar temporal trends between 1991 and 1998 (Fig. 7). However, the increase in breeding effort in kittiwakes in the second half of the period was more marked than that of guillemots.

Predator performance in relation to sandeel availability

Breeding success of all 3 seabird species was significantly correlated with either the May/June CPUE index, May CPUE or June CPUE (Fig. 8, Table 2). However, while the correlation was positive for the comparisons involving June CPUE, indicating that low breeding success was associated with reduced availability of 1+ group sandeels to

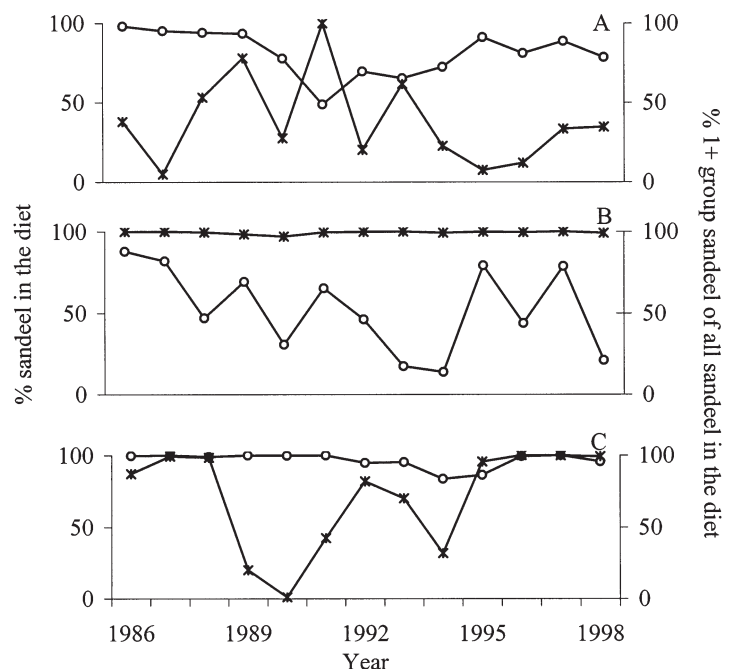


Fig. 6. Temporal changes in the percentage of sandeels in the diet (\circ) and the percentage of sandeels taken that were 1+ group (\times) in (A) kittiwakes, (B) guillemots and (C) shags on the Isle of May between 1986 and 1998

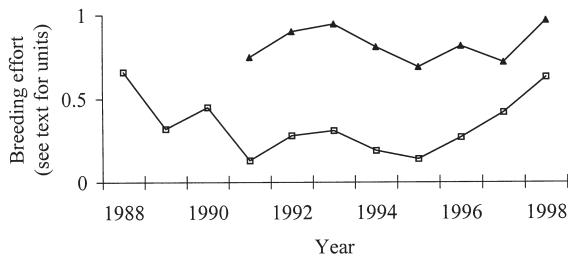


Fig. 7. Temporal changes in indices of breeding effort in kittiwakes (□) and guillemots (▲) on the Isle of May between 1988 and 1998. See 'Methods' for details of how effort was estimated

the fishery at this time, all the correlations with the May and May/June CPUE index were negative. This suggested that reproductive output was affected not only by the absolute level of 1+ group sandeel availability but also by the timing of peak availability, with success being lower in seasons when availability peaked early. Interspecific comparisons of the strength of the response indicated that, over the observed range of CPUE, kittiwakes and shags showed proportionately greater changes in productivity than guillemots (Fig. 9). Additional data for guillemots on chick condi-

tion at fledging indicated that the effect could have been more severe than indicated simply by breeding success because weights tended to be lower in years when the May/June CPUE index was high ($r = -0.803$, $p = 0.10$). In none of the species was breeding success significantly correlated with CPUE in July or the ratio between June and July CPUE.

Comparisons between the proportion of 1+ class sandeels in the diet of seabirds and the estimates of 1+ group sandeel availability indicated that in all 3 species the strongest correlations were with May CPUE and with the May/June CPUE index, although none of the relationships were statistically significant (Table 2). However, the direction of the relationship differed between the predators, with a lower CPUE index, indicating a late peak in 1+ group sandeel availability, associated with a higher proportion of 1+ class sandeels in the diet of the 2 diving species but with a lower proportion in the diet of the surface-feeding kittiwake.

