Seabird–fishery interactions: Quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea

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Seabird-fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea

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ABSTRACT: Sandeels *Ammodytes marinus* are important food for many breeding seabirds in the North Sea, and are harvested in large quantities by an industrial fishery. There is very little evidence of the fishery reducing availability of sandeels to breeding seabirds, but there is concern that fishery managers should take account of the needs of breeding seabirds. Here we present a quantitative index of the sensitivity of different seabird species' breeding success to reduced abundance of sandeels. The index is based on seabird size, cost of foraging, potential foraging range, ability to dive, amount of 'spare' time in the daily budget, and ability to switch diet. Testing the index with empirical data from Shetland during periods of reduced sandeel abundance shows a close correlation between seabird breeding performance and predictions from the index. Mapping the distributions around the North Sea of seabirds with breeding success highly sensitive to sandeel abundance shows that the majority of sensitive seabirds breed in Shetland and Orkney. Industrial fishing in those regions should be closely controlled to avoid depleting the local sandeel stocks on which seabirds depend. This analysis considers only impacts on seabird breeding. There is a need for analysis of possible influences on other aspects of seabird demography.

KEY WORDS: Fisheries management · Conservation · Breeding success · Predator-prey · Seabird · Sandeel · Ammodytes · Industrial fishing

INTRODUCTION

The lesser sandeel *Ammodytes marinus* is a very abundant and widely distributed fish in the North Sea (Daan et al. 1990, Gislason & Kirkegaard 1996, Pedersen et al. in press). As a small, lipid-rich, shoaling fish, it provides an important food resource for many predatory fish (ICES 1997), seabirds (Furness & Tasker 1997) and marine mammals (Pierce et al. 1991, Hammond et al. 1994, Santos et al. 1994, Haug et al. 1996). In the case of seabirds, it is particularly important in the diet of many species during the breeding season (Furness & Tasker 1999) and often represents a major food for growing chicks (Hamer et al. 1991, Harris & Wanless 1997). The breeding success of some seabirds can be reduced dramatically when sandeel abundance decreases, as seen in Shetland during the late 1980s (Bailey et al. 1991, Hamer et al. 1991, 1993, Danchin 1992, Monaghan 1992, Phillips et al. 1996a,b).

The sandeel is also the target of the largest single-species fishery in the North Sea (Gislason & Kirkegaard 1996). The North Sea industrial fishery for sandeels increased from the 1950s to 1970s, reaching a level generally between 500 000 and 1 000 000 t from the late 1970s to the present. Sandeels are short-lived fish with highly variable recruitment and high natural mortality, features that make analytical stock assessment very difficult (Cook & Reeves 1993). They are also not amenable to acoustic survey, and so it has not been practical to set varying annual quotas based on stock assessments. The recent setting of a total allow-

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able catch (TAC), of 1 million t for the North Sea as a whole, was a precautionary measure based on the empirical observation that catches of about this size in recent years appear to be sustainable (ICES 1998a,b). However, the possibility that this fishery might reduce sandeel abundance locally in areas where seabirds depend on sandeels to maintain their population and breeding success, requires that a management plan for the fishery should take account of the food needs of breeding seabirds (Furness 1999) and other top predators (ICES 1998a).

The needs of seabirds vary between species. Some seabirds feed predominantly on sandeels, while others rarely eat sandeels. Seabird species also differ considerably in their responses to reductions in food abundance. Furness & Ainley (1984) reviewed the hazard of industrial fishing to seabirds, pointing out that certain kinds of seabirds are likely to be particularly vulnerable. These include species with energetically expensive foraging methods, species restricted to foraging close to the colony, species limited to using a specialised and inflexible foraging method, those unable to dive below the sea surface, and those lacking 'spare' time in their activity budget that could be allocated to foraging if food were scarce. Other species, with characteristics such as large foraging ranges, low foraging costs and large amounts of 'off-duty' spare time, are likely to be somewhat buffered against reductions in food abundance (Cairns 1987, Montevecchi 1993). These theoretical predictions have largely been supported by subsequent studies comparing seabird breeding performance between years of high and low food abundance. For example in Shetland, Arctic terns, *Sterna paradisaea* (small, surface-feeding seabirds with expensive foraging and little spare time), tend to abandon breeding attempts when sandeel abundance is low (Monaghan et al. 1992); whereas common guillemots, *Uria aalge* (large, deep-diving seabirds able to increase time allocated to foraging), continue to breed successfully even when sandeel abundance is greatly reduced (Monaghan et al. 1996).

In this paper we construct a quantitative 'vulnerability index' based on the qualitative theoretical model in Furness & Ainley (1984), and defined as the vulnerability of the breeding performance of seabird species to reduced food abundance. We then combine this index with data on the importance of sandeels in the diet of these seabirds while breeding in different parts of the North Sea (we use the ICES definition of the North Sea [Fig. 1] as ICES Fishing Area IV), to give a spatially resolved 'sensitivity index' of seabirds as a function of reduced sandeel abundance. This theoretically-derived index is then tested by comparing its predictions with empirical data from Shetland showing the magnitude of reduction in seabird breeding success for different species during a period of drastically reduced sandeel abundance in the late 1980s. The sensitivity index is then combined with data on the numbers of seabirds breeding in different parts of the North Sea, in order to map the key areas of the North Sea for sandeel-dependent seabirds.

