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Management implications of interactions between fisheries and sandeel-dependent seabirds and seals in the North Sea

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The lesser sandeel, *Ammodytes marinus*, is a key food for many seabirds and seals, and is also the target of the largest single-species fishery in the North Sea. Despite claims that sandeel fishing has harmed dependent predator populations, census data show that most seabirds and grey seals increased in numbers as the fishery grew and reached peak harvest. Generally high breeding success of black-legged kittiwakes at North Sea colonies also suggests that sandeel abundance has remained good for breeding seabirds at the broad scale, though local and small-scale effects of sandeel fishing should not be overlooked. VPA and CPUE data suggest that abundance increased as the fishery grew. A negative correlation between sandeel recruitment and total stock size preceding spawning suggests that there is now resource competition (bottom-up control). Bioenergetics modelling indicates that predatory fish take far more sandeel than taken by the industrial fishery or wildlife. Effects of decreases in predatory fish stocks have been greater than increases in the take by seabirds and seals and by the fishery. Thus, overall, there appears to have been a reduction in mortality during the last 30 years. Changes in predatory fish abundances, especially mackerel and whiting, may influence sandeel stocks more than changes in industrial fishery, at least at the scale of the North Sea as a whole. These interactions imply that seabird and seal food supply in terms of sandeel may be strongly dependent on decisions regarding management of stocks of mackerel and gadoids. The overwhelming influence of predation on "food-fish" by predatory fish may be a feature of many marine food webs worldwide, where "fishing down the food web" has occurred, and this has clear management implications if wildlife and fisheries are to coexist.

Keywords: fishery management, conservation, *Ammodytes marinus*, industrial fishing, predator-prey interactions, harvesting, trophic transfer, top predator, bioenergetics.

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Introduction

The North Sea has been intensively fished over many decades (Greenstreet *et al.*, 1999a,b). There are detailed data to describe the fisheries and fish stocks (Greenstreet *et al.*, 1999a,b; ICES, 2000), and populations, diets, and breeding success of both seabirds (Lloyd *et al.*, 1991; Furness and Tasker, 1999; Upton *et al.*, 2000) and seals (Hammond *et al.*, 1994; Brown and Pierce, 1998; Pomeroy *et al.*, 2000). Because of detailed data, the history of intensive fishing, and the large populations of seabirds and seals, the North Sea is an ideal area for the investigation of interactions between fisheries and wildlife. This topic has been the focus of much recent attention (Furness, 1990, 1999; Harris and Wanless, 1997; Rindorf *et al.*, 2000), such that the North Sea example features as a text book case study on fishery-wildlife interactions (Jennings *et al.*, 2001). Certainly, the North Sea provides an outstanding example of "fishing down the food web" (Pauly *et al.*, 1998). Concern about overexploitation of large predatory fish such as cod, *Gadus morhua*, was expressed as long ago as the 1880s (Daan *et al.*, 1990). Since the 1950s there has been a large increase in the harvest of sandeel (predominantly the lesser sandeel, *Ammodytes marinus*, but several different species as well as different sub-stocks are managed as a single unit in this fishery). Growth of sandeel stocks followed major reductions in the stocks of cod, haddock, *Melanogrammus aeglefinus*, whiting, *Merlangius merlangus*, herring, *Clupea harengus*, and

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mackerel, *Scomber scombrus*, and one hypothesis suggests that sandeel increased as a result of the reduced predation and competition with other fish (Sherman *et al*., 1981). Fishery landings increased during the 20th century, but with an increasing proportion of the catch comprising industrial fish rather than human consumption fish. The North Sea fish community shows the effect of intensive harvesting as reductions in the size of the individual fish in the community, and a reduction in the proportion of large predatory fish (Greenstreet *et al*., 1999a,b; Jennings *et al*., 2001).