Data on attendance patterns provided some evidence that guillemots were able to compensate for changes in sandeel availability, with the amount of time the pair spent together at the site tending to be lower in years when availability peaked early

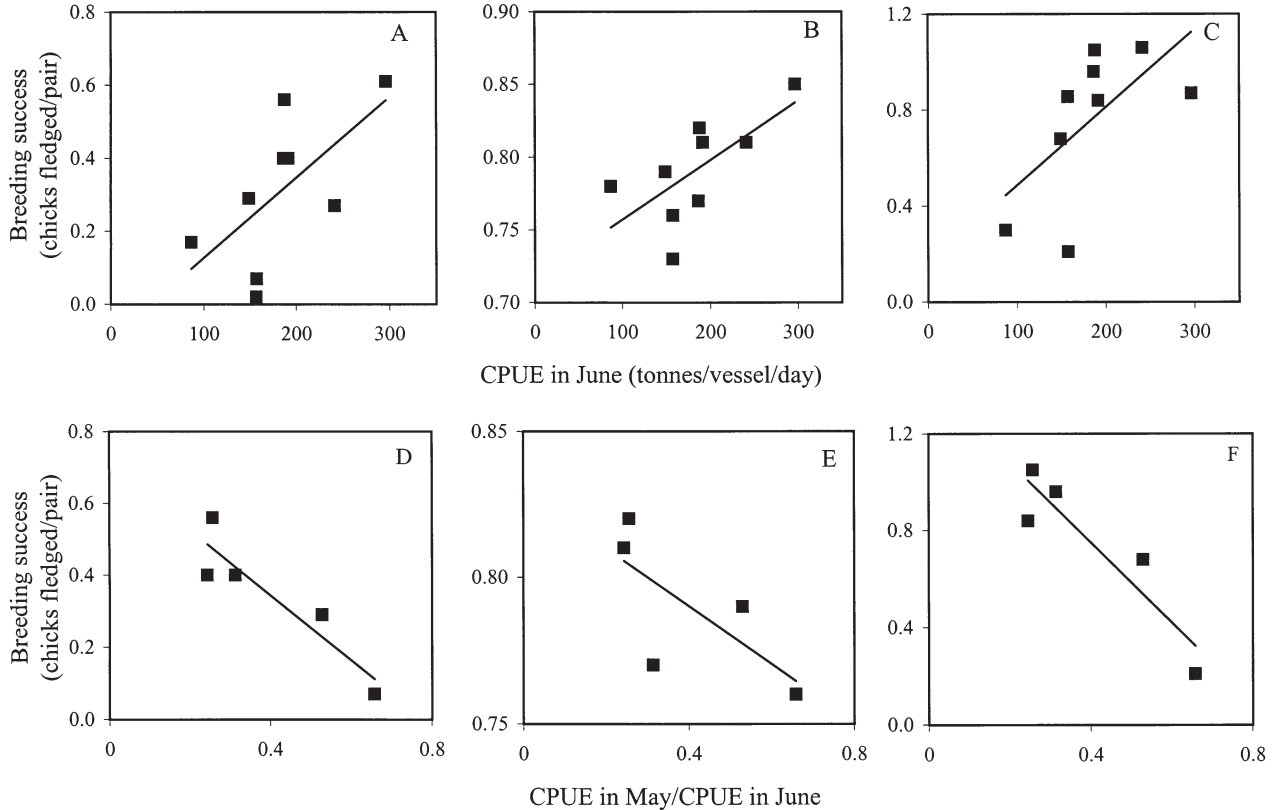


Fig. 8. Breeding success of (A, D) kittiwakes, (B, E) guillemots and (C, F) shags as a function of June CPUE (upper panels) and May/June CPUE (lower panels). Correlation coefficients are given in Table 2

Table 2. Correlations, and probabilities of the correlations being zero, between breeding success (chicks fledged per pair), chick quality (mass at fledging), breeding effort (parental attendance) and diet (proportion of biomass made up of 1+ group sandeels) for seabirds on the Isle of May and the availability of 1+ group sandeels estimated from catch per unit effort (CPUE) data for the sandeel fishery in May, June and the May/June ratio

		Correlation between:					
		May CPUE (n = 5)		June CPUE (n = 9)		May/June CPUE (n = 5)	
		r	p	r	p	r	p
Breeding success	Kittiwake	-0.94	0.02	0.64	0.06	-0.92	0.03
	Guillemot	-0.77	0.13	0.68	0.05	-0.72	0.17
	Shag	-0.94	0.02	0.62	0.07	-0.92	0.03
Chick quality	Guillemot	-0.857	0.06	0.360	0.34	-0.803	0.10
Breeding effort	Kittiwake	0.178	0.77	-0.425	0.25	0.091	0.88
	Guillemot	0.837	0.08	-0.097	0.82	0.823	0.09
Diet	Kittiwake	0.794	0.11	0.020	0.96	0.719	0.17
	Guillemot	-0.765	0.13	0.458	0.22	-0.821	0.09
	Shag	-0.582	0.30	0.433	0.24	-0.680	0.21

(Table 2). In contrast, there was no evidence of a similar effect in kittiwakes. None of the comparisons between attendance and June CPUE approached statistical significance.