Although larval drift carries sandeels between areas of the North Sea (Wright & Bailey 1996, Proctor et al. 1998), once over 4 to 6 mo of age sandeels show only very local horizontal movements, suggesting that the North Sea can be subdivided into several different stocks (Pedersen et al. in press). Concentration of fishing effort in a particular local patch might then reduce sandeel abundance for seabirds breeding in the vicinity. Thus, the mapping of the distribution of seabirds with high sensitivity to sandeel abundance may then provide a basis for recommendations regarding the limitation of sandeel fishing effort in specific areas of the North Sea in order to minimise the risk of the fishery causing a reduction in the breeding success of seabirds. Conversely, it may help to identify areas of the North Sea where local reductions in sandeel abundance would affect few seabirds.

Although this is the first time that such an approach has been applied to identify the key geographical locations in which conflict between seabirds and an industrial fishery might arise, we are using an approach analogous to one that is well established in the identification of key areas of seabird vulnerability to oil spills. In that field, the use of seabird sensitivity indices is widespread (King & Sanger 1979, Wiens et al. 1984), as is the plotting of the geographical distribution of concentrations of seabirds of high vulnerability (Tasker et al. 1990, Skov et al. 1995). We also believe that this paper, although very specific to the North Sea, has general applicability because the potential effect of fisheries on seabirds is a topic of concern worldwide, and our approach could be applied in any geographical region. We also believe that this approach could potentially be extended to other groups of dependent predators such as marine mammals and large fish, although the required data on those are less detailed than for seabirds. The approach could provide a basis for identification of candidate marine nature-reserves for top predators.

METHODS

Vulnerability of breeding success of different seabird species to reduced abundance of food in vicinity of colonies. Following the theoretical model described, but not quantified, by Furness & Ainley (1984), we constructed a 'vulnerability index' based on 5-point scales for 6 variables:

(1) Small size: Score 4 was given for species with a breeding-season mean adult body-mass <125 g, 3 for 125–250 g, 2 for 250–500 g, 1 for 500–1000 g, and 0 for species with body mass >1000 g.

(2) High cost of foraging: Score 4 was given for species using flapping flight with frequent change of direction and hovering, 3 for flapping flight or underwater swimming or birds with high wing loading, 2 for birds combining flapping flight with some gliding or soaring flight, 1 for birds with predominantly gliding flight, and 0 for birds adapted to economical gliding flight.

(3) Short foraging range: Score 4 was given for birds mainly foraging within 5 km of the nest, 3 for birds foraging mainly within 10 km of nest, 2 for birds foraging mainly within 20 km of nest, 1 for birds foraging mainly within 50 km of nest, and 0 for birds foraging regularly >50 km from the nest.

(4) Little ability to dive: Score 4 was given for surface feeders, 3 for birds feeding in the upper 1 m of sea, 2 for birds regularly foraging down to 10 m depth, 1 for birds regularly foraging down to 30 m depth, and 0 for birds able to forage down to the seabed throughout most of the North Sea (i.e. able to dive to at least 60 m).

(5) Lack of spare time in daily budget: Score 4 was given for species that spend very little time 'off-duty' during chick-rearing, and 0 was given for species that feed chicks only infrequently and/or spend considerable periods 'off-duty' during chick-rearing. Intermediate scores were given to birds between these extremes.

(6) Low ability to switch diet: Score 4 was given for seabird species where the diet is predominantly composed of only a single prey type caught by a specialised feeding method, 3 for birds where the diet is predominantly composed of only a few prey types caught by a specialised feeding method, 2 for birds taking a moderate variety of prey, often by varied methods, 1 for birds taking a wide range of prey, often in different habitats, and 0 for birds taking a very wide range of prey and using many different feeding habitats or methods.

Given that some of these categorizations involve subjective assessments, we sent the first iteration of this vulnerability table to 10 seabird ecologists to determine whether there were consensus views that any of the classifications should be altered; we decided *a priori* to make changes if 2 or more reviewers indicated that our initial categorisation should be altered (in the same direction).

Seabird diets. Reviews of the diets of seabirds in different areas of the North Sea by Tasker & Furness (1996) and Furness & Tasker (1999) and a paper on sandeel consumption by seabirds in the Firth of Forth area (Wanless et al. 1998) provided the source for a tabulation of the proportion of the breeding season diet comprising sandeels. We chose median estimates across years and across colonies and studies. We divided the North Sea into 4 areas based on the consistency of dietary data within areas and differences between areas. These areas largely reflect the distributions of small shoaling pelagic fish within the North Sea (Daan et al. 1990). Shetland to the Moray Firth is an area with no young herring *Clupea harengus* and few sprats *Sprattus sprattus* (see maps in Daan et al. 1990), so that sandeel is the only abundant food fish available to seabirds; sprats and young herring are very rare or absent from seabird diets in this area (Furness 1990, Furness & Tasker 1997). Peterhead to Farne Islands is an area with sandeels and some sprats but very few young herring (Daan et al. 1990), and seabird diets reflect this mix of food-fish (Wanless et al. 1998). The southern and south-eastern North Sea is an area with abundant juvenile herring and sprats (Daan et al. 1990), and sandeels are less important in seabird diets there (Frank 1992, Becker 1996). The Norwegian (north-eastern) sector of the North Sea (to 62° N) is an area with important stocks of young herring as well as sandeels, and seabird diets there often consist of a mix of herring and sandeels (Dunnet et al. 1990, Anker-Nilssen et al. 1997).