A recent review of the effects of aquaculture on world fish supplies (Naylor *et al*., 2000), suggested that the growth of aquaculture posed a threat to worldwide marine food chains through its demand for aquafeeds. These are manufactured predominantly from fishmeal and fish oils derived from industrial fisheries. The authors claimed that large-scale industrial fisheries are incompatible with thriving populations of marine predators, and stated

> "The impact of pelagic fisheries depletion is thought to reduce available food supplies for marine predators. . . . In the North Sea, for example, overexploitation of many capelin [*sic*], sandeel and Norway pout stocks, mainly for reduction to fishmeal, has been implicated in the declines of certain stocks of other wild fish . . . and in the distribution, population sizes and reproductive success of various seal and seabird colonies."

This is both factually inaccurate, and highly misleading. As pointed out by Furness and Tasker (2000) and Yodzis (2001), North Sea seabirds have not shown declines in numbers or dramatic reductions in breeding success that can be attributed to overexploitation of food-fish by industrial fisheries. This lack of a damaging effect contrasts with various predictions that wildlife will suffer through competition for food-fish (Yodzis, 1994, 2001), and so could be considered counter-intuitive. I review the evidence for interactions between industrial fisheries, stocks of industrial fish, and populations of "top predators" in the North Sea (seabirds, seals, and those larger fish that feed extensively on industrial fish stocks) in trying to explain the apparently counter-intuitive observation that a very large industrial fishery has developed in the North Sea alongside growing populations of sandeel-dependent seabirds and seals. Finally, I consider fisheries management and wildlife conservation implications of these relationships among North Sea fisheries, fish stocks and wildlife, and comment on the extent to which the observed scenario may be typical of heavily fished shelf-sea ecosystems elsewhere in the world.

The sandeel fishery is the largest industrial fishery in the North Sea, and the principal fishery of concern as potentially in competition with wildlife, because sandeel provide an important part of the diet of many top predators. The other major industrial fishery is for Norway pout, *Trisopterus esmarkii*, but Norway pout is either not eaten or forms only a tiny part of the diet of seabirds and seals in the North Sea (Hammond *et al*., 1994; Furness and Tasker, 1997; ICES, 1997; Brown and Pierce, 1998; Tasker *et al*., 2000). Therefore any effects of the pout fishery on these top predators are likely to be very much less than those of the sandeel fishery. For this reason, the pout fishery will not be discussed.

The spatial scale of interactions

Sandeels are small, short-lived, lipid-rich, shoaling fish. They are especially important in the diet of seabirds during the summer, as sandeel then spend much time feeding in the upper layers of the sea on zooplankton. At other times of year they spend most of the time buried in the sand, where they are inaccessible to many predators, though they continue to be eaten by some, such as seals, Eurasian shags, *Phalacrocorax aristotelis*, and common guillemots, *Uria aalge*, which apparently can dig them out of the seabed (Hammond *et al*., 1994). Although the larvae drift with currents, once metamorphosed at around six months, sandeel do not show extensive horizontal movements, but tend to remain associated with a particular patch of suitable substrate (Gauld and Hutcheon, 1990; Pedersen *et al*., 1999).

The management of North Sea sandeel stocks is based on the assumption that there are two separate stocks. One is a small, local stock at Shetland (Bailey *et al*., 1991; Wright and Bailey, 1996; ICES, 2001). The Shetland sandeel stock has supported a very small industrial fishery in some years, but the highest catch from that stock (52 000 t) is less than 4% of the maximum catch taken from the North Sea (ICES, 2001). The remainder of the North Sea is treated as if it contains only a single stock (ICES, 2001). This is clearly a gross simplification based on incomplete understanding of sandeel stocks and biology, because this management area includes not only three different species of sandeel taken by the fishery, but also sub-stocks of *A. marinus* that are probably quite distinct in terms of recruitment process (Pedersen *et al*., 1999). Although the North Sea stock may be further subdivided on the basis of larval drift and settlement patterns (Proctor *et al*., 1998), there is little evidence to suggest that the various sub-stocks around the North Sea differ in dynamics from each other. Recruitment data suggest that years of high or low recruitment are synchronous throughout the area, whereas the Shetland stock shows quite independent dynamics (ICES, 2001). Lacking further understanding of unit stocks, I follow the tradition of separating the Shetland and North Sea stocks, and treating the latter as a single unit.