DISCUSSION

Sandeel availability

The availability, and thus catchability, of sandeels to the fishery varies during the season, presumably as a result of changes in biomass and/or behaviour of the fish (Winslade 1974b, Reeves 1994). If behaviour only differed between months and not between years in a given month, a high CPUE in May would be expected

to be followed by a high CPUE in June. However, our results clearly indicate the opposite effect, with CPUE on the Wee Bankie in May and June being inversely, not directly, correlated. It seems unlikely that the main reason for this was fishing mortality in May, since effort and catch were always low in this month compared to June. It is possible that the change in CPUE was affected by the fishery in June, as CPUE is a monthly average and large catches may deplete biomass at an even smaller temporal scale. However, most of the variation in the ratio between the CPUEs is caused by variation in May CPUE rather than June CPUE (the highest value being 225% of the smallest in May, whereas the percentage in June was 125%). A more likely explanation is that the timing of peak availability varies from year to year due to behavioural changes which alter the proportion of sandeels buried in the sediment in June and hence their catchability to the fishery. CPUE in May relative to that in June therefore provides a measure of the timing of the onset of sandeel burying behaviour as well as a change in biomass caused by mortality. If the key factor affecting sandeel behaviour operates at a North Sea scale, for example warm or cold years or early or late zooplankton blooms (Winslade 1974a,b), CPUE ratios on the Wee Bankie and the North Sea should be correlated. At first glance, this does not appear to be the case. However, in June 1993 the fishing effort on the Wee Bankie was 3 times higher than in any other year. Therefore in this case the main reason for the high value of the May/June CPUE ratio may have been the large fishing mortality that year, which resulted in a low CPUE in June. In the remaining years, fishing effort in June was much lower, and values for these years accord well with those estimated elsewhere in the northern North Sea. The factor(s) responsible for

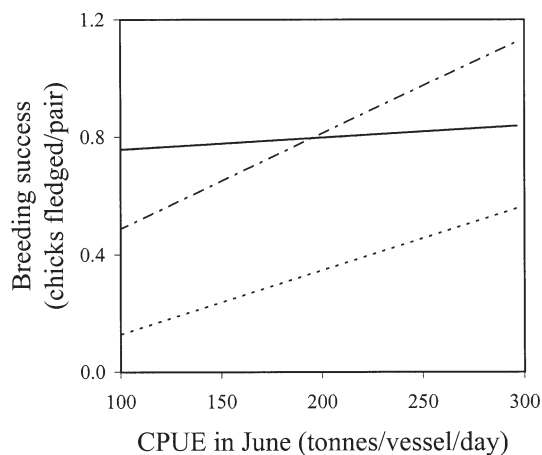


Fig. 9. Comparisons of the fitted lines for breeding success as a function of CPUE in June for kittiwake (.....), guillemot (—) and shag (---)

annual variation in the timing of the onset of burying behaviour in 1+ group fish is unknown, but the results of Petersen et al. (1998) suggest that sandeels stop growing earlier in years when CPUE in the North Sea peaks in May. If growth levels off, there would appear to be little reason for the sandeels to remain in the water column, where mortality is likely to be much higher than in the sediment (Winslade 1974a, Hobson 1986).

The CPUE data indicated that 1+ group sandeel availability to the fishery did not fluctuate dramatically between 1993 and 1998 (all values fell between 87 and 112% of the mean). Prior to this, there was a 3-fold change in availability between 1990 and 1992. This can be compared to the 40-fold change in 1+ group biomass at Shetland from 1983 to 1987, when severe problems were encountered by the seabirds dependent on this species (Monaghan et al. 1989, ICES 1998a, Furness 1999a,b). However, it should be stressed that little variation in CPUE does not necessarily mean that sandeel biomass remains constant since, if sandeels migrate into the areas where the fishery operates, high CPUEs can be maintained even when total biomass is low. Further, catchability may actually increase at low densities, as fishermen spend a higher proportion of their time searching for the fish (Crecco & Overholtz 1990). We therefore prefer to use CPUE as a measure of sandeel availability to the fishery rather than as an estimate of biomass in the area.