Sensitivity-index calculation. The vulnerability index (described above) quantifies the vulnerability of seabird breeding success to reductions in food supply. Since seabirds in some parts of the North Sea are able to feed on sandeels, sprats or young herring, all of which provide high quality (lipid-rich) food that can sustain high breeding success, seabirds with high vulnerability may not be affected by reductions in sandeel abundance if the abundance of herring or sprat remains high. In contrast, seabirds in areas where sandeel represents the only 'food-fish' (Springer & Speckman 1997), seabird breeding success will not be buffered by availability of alternative food-fish prey. In order to capture this geographical variation in prey alternatives, we computed a regional 'sensitivity index' as 'vulnerability index' times the proportion of sandeel in the diet of breeding seabirds in that part of the North Sea. This index is thus spatially variable, and the vulnerability value is downweighted to the extent that foods other than sandeels figure in the average diet of the species in the defined area.

Testing indices against empirical data. It is possible to use empirical data on the breeding success of seabirds during periods of reduced food supply to test the predictions of the vulnerability and sensitivity indices. We used data on the breeding success of seabirds in Shetland during 1986 to 1990, a period when sandeel stock was reduced to less than 20 % of its abundance in 1974 to 1986 (Bailey et al. 1991, ICES

1998b), and during 1991 to 1997 when sandeel stock was at a moderate level between 25 and 75% of the abundance in 1974 to 1986 (seabird breeding success data for 1998 and 1999 are not considered since the abundance of sandeels in those years has not yet been published). Data on seabird breeding success were taken from the annual reports published by the Joint Nature Conservation Committee (Walsh et al. 1990, 1991, 1992, 1993, 1994, 1995, Thompson et al. 1996, 1997, 1998) and from annual Shetland Bird Reports and unpublished reports to Sullom Oil Terminal Environmental Advisory Group of seabird monitoring at Foula, where these data add to the Joint Nature Conservation Committee summaries. We calculated the median value (because values were highly skewed and thus precluded use of means) of breeding success in the 20% most successful of all sites monitored in Britain and Ireland each year from 1989 to 1998 (since data presented for years before 1989 were not in a suitable form to use for this) as a measure of breeding success achieved under what we can assume to be the best conditions (henceforth termed 'best performance'). These estimates are variable in quality and quantity because some are based on large numbers of estimates of breeding success at many colonies in many years, while others are based on only a few estimates, but we assume that small sample sizes for some species simply increase the noise rather than causing bias. We then expressed for each species the breeding success achieved at monitored sites in Shetland during the 2 study periods as a percentage of 'best performance'. These results were then correlated (using a Pearson product-moment correlation coefficient) with the vulnerability index and sensitivity index scores for the 14