Breeding seabirds feed in relatively small areas around their colonies, and not uniformly throughout the North Sea, so that it would be preferable to examine their performance in relation to the local abundance of sandeel within the foraging range of the seabirds. Such small-scale analysis is possible through intensive and expensive survey research dedicated to investigating the feeding ecology of seabirds, but has only been undertaken in a small area [i.e. Firth of Forth over a small number of years (Lewis *et al*., 2001)], though slightly larger scale surveys at Shetland can be used to compare seabird breeding performance in that local area (Phillips *et al*., 1996; Ratcliffe *et al*., 1998; Furness, 1999). For the North Sea sandeel stock, it is only possible to compare local or regional seabird performance with sandeel population data aggregated over the entire area. Notwithstanding this constraint, variations in breeding success of sandeel-dependent seabirds such as black-legged kittiwakes, *Rissa tridactyla*, show similar patterns across years in colonies along the entire length of the UK coasts from Orkney to Kent, and these variations correlate with the overall abundance of sandeel (Furness, 1999). This pattern further supports the view that sandeel dynamics in the various sub-stocks is relatively coherent or is predominantly influenced by factors acting at the North Sea scale rather than at more local scales. This coherence makes up for the poor spatial fit between predator foraging ranges and the area covered by fishery-derived assessment data (ICES, 2001). The advantage of using the latter is they provide a long time-series against which predator populations can be compared. My approach is therefore complementary to the detailed local study of seabird-sandeel interactions as carried out off the Firth of Forth (Harris and Wanless, 1997; Wanless *et al*., 1998; Rindorf *et al*., 2000; Lewis *et al*., 2001) or Shetland (Phillips *et al*., 1996; Ratcliffe *et al*., 1998; Furness, 1999).

Fishery data

Annual estimates of North Sea sandeel stock size (numbers of fish on 1 January) and recruitment (number of 0-group recruiting to the stock in July) are routinely obtained from virtual population analysis (VPA; ICES, 1989, 2001). The high natural mortality rate, short life-span, seasonal changes in behaviour, the tendency of the fishery to concentrate in restricted areas that often differ from year to year, and the small percentage of catch sampled for age structure, are all features that are less than ideal for accurate VPA. Therefore, a large noise in the stock estimates must be expected that may obscure or weaken correlations with other data sets.

Another measure of annual abundance is the standardised catch per unit effort (cpue) in the industrial fishery, which is available for two areas (northern and southern) and two seasons (January–June and July–December; ICES, 2001). Data for the first half of the year represent catches of group 1+ sandeel, while the catches in the second half include a variable proportion of 0-group recruits (Gislason and Kirkegaard, 1998).

Annual landings from the North Sea (excluding Shetland) were extracted from ICES (2001).

Predator population trends and breeding productivity

Seabird breeding numbers on all coasts of Britain and Ireland were counted in 1969 and again in 1985–1987 (Lloyd *et al*., 1991). These counts span the period during which the sandeel fishery expanded. Data on numbers by species breeding on British North Sea coasts from Orkney to Kent (excluding birds within the region of the local Shetland sandeel stock) were extracted from Lloyd *et al*. (1991), and the percentage change between the two surveys was calculated as a measure of population trend. Grey seal, *Halichoerus grypus*, and harbour seal, *Phoca vitulina*, population trends were taken from the literature. These data are used to test the hypothesis that sandeel fishing has caused declines in seabird and seal populations.

Consideration of the life history of different species suggests that breeding success of black-legged kittiwakes should be particularly responsive to sandeel abundance (Furness and Tasker, 2000), and hence a good indicator of the impact of sandeel fishing on seabirds. Kittiwake productivity (chicks per nest) is easy to measure and has been monitored annually in a standardised way in a large number of colonies on British coasts since 1986 (Upton *et al*., 2000). Empirical data show that breeding success is lower in years when sandeel abundance is lower, for both Shetland and North Sea sandeel stocks (Furness, 1999), as well as for individual colonies (Rindorf *et al*., 2000). Kittiwake productivity monitoring data are used to test the hypothesis that breeding success in North Sea colonies would be less than in western colonies because only the former are affected by industrial fishing for sandeel.