S seabird performance in relation to sandeel availability

Ideally, evaluation of predator/prey responses requires not only information on the diet and performance of the predator but also an assessment of the availability of the prey at a spatial and temporal scale that matches that of the predator concerned. In practice, these criteria are hard to meet, especially for highly mobile predators such as seabirds, which exploit complex, 3-dimensional feeding environments. In our analyses we used data from the industrial fishery which was operating in localised areas situated about 30 to 50 km away from the seabirds' breeding colony (Wanless et al. 1998). This approach undoubtedly represents a major advance on most previous analyses which have used estimates of sandeel abundance at a North Sea scale, but it is still unlikely to have provided a perfect estimate of prey availability for any of the avian predators concerned.

Concordance between sandeel availability to the fishery and availability to the avian predators was potentially greatest for guillemots, since both the horizontal and vertical feeding distributions of this species

overlap that of the Wee Bankie fishery (Wanless et al. 1998, unpubl. data). Kittiwakes are also known to utilise the same area as the fishery (Wanless et al. 1998), but CPUE data derived from trawls covering the lower half of the water column may not be a very good measure of sandeel availability to a specialised surface feeder like the kittiwake. Coincidence was likely to be poorest for shags, which never feed in areas used by the sandeel fishery but instead have a coastal feeding distribution (Wanless et al. 1998). However, as sandeels in these areas are unlikely to be reproductively isolated from those at the Wee Bankie (Wright et al. 1998), the availability of sandeels in both areas is likely to be dominated by the previous year's recruitment and thus of similar size. If sandeels do not move within the overall area, June availability could potentially be higher near the coast, since this area is not directly affected by fishing mortality.

Whilst these points should be borne in mind, our results provide compelling evidence of a highly consistent relationship between the breeding success of seabirds and prey availability as measured by CPUE of the sandeel fishery, with success maximised when (1) June CPUE was high and (2) the May/June CPUE ratio was low. If our suggestion that this ratio provides a measure of the timing of the peak of 1+ group sandeel availability is correct, these findings suggest that both the abundance and the temporal dynamics of sandeels influence the reproductive output of 3 seabird species with very different feeding adaptations. Our assessment of the importance of temporal effects was hampered by the fact that May CPUE data were only available for 5 of the years between 1990 and 1998. Whilst more data are clearly needed to confirm our findings, they currently suggest that relatively small-scale differences in the timing of peak sandeel availability may be a major determinant of seabird breeding output on the Isle of May, with success dependent on 1+ group availability peaking late rather than early.

Both diving and surface-feeding species suffered reduced breeding success in years with low sandeel availability, indicating that none of them was able to compensate fully for the change. In all 3 species it appeared that the range of CPUEs recorded during the study fell within the linear part of the response function (Murdoch & Oaten 1975). Similarly Furness (1999b) also found that the relationship between kittiwake productivity and sandeel abundance in the North Sea as a whole was apparently linear. Breeding success clearly cannot increase indefinitely, and beyond some threshold value of CPUE no further improvement in productivity would be expected. However, with the data currently available, such a threshold was not clearly defined in any of the species considered here. There was, however, evidence of marked interspecific differences

in the magnitude of the change in breeding success as a function of June CPUE. The effect was greatest in kittiwakes, a result that accords well with the prediction that species which have a small body size, high reliance on sandeels and specialised or energetically expensive feeding methods are more likely to be adversely affected by reduced abundance of sandeels in the vicinity of their breeding colony (Furness 1999a).

CPUE on the Wee Bankie is generally high relative to elsewhere in the North Sea (Wright et al. 1998). Our findings that even small reductions in June CPUE have a detectable effect on seabird breeding success suggest that, if levels were further reduced to those more typical of the North Sea as a whole, the effect on seabird productivity might be severe. The reason for this is unclear, but the relatively large commuting distance from the Isle of May breeding colony to the feeding grounds on the Wee Bankie could be a contributing factor.

There was no strong evidence to suggest that changes in 1+ sandeel availability were well reflected in the diets of the predators studied. In the case of kittiwakes and shags the main alternate prey was a younger age class of sandeels, only guillemots showed an actual change in the species taken. Hence, it appeared that none of the species was able to effectively compensate for changes in 1+ sandeel availability through changes in diet. In terms of behaviourally mediated compensation, attendance data for guillemots indicated that breeding birds tended to work harder in years when 1+ group sandeel availability peaked early but this increase in effort was insufficient to offset the reduction in sandeel availability. Indeed in this species both the quantity, in terms of productivity, and quality, in terms of chick weight at fledging, appeared to be adversely affected. In kittiwakes there was no evidence of any effective behavioural compensation in response to changes in sandeel availability. Similar interspecific differences were also recorded during a period of reduced sandeel abundance in Shetland, when kittiwakes were shown to be less able than guillemots to compensate by altering behaviour (Monaghan 1996).