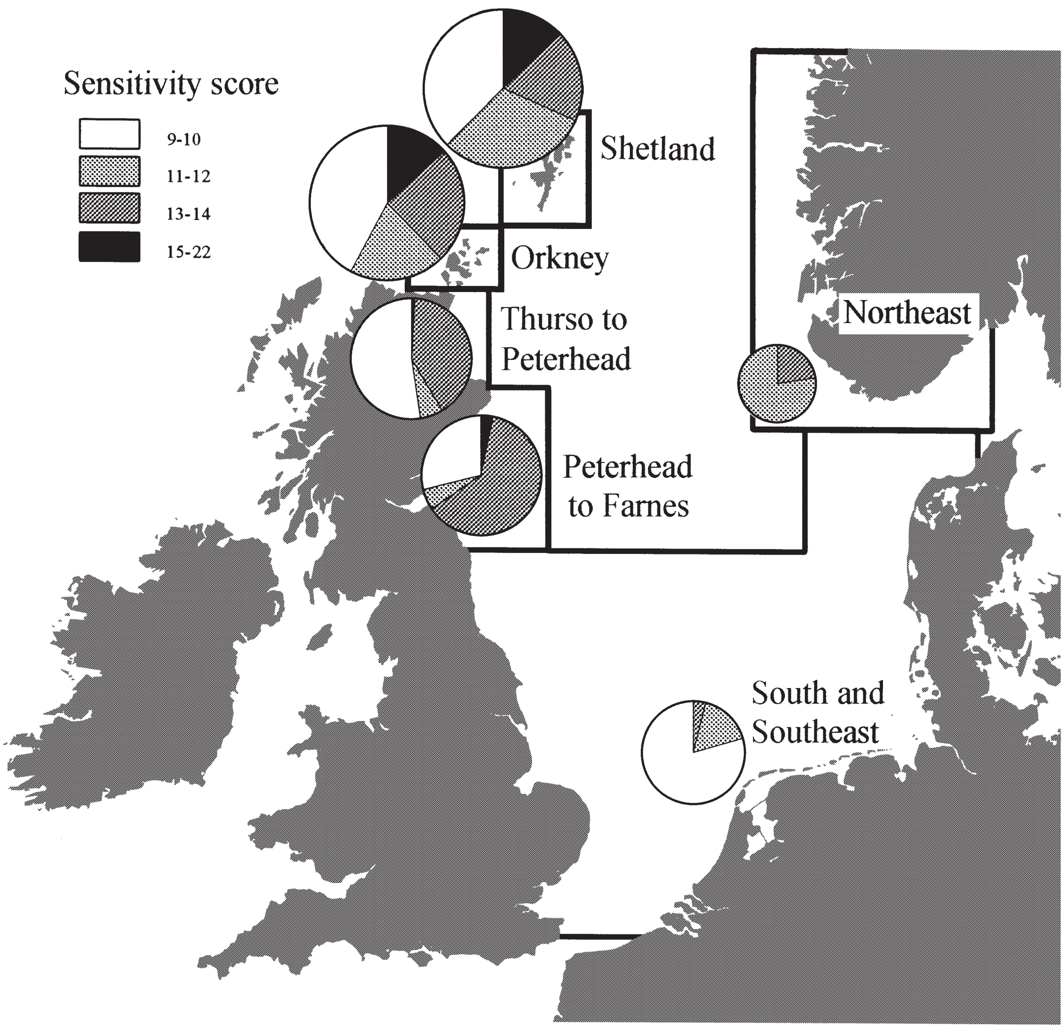

Fig. 1. Numbers of pairs of seabirds of high sensitivity to sandeel abundance (index scores ≥9), breeding in different parts of North Sea. Areas are defined as Shetland, Orkney, Thurso to Peterhead, Peterhead to Farnes (inclusive), southern and south-eastern North Sea, and north-eastern North Sea. Size of each circle indicates size of local breeding population of seabirds of high sensitivity score

species of seabirds at Shetland for which breeding success data were available, using arcsine-transformed percentages for statistical tests.

Distributions of breeding seabirds. Data on numbers of seabirds breeding on North Sea coasts have been tabulated by Dunnet et al. (1990), Lloyd et al. (1991), and by Tasker & Furness (1996). We extracted relevant counts from these publications to obtain total numbers of pairs of seabirds in Shetland, Orkney, Thurso to Peterhead, Peterhead to Farnes, Southern and south-eastern North Sea and north-eastern North Sea (Fig. 1), regions chosen to correspond to the broad distributions of major food-fish species (Daan et al. 1990).

RESULTS

Index of vulnerability of breeding success to reduced abundance of food

Feedback on our first estimate of the scores for each attribute in the vulnerability index for each seabird species from 10 leading seabird ecologists resulted in 5 changes to species' vulnerability scores, 3 by a single point and 2 by 2 points. These changes had almost no effect on the ranking of species, since the variations in species' scores, from 5 to 22 points, was very large in relation to these small adjustments for individual species and species were well spread across this range of scores. There was broad agreement amongst these ecologists that the 6 criteria included in the index (Table 1) were appropriate, but some concern that these did not necessarily merit equal weight in determining the final index score. However, we could not find any consensus for a change from the equal weighting proposed here.

The index (Table 1) shows terns and the black-legged kittiwake *Rissa tridactyla* as the species with the highest vulnerability scores. Skuas, small larus gulls, divers and most auks share moderate vulnerability scores, while common guillemot, shag *Phalacrocorax aristotelis*, great cormorant *P. carbo*, Manx shearwater *Puffinus puffinus*, northern fulmar *Fulmarus glacialis* and northern gannet *Morus bassanus* have particularly low vulnerability scores.

Sensitivity index

The proportion of sandeels in the diet varies considerably between species, but also between areas, being highest in Shetland to Moray Firth and lowest in the

Table 1. Vulnerability of breeding success of different seabird species to reduced abundance of food in vicinity of colonies (species ranked by vulnerability index score). See 'Methods' for details of individual score criteria

Species	Small size	High cost of foraging per unit of time	Constrained to short foraging range	Little ability to dive	Lack of spare time in daily budget	Low ability to switch diet	Score
Arctic tern	4	4	4	3	4	3	22
Roseate tern	4	4	4	3	4	3	22
Little tern	4	4	4	3	4	2	21
Common tern	3	4	4	3	4	2	20
Sandwich tern	3	4	3	3	3	3	19
Black-legged kittiwake	2	2	1	4	4	3	16
Arctic skua	2	2	3	4	1	3	15
Black-headed gull	3	3	3	4	2	0	15
Common gull	2	3	3	4	2	0	14
Black guillemot	2	3	3	1	3	2	14
Great skua	0	3	3	4	1	2	13
Atlantic puffin	2	3	1	2	3	2	13
Razorbill	1	3	2	1	2	3	12
Red-throated diver	0	3	4	0	2	3	12
Lesser black-backed gull	1	2	2	4	1	1	11
Herring gull	1	2	3	4	1	0	11
Greater black-backed gull	0	2	3	4	1	0	10
British storm petrel	4	2	1	3	0	0	10
Leach's petrel	4	2	1	3	0	0	10
Common guillemot	1	3	1	0	2	2	9
Shag	0	3	3	0	0	2	8
Great cormorant	0	3	4	0	0	0	7
Manx shearwater	2	1	0	2	0	2	7
Northern fulmar	1	0	0	4	2	0	7
Northern gannet	0	2	0	2	1	0	5