Modelling sandeel consumption

ICES (1997) constructed a bioenergetics model to estimate the quantities of sandeel consumed each year by mackerel, gadoids, other fish, marine mammals, and seabirds. The model used diet data for fish from stomach sampling and for seals and seabirds from the literature, combined with estimates of consumption rates and predator population sizes and/or biomasses. Details of the model, and its limitations, are provided in ICES (1997) and the submodel for seabirds is described in Furness and Tasker (1997). The model was extrapolated to add estimates for 1969–1973 and 1997–1999, based on predator abundance estimates for those years [fish

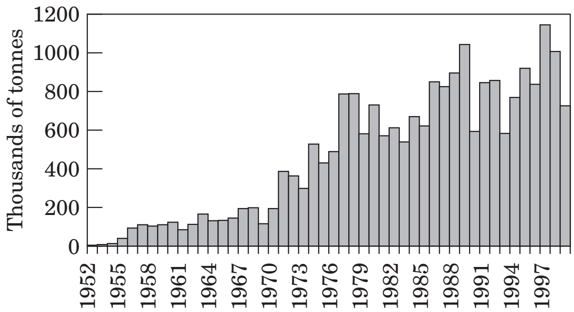

Figure 1. Time-series of sandeel landings from the North Sea (excluding Shetland), 1952–2000 (from ICES, 2001).

biomass based on ICES (2001); extrapolated linear trends for seals; no change in numbers for seabirds], and assuming no changes in diet.

Results

The sandeel fishery in the North Sea started in the early 1950s and catches increased to around 150 000 t during the 1960s (Figure 1). Catches grew rapidly during the 1970s to reach 800 000 t by 1977. From 1977 onwards, catch has fluctuated around 800 000 t, with little or no trend and rarely falling below 600 000 t or exceeding one million tonnes. This would suggest that effects on seabirds or seals might be expected either during the period of rapid increase in landings during the 1970s, or during the period of high volume catches since 1977.

Numbers of grey seals were increasing before sandeel fishing began, but have continued to increase alongside the fishery (Reijnders *et al.*, 1995; Pomeroy *et al.*, 2000). Between 1969 and 1987, breeding numbers of seabirds on North Sea coasts decreased in four species (herring gull, great black-backed gull, roseate tern, and common tern) and increased by 10% or more in 15 species (Table 1). Herring gull declines may be related to reduced availability of domestic refuse, gull control programmes, and outbreaks of botulism (Lloyd *et al.*, 1991; Walsh and Gordon, 1994). Industrial fishery effects are unlikely because herring gulls do not particularly depend on sandeel in the summer diet (Table 1). Roseate and common tern declines may be related to trapping in west Africa (Lloyd *et al.*, 1991; Cabot, 1996). Seven species have increased by 100% or more, including species that feed extensively on sandeel while breeding (Table 1), such as common guillemots and Eurasian shags.

In the mid-1980s, kittiwake productivity tended to be higher at North Sea colonies between Orkney and Kent than at UK, Irish Atlantic, and Irish Sea colonies, although the difference had declined to zero by the late 1990s (Figure 2). The change has been due largely to increasing breeding success at Atlantic colonies while success at North Sea colonies has remained high at around one chick per nest (Figure 2). This suggests that

Table 1. Changes in breeding population size of seabirds on UK coasts from Orkney to Kent, between national censuses in 1969 and 1987 (Lloyd *et al.*, 1991), and approximate proportion of sandeel in diet of North Sea seabirds in summer by region (N: northern; S: southern North Sea; Furness and Tasker, 2000).