Although our results indicate that temporal variations in sandeel availability have important implications for seabird reproductive output, our conclusions are based on correlations. It is not possible from the available commercial catch data to determine the biological mechanism(s) that underlie(s) annual variations in the timing of the peak of 1+ group sandeel availability, and we cannot rule out the possibility that both this timing variable and seabird breeding success may be responding to some third environmental parameter such as temperature, sea conditions or solar radiation. The high correlation between seabird breeding suc-

cess and sandeel availability to the fishery naturally leads to the question of how much fish can be caught on the Wee Bankie without adversely affecting seabird breeding success. The answer to this depends crucially on understanding the magnitude and scale of sandeel migration into the fishing grounds, and thus assessing the risk of fishing down the population without realising it. With the information currently available, it is only possible to conclude that the large catches in 1993 may have reduced sandeel biomass to an extent that the breeding success of the 3 seabird species considered here was affected. However, in the remaining years such effects are not evident and it seems more likely that changes in the behaviour of the sandeels, possibly associated with environmental factors, had a greater effect on seabird breeding success than the fishery. It is unlikely that the small fishery in 1990 caused the sandeel stock to decrease to such an extent as to cause the marked drop in breeding success for kittiwakes. Further research is needed to investigate if other factors are contributing to the long-term decline in kittiwake breeding success and survival on the Isle of May (Wanless et al. 1999).

In the analyses presented here we were only able to consider changes in the availability of 1+ group sandeels, since this is the age category of fish taken by the fishery. However, from the dietary data for the seabirds it is clear that in some years 0 group sandeels also form an important component of the diet of kittiwakes and shags. Moreover, while there was no evidence that 0 group sandeels formed a major item in the diet of guillemot chicks, they could have been taken by adults. In the case of kittiwakes, intensive sampling throughout the 1997 and 1998 seasons demonstrated that this species shows a consistent seasonal shift from 1+ group to 0 group sandeels, with the transition occurring over a 3 wk period in June (Wanless et al. 1999). If this pattern reflects the progressive decline in availability of 1+ group sandeels due to the shift from a pelagic to a buried phase, coupled with increased availability of 0 group sandeels after metamorphosis, then it is possible that kittiwakes may be particularly sensitive to temporal variations in sandeel life history events. Conditions could become critical if an early peak in 1+ group sandeel availability, and thus an early onset of burying, was accompanied by a late and/or poor recruitment of the 0 group. Clearly, targeted research is needed to investigate the factors involved in the timing of 0 group metamorphosis and how this is related to the behaviour of older fish.

In conclusion, these analyses of data on seabird breeding performance and CPUE data for the sandeel fishery have highlighted the importance of examining sandeel availability, not only at a fine spatial scale but also at a fine temporal scale. We suggest that the tim-

ing of sandeel life history events, in particular the switch from a pelagic to a buried phase in 1+ group fish and the metamorphosis of 0 group, plays a key role in the predator/prey dynamics of the North Sea ecosystem. Although the timing of these events is unlikely to be directly influenced by the sandeel fishery, most catches are taken in June and it is possible that the fishery could exacerbate the situation by further reducing the biomass of available fish. It is possible that this happened in 1993. Understanding the ecological mechanisms underlying this temporal variation is therefore essential both in order to evaluate the suitability of various stock assessment methods and also to provide advice on possible management options which take account of wildlife as well as commercial requirements.

Acknowledgements. This study was carried out with financial support from the European Commission Study Contract 95/C76/15 'Effects of Large-Scale Industrial Fisheries on Non-Target Species' and the UK Ministry of Agriculture, Fisheries and Food Contract CSA 4405. We also used data collected by the Institute of Terrestrial Ecology (Natural Environment Research Council) under a contract with the Joint Nature Conservation Committee. We thank all the people who have helped collect the seabird data, and the Institute of Fisheries Research Services, Marine Laboratory, Scotland, UK, and the Norwegian Directorate of Fisheries for supplying data on sandeel commercial catches in the Firth of Forth. John Harwood, Henrik Gislason, Henrik Jensen and Eskild Kirkegaard provided helpful comments on an earlier version of the paper.

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Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany

*Submitted: October 18, 1999; Accepted: February 1, 2000
Proofs received from author(s): July 7, 2000*