Table 2. Proportion of sandeels in diet of breeding seabirds in each sector of North Sea. Data from Tasker & Furness (1996), Wanless et al. (1998), Furness & Tasker (1999)

Species	Shetland, Orkney, Thurso to Peterhead	Peterhead to Farnes	Southern and south-eastern North Sea	North-eastern North Sea
Arctic tern	1.0	0.8	0.6	0.6
Roseate tern	–	0.5	0.3	–
Little tern	–	0.2	0.2	–
Common tern	0.8	0.6	0.4	0.6
Sandwich tern	–	0.6	0.6	–
Black-legged kittiwake	0.9	0.8	0.6	0.8
Arctic skua	1.0	–	–	0.8
Black-headed gull	0.1	0.1	0.1	0.1
Common gull	0.1	0.1	0.1	0.1
Black guillemot	0.6	–	–	0.6
Great skua	0.6	–	–	0.6
Atlantic puffin	0.9	0.8	0.6	0.6
Razorbill	0.9	0.8	0.6	0.6
Red-throated diver	0.8	–	–	0.6
Lesser black-backed gull	0.6	0.6	0.4	0.4
Herring gull	0.4	0.1	0.1	0.1
Greater black-backed gull	0.6	0.4	0.4	0.4
British storm petrel	0.1	–	–	0.1
Leach's petrel	0.1	–	–	–
Common guillemot	1.0	0.8	0.6	0.4
Shag	1.0	1.0	1.0	0.8
Great cormorant	0.1	0.1	0.1	0.1
Manx shearwater	0.1	–	–	–
Northern fulmar	0.4	0.2	0.2	0.2
Northern gannet	0.4	0.3	0.2	0.2

Table 3. Sensitivity to sandeel abundance. Index scores for seabirds in different sectors of North Sea. Sensitivity index is defined as vulnerability score times proportion of sandeels in breeding season diet (see 'Methods')

Species	Vulnerability score	Shetland, Orkney, Thurso to Peterhead	Peterhead to Farnes	Southern and south-eastern North Sea	North-eastern North Sea
Arctic tern	22	22	18	13	13
Roseate tern	22	–	11	7	–
Little tern	21	–	4	4	–
Common tern	20	16	12	8	12
Sandwich tern	19	–	11	11	–
Black-legged kittiwake	16	14	13	10	13
Arctic skua	15	15	–	–	12
Black-headed gull	15	1	1	1	1
Common gull	14	1	1	1	1
Black guillemot	14	8	–	–	8
Great skua	13	8	–	–	8
Atlantic puffin	13	12	10	8	8
Razorbill	12	11	10	7	7
Red-throated diver	12	10	–	–	8
Lesser black-backed gull	11	7	7	4	4
Herring gull	11	4	1	1	1
Greater black-backed gull	10	6	4	4	4
British storm petrel	10	1	–	–	1
Leach's petrel	10	1	–	–	–
Common guillemot	9	9	7	5	4
Shag	8	8	8	8	6
Great cormorant	7	1	1	1	1
Manx shearwater	7	1	–	–	–
Northern fulmar	7	3	1	1	1
Northern gannet	5	2	2	1	1

Table 4. Breeding success of seabirds in Shetland during periods of low (1986 to 1990) and moderate (1991 to 1997) sandeel abundance in relation to median breeding success achieved by these species in most productive regions of Britain and Ireland over period 1986 to 1997 (data from annual reports 'Seabird Numbers and Breeding Success in Britain and Ireland' published by Joint Nature Conservation Committee). Species ranked according to vulnerability index score. See 'Methods' for further details

Species	Vulnerability to low food abundance	Sensitivity to low sandeel abundance	Mean breeding success 1986–1990	Mean 1986–1990 as % median of best 20%	Mean breeding success 1991–1997	Mean 1991–1997 as % median of best 20%	Breeding success in best 20% of sites 1989–1998 Range	Median
Arctic tern	22	22	0.00	0	0.41	48	0.7–1.2	0.85
Common tern	20	16	0.00	0	0.20	18	0.8–1.5	1.10
Black-legged kittiwake	16	14	0.32	28	0.62	54	1.0–1.3	1.15
Arctic skua	15	15	0.24	20	0.87	72	0.8–1.3	1.20
Black guillemot	14	8	0.73	66	0.80	73	0.7–1.4	1.10
Great skua	13	8	0.52	47	0.76	69	1.0–1.3	1.10
Atlantic puffin	13	12	0.27	33	0.77	94	0.76–0.86	0.82
Razorbill	12	11	0.38	51	0.62	83	0.69–0.86	0.75
Red-throated diver	12	10	0.51	54	0.68	72	0.6–1.6	0.95
Common guillemot	9	9	0.74	91	0.71	88	0.77–0.85	0.81
Shag	8	8	1.24	69	1.39	77	1.5–2.2	1.80
Great cormorant	7	1	2.60	91	2.83	99	2.3–3.1	2.85
Northern fulmar	7	3	0.44	70	0.49	78	0.52–0.71	0.63
Northern gannet	5	2	0.68	89	0.68	89	0.71–0.87	0.76

southern North Sea and Norway (Table 2). These dietary differences result in the 'sensitivity of breeding success to sandeel abundance' index for most species being higher in the Shetland to Moray Firth area than elsewhere in the North Sea (Table 3). The highest sensitivity scores were found for Arctic terns in Shetland to Peterhead (22), Arctic terns in Peterhead to Farnes (18), common terns *Sterna hirundo* in Shetland to Peterhead (16), Arctic skuas *Stercorarius parasiticus* in Shetland to Peterhead (15), black-legged kittiwakes in Shetland to Peterhead (14), Arctic terns in southern North Sea and Norway (13), and black-legged kittiwakes (13) in Peterhead to Farnes and Norway.