Species	Scientific name	Change (%)	Diet fraction N	Diet fraction S
Northern fulmar	*Fulmarus glacialis*	+110%	0.3	0.2
Northern gannet	*Morus bassanus*	+130%	0.4	0.2
Great cormorant	*Phalacrocorax carbo*	+120%	0.1	0.1
Eurasian shag	*Phalacrocorax aristotelis*	+100%	1	1
Arctic skua	*Stercorarius parasiticus*	+200%	1	—
Great skua	*Catharacta skua*	+2000%	0.6	—
Black-headed gull	*Larus ridibundus*	+10%	0.1	0.1
Mew gull	*Larus canus*	+10%	0.1	0.1
Lesser black-backed gull	*Larus fuscus*	+10%	0.6	0.4
Herring gull	*Larus argentatus*	− 30%	0.4	0.1
Great black-backed gull	*Larus marinus*	− 50%	0.5	0.4
Black-legged kittiwake	*Rissa tridactyla*	+50%	0.9	0.6
Sandwich tern	*Sterna sandvicensis*	+90%	0.6	0.6
Roseate tern	*Sterna dougallii*	− 85%	0.5	0.3
Common tern	*Sterna hirundo*	− 40%	0.6	0.4
Arctic tern	*Sterna paradisaea*	0%	0.9	0.6
Little tern	*Sterna albifrons*	+20%	0.2	0.2
Common guillemot	*Uria aalge*	+130%	0.9	0.6
Razorbill	*Alca torda*	+20%	0.8	0.6
Black guillemot	*Cepphus grylle*	+50%	0.6	—
Atlantic puffin	*Fratercula arctica*	+2%	0.8	0.6

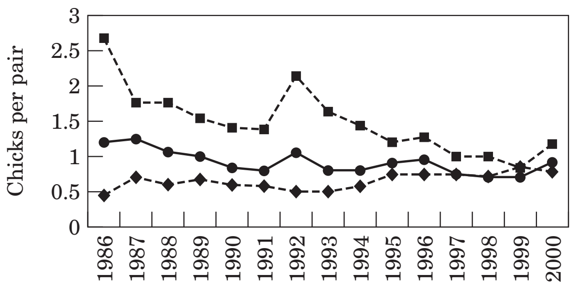

Figure 2. Time-series of breeding success of black-legged kittiwakes in colonies on the UK North Sea coast from Orkney to Kent (continuous line and dots), in colonies to the west of the UK and in Ireland (broken line and diamonds), 1986–2000, and the ratio between the two (large squares and broken line). Data from JNCC Annual Reports on seabird numbers and breeding success in Britain and Ireland.

sandeel abundance in the North Sea was generally more than adequate for this species throughout the entire period.

The success of most seabirds and grey seals alongside the growing sandeel fishery invites examination of relevant aspects of sandeel abundance, recruitment and mortality over this period. Stock size on 1 January (VPA) and cpue during the first half of the year are correlated for both regions distinguished ($p<0.01$), although cpue tends to an asymptote as stock size increases (Figure 3). Correlations between cpue in the second half of the year and VPA estimates of stock size were weaker ($r=0.4$; $p<0.05$), while cpue in the second half of the year and VPA estimates of recruitment were not significant ($r=0.3$). Apparently, the variable mixture of 0-group and older fish in the cpue estimate (Gislason and Kirkegaard, 1998) masks the recruitment signal. There is no evidence from ICES data that sandeel fishing has caused long-term depeletion of the stock. Indeed, abundance (ICES, 2000) shows a slight positive trend from 1976–2000 (Figure 4). The cpue data are partly consistent with an increase in abundance (linear regression for the northern North Sea, 1976–2000, has a significant positive slope: $r=0.70$, $p<0.01$; for the southern North Sea, 1982–2000, the correlation is not significant: $r=0.30$). There is a marked negative density-dependence of sandeel recruitment on total stock size (Figure 5), suggesting resource competition between older and recruiting sandeel. This relationship would tend to buffer the stock against depletion by fishery or by predator stocks.

Bioenergetic estimates of the quantities of sandeel taken by each consumer group indicate that the industrial fishery takes much less than the amount consumed by the major fish predators. Furthermore, the reduction in the consumption by mackerel and gadoids since 1969 was larger than the increase in industrial catch. The net