Empirical data to test indices

Mean breeding success of seabirds in Shetland during 1986 to 1990, the period of greatly reduced sandeel abundance, varied among 14 species between 0 and 91% of that of the median performance of the best 20% of monitored sites in Britain and Ireland over the period 1989 to 1998 (Table 4). By comparison, performance was much better in Shetland during 1991 to 1997, ranging from 18 to 99% of 'best performance'. When related to the vulnerability index or sensitivity index for each of these species, a correlation was clearly evident. For 1986 to 1990, the percentage reduction in breeding success from 'the best' correlated with the vulnerability index ($r = 0.92$, $p < 0.001$), and with the sensitivity index ($r = 0.88$, $p < 0.001$, Fig. 2). For 1991 to 1997, the percentage reduction in breeding success from 'the best' correlated with the vulnerability index ($r = 0.77$, $p < 0.01$), and with the sensitivity index ($r = 0.67$, $p < 0.01$, Fig. 3). In neither time period is the correlation of the reduction in breeding success significantly stronger with the sensitivity index than with the vulnerability index. As might be anticipated given that breeding success of seabirds was reduced much more in Shetland during 1986 to 1990 than in 1991 to 1997, the slope of the relationship with the sen-

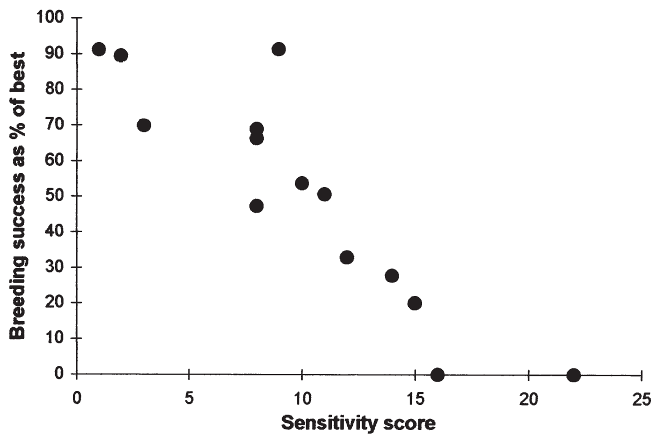

Fig. 2. Mean breeding success of each species of seabird monitored in Shetland between 1986 and 1990 expressed as percentage of median breeding success achieved by 20% of sites with highest performance each season in Britain and Ireland between 1989 and 1998, in relation to the sensitivity index score of that species. Correlation ($n = 14$ species) with percentages arcsine-transformed is 0.88, $p < 0.001$. Slope is 4.9% per unit sensitivity

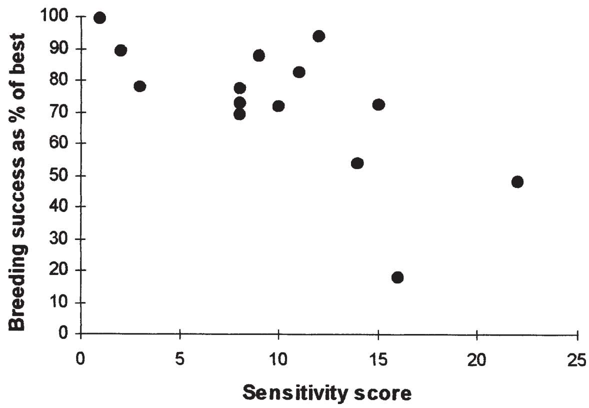

Fig. 3. Mean breeding success of each species of seabird monitored in Shetland between 1991 and 1997 expressed as percentage of median breeding success achieved by 20% of sites with highest performance each season in Britain and Ireland between 1989 and 1998, in relation to the sensitivity index score of that species. Correlation (n = 14 species) with percentages arcsine-transformed is 0.67, $p < 0.01$. Slope is 2.5% per unit sensitivity

sitivity index is greater during 1986 to 1990 (4.9% per unit sensitivity) than in 1991 to 1997 (2.5% per unit sensitivity).

Distribution around North Sea of seabirds with high sensitivity scores

Breeding numbers of seabirds highly sensitive to sandeel abundance (arbitrarily defined here as having a sensitivity index score of ≥9) are highest in Shetland (268 000 pairs) and Orkney (261 000 pairs). This represents over half of the total in the entire North Sea (one million pairs), despite the small area represented by these 2 archipelagos. Most of the remaining seabirds with high sensitivity scores are distributed on the east coasts of Scotland and England (Fig. 1). The regions with the lowest numbers of seabirds sensitive to sandeel abundance are the north-eastern North Sea, and the southern and south-eastern North Sea, which are also the 2 regions of largest geographical area (Fig. 1).

DISCUSSION

Vulnerability index

Since the model proposed by Furness & Ainley (1984), a number of studies have identified particular aspects of seabird ecology that affect the extent to which their breeding success is determined by variations in food abundance (Heubeck 1989, Furness & Barrett 1991, Montevecchi 1993, Barrett & Krasnov 1996, Becker 1996, Phillips et al. 1996a,b, Anker-Nilssen et al. 1997, Croxall et al. 1999). These have confirmed the importance of limited foraging range, limited ability to dive, lack of 'spare time' and low ability to switch to alternative diet. The other variables included in our index, small body size and high cost of foraging per unit time, have received little attention in this context, and so the relative importance of each of these factors remains uncertain. For simplicity, we gave each factor equal weight in computing the vulnerability index, but this approach may be refined as further data become available.

The position of each species on the 'index of vulnerability to reduced food-fish abundance' was broadly agreed by a range of seabird ecologists. Furthermore, the position of each species on this index is fairly robust to small alterations of individual scores since the index ranges over 18 points, with species fairly evenly spread across this range of scores (Table 1). It seems likely that this index would be widely appropriate for seabirds, not only for North Sea populations but also in other seas and oceans, and for other seabird species where scores have not yet been assigned, but this remains to be tested. However, Harris & Wanless (1990) identified the kittiwake as 1 species in which breeding success is highly vulnerable to reduced food abundance. The high vulnerability of terns is also widely recognised (Frank & Becker 1992, Monaghan et al. 1992), but terns may be less useful as indicators of reduced food-fish abundance because their breeding success also shows high variability as a result of impacts of predators and stochastic effects of weather (Thompson et al. 1996, 1997, 1998).

Sensitivity index

In the particular context of the North Sea and the importance of sandeels to seabirds, it is evident that the vulnerability index needs to be modified to account for the fact that some seabird species feed heavily on sandeels while others do not. The data on seabird diets (Table 2) show that there are distinct differences in the importance of sandeels in the breeding season diets of seabirds in different parts of the North Sea. In general, sandeels are more important for seabirds in the north-western North Sea and less important in the eastern and southern North Sea where other small-shoaling lipid-rich food-fish are available as alternatives to sandeels. For seabirds in the north-western North Sea (such as Shetland and Orkney), the sensitivity index (predicting sensitivity of breeding success to reduced abundance of sandeels) and the vulnerability index (predicting sensitivity of breeding success to reduced abundance of food-fish) are very closely similar, because there are no food-fish other than sandeels and adult herring and adult mackerel *Scomber scombrus*. These latter adult fish are too big for most seabirds to eat, and so most seabirds in this region feed predominantly on sandeels while breeding (though some exceptions to this are evident in Table 2). However, in the southern and eastern North Sea, the fact that sandeels form only a small part of the diet of many seabirds and that clupeids are predominant in many diets, suggests that clupeid abundance may be more important in determining breeding success than is sandeel abundance. This is supported by detailed studies of common tern breeding success in the south-eastern North Sea, where it has been found that chick growth rate and fledging success are closely correlated with abundance of young herring (Greenstreet et al. 1999).

Testing indices against empirical data

The empirical test of the sensitivity index showed that the relative reductions in breeding success of each species in Shetland during periods of exceptionally low and moderate sandeel abundance were close to predictions. The 1 conspicuous outlier in the graph relating breeding success to sensitivity in 1986 to 1990 (Fig. 2), the period of exceptionally low sandeel abundance, is the common guillemot, which achieved 91% of 'best performance' despite a sensitivity score of 9. A number of reasons for this anomaly can be put forward, but only as speculation at this stage. Unlike most other seabirds, common guillemot chicks fledge when only partly grown, and variation in chick survival between leaving the ledges and achieving adult size might occur but is impossible to detect from current monitoring methods, which define success as a chick surviving to the age at which it descends to the sea. It appears to be a feature of common guillemot biology that breeding success, defined in terms of chicks leaving the colony, is almost invariably high at colonies in many different locations and food availabilities (Furness & Barrett 1991, Monaghan et al. 1996, Thompson et al. 1998), although common guillemot breeding numbers can be severely affected by reduced food abundance (Vader et al. 1990, Heubeck et al. 1991). Possibly the common guillemot sensitivity score should be lower than the estimate, which assumes that foraging cost in this species is relatively high because the wing-loading of guillemots is exceptionally high and so will increase flight costs.