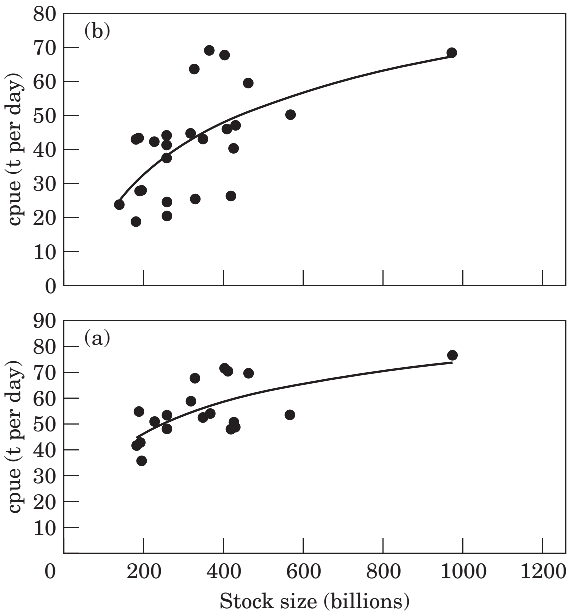

Figure 3. Standardised cpue of sandeel (t d^{-1}), during the first half of the year in (a) the northern (b) the southern North Sea in relation to the VPA estimate of total North Sea stock size in numbers (billions of fish) on 1 January (ICES, 1989, 2001). Lines represent best-fitted logarithmic regressions [(a) 1976–2000, $r=0.62$, $p<0.01$; (b) 1982–2000, $r=0.66$, $p<0.01$].

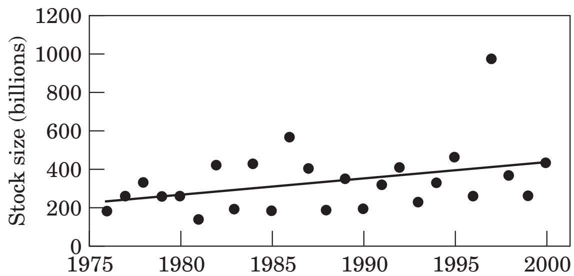

Figure 4. Time-series of VPA estimates of the total North Sea sandeel stock size (billions of fish) on 1 January 1976–2000 (from ICES, 1989, 2001) and fitted regression ($r=0.39$, $p=0.05$).

effect is that sandeel appear to have experienced a reduction in mortality (Figure 6).

Discussion

Naylor *et al.* (2000) cite several references in supporting their claim that sandeel fishing in the North Sea has caused declines in seabird and seal populations and breeding success. One of these (Phillips *et al.*, 1996), demonstrated that breeding success of Arctic skua, *Stercorarius parasiticus*, in Shetland was much lower in years when the local abundance of sandeel was severely reduced. However, that study did not identify industrial

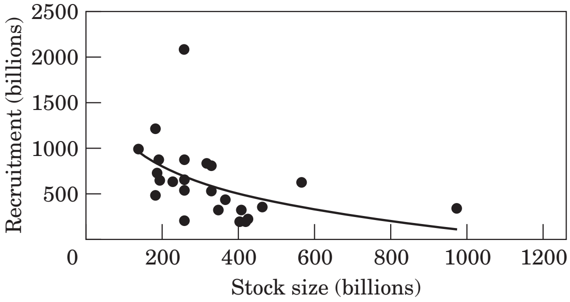

Figure 5. Relationship between VPA estimates of recruitment and total stock size for North Sea sandeel, 1976–1999 (from ICES, 1989, 2001). The line represents the best-fitted logarithmic regression ($r=0.45$, $p<0.05$).

fisheries as causing the reduction in sandeel abundance. The other studies cited show that seals and some seabirds feed on sandeel, and that their spatial distribution in the North Sea may correlate with sandeel distribution, but none shows sandeel fishing to have caused numerical declines or breeding failures of wildlife as claimed. The available data on numbers of seals and seabirds, and breeding success of seabirds, clearly show that grey seals and most sandeel-dependent seabirds have increased in numbers during the period of expansion of the fishery. Because many seabirds do not start breeding until several years old, an impact on immature survival rate may not be evident in counts of breeding numbers until several years after the event. However, the 1985–1987 seabird census took place eight to ten years after the sandeel fishery had reached a plateau around 800 000 t yr^{-1}, and 15–17 years after the fishery first exceeded 350 000 t yr^{-1} (Figure 1). By then, any major effect of the fishery should have been detected. However, contrary to assertions of Naylor *et al.* (2000), breeding numbers of several species relying heavily on sandeel for their food show large increases (Table 1).

Numbers of breeding seabirds may be a relatively insensitive measure of environmental impacts, because they may vary for many different reasons. Breeding numbers can be buffered by pools of potential recruits in the non-breeding component of populations, which are normally ignored during population census (Klomp and Furness, 1992). Breeding success may be a more sensitive measure (Hamer *et al.*, 1991; Furness and Tasker, 2000). Since monitoring started in 1986, black-legged kittiwake breeding success has generally been quite high at North Sea colonies. A mean of round one chick per nest is higher than achieved in Atlantic colonies in Britain and Ireland, and much higher than achieved in many other north-west Atlantic colonies and by kittiwakes in most North Pacific colonies (Barrett and Krasnov, 1996; Regehr and Montevecchi, 1997). Also breeding success in Shetland colonies is lower during years of low sandeel abundance (Danchin, 1992; Hamer *et al.*, 1993). Although sandeel fishing may influence food availability to kittiwakes at a local scale where fishing occurs close to a colony (Rindorf *et al.*, 2000), the extensive data set used here provides no evidence of the sandeel fishery adversely affecting seals or seabirds at the North Sea scale.

This counter-intuitive result, given an annual catch of 800 000 t of sandeel, may be explained by several

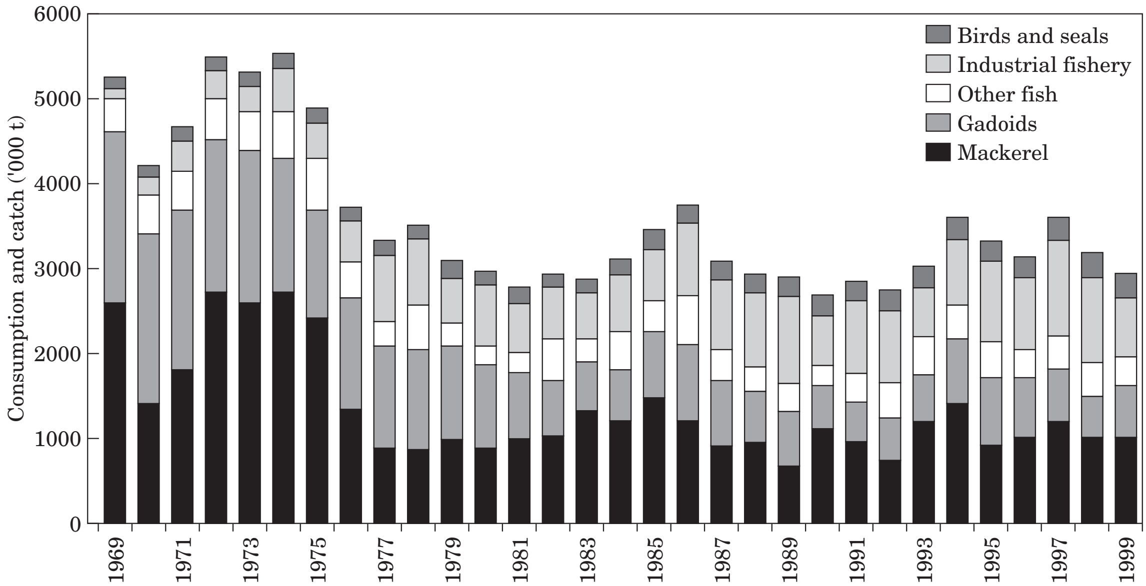

Figure 6. Time-series of estimated consumption of North Sea sandeel by consumer group and industrial catch, 1969–1999 (million t); for details see Data section.

factors. First, sandeel recruitment shows inverse density-dependence (Figure 5). This suggests that sandeel abundance is controlled by "bottom-up" processes, rather than by predation. Increased fishing harvest or natural predation may simply tend to increase recruitment. Second, the VPA and cpue data suggest that the sandeel stock has probably increased over the past 30 years rather than decreased (Figure 4). This appears, to be a continuation of an increasing trend identified in the 1960s and 1970s (Sherman *et al*., 1981). The absence of a decline in response to the expansion of the industrial fishery may reflect that the catch represents only a small proportion of the total mortality of sandeel: the multi-