During 1991 to 1997, a period of rebuilding sandeel stock at Shetland after the years of low abundance, the relationship between breeding performance and sensitivity score was not as strong as in the earlier period. The most conspicous outlier in that graph (Fig. 3) is the common tern, which achieved a breeding success only 20% of 'best performance' yet had a sensitivity score of 16, which would predict a breeding performance around 60% of best performance. This outlier may simply be due to the very small amount of data on common tern breeding-success in Shetland. However, in this species, breeding success may have been reduced further by nest predators, since the breeding numbers of terns decreased during the period of low abundance of sandeels (Heubeck 1989, Thompson et al. 1996, 1997, 1998) and nest predators may have become more concentrated at remaining tern colonies. The common tern shows less defence of nests against predators than the Arctic tern, and tends in Shetland to breed in smaller and hence more vulnerable colonies (Heubeck 1989, Uttley 1992). Similarly, breeding success of some other seabirds in Shetland during 1990 to 1997 has been reduced at some colonies by predation (Furness 1997, Heubeck et al. 1997), so that there is much variation in breeding success in this data set due to factors other than food supply. Of course, the effects of kleptoparasitism or predation and reduced food supply can interact such that birds having difficulty in provisioning chicks may suffer higher rates of predation as a consequence of reduced nest attendance or cooperative defence against predators, or higher rates of kleptoparasitism by hungry competitors (Oro 1996, Gonzalez-Solis et al. 1997, Regehr & Montevecchi 1997).

The empirical data from Shetland strongly support the rankings obtained from the sensitivity index and vulnerability index, by showing high correlations with both indices. However, since the rankings of Shetland seabirds on these 2 indices are very similar because of the lack of other food-fish in this region, it is not possible to demonstrate that the sensitivity index is a better measure than the vulnerability index. Indeed, the correlations with the empirical data are slightly higher for the vulnerability index, although not significantly so.

Distribution around North Sea of seabirds with high sensitivity scores

We take these high correlations, despite known effects of predators on breeding performance adding noise to these data, as strong support for the use of such an index as a means of identifying areas of the North Sea with more or less seabirds whose breeding success would be sensitive to sandeel abundance. It has already been recognised that the consumption of sandeels by seabirds tends to be concentrated in the north-western North Sea, whereas historically the industrial fishery has tended to concentrate its fishing effort somewhat in the southern and eastern North Sea (Furness 1999), but this study is the first attempt to map the distribution around the North Sea of breeding concentrations of seabirds sensitive to reduction in sandeel abundance. The result (Fig. 1) indicates that particular attention should be paid to whether sandeel fishing will reduce the abundance of sandeels in Shetland or Orkney, where we find the highest breeding concentrations of seabirds whose breeding success is sensitive to sandeel abundance. The small fishery for sandeels at Shetland is now limited by a quota reviewed regularly on the basis of research-survey trawl estimates of sandeel abundance at Shetland, while there has never been a sandeel fishery at Orkney due to the unsuitable nature of the seabed for sandeel trawling in that area. There has, however, been an increase in sandeel fishing close to the south-east coast of Scotland, and a long tradition of high catches of sandeels from the banks off the east coast of England. These sandeel fishing areas are relatively close to large aggregations of breeding seabirds that are classified as vulnerable by our index, particularly in the Firth of Forth. This would suggest that the breeding performance of this population of seabirds should be monitored with particular attention to variations that may relate to changes in sandeel abundance.

Another implication from Fig. 1 is that reductions in sandeel abundance, whether caused through depletion by fishing or by natural processes, are less likely to affect many breeding seabirds in the eastern North Sea, since the numbers of seabirds which have breeding performance with high sensitivity to sandeel abundance are low in most of that region. At present, seabirds in that region appear to be more likely to show variations in breeding performance as a consequence of changes in the abundance of young herring and possibly sprats (Becker 1996).

Further considerations

It is important to note that we are not in this analysis considering effects of sandeel abundance on survival rates of adults or immature seabirds, or effects on other potentially important demographic parameters such as immigration rates or ages at first breeding. Life-history theory as applied to seabirds predicts that seabirds should buffer themselves against impacts of food supply on adult survival, for example by refraining from breeding in years when food is scarce, or through brood reduction (Cairns 1987, Furness 1996). There is evidence that seabirds may invest less in reproduction (Ratcliffe et al. 1998, Wernham & Bryant 1998), or refrain from breeding, when food is in short supply, but nonbreeding varies in extent among species and is an infrequent response in some species (Catry et al. 1998). There are examples of catastrophic reductions in food-fish abundance that have led to increased mortality rates of adult seabirds (Krasnov & Barrett 1995, Barrett & Krasnov 1996, Vader et al. 1990), but these appear to relate to high rates of adult mortality during winter among species that depend on the particular food-fish species as prey during winter.

However, despite predictions of life-history theory, recent studies of black-legged kittiwakes suggest that adult survival rates are reduced when birds have to work hard to provision chicks, either as a result of enlarged brood size or reduced food abundance (Jakobsen et al. 1995, Golet et al. 1998, Golet & Irons 1999, Oro & Furness unpubl. data). Changes in numbers of common guillemots attending ledges in Shetland in response to reduced sandeel stock (Heubeck et al. 1991) despite almost no effect of this on common guillemot breeding success (Table 4), suggest a need to investigate the effects of sandeel abundance on more than just breeding success. Harris & Bailey (1992) found no correlation between sandeel abundance and overwinter survival of first-year common guillemots in the North Sea, but found a relationship with sprat abundance. While it is relatively easy to monitor breeding success of seabirds, monitoring adult survival rates is much more difficult, and there are few relevant data sets. Population dynamics of seabirds may be very sensitive to changes in adult survival rates, and there is a need for research into the relationship between seabird survival rates and prey abundance to complement the detailed data currently being gathered on breeding success.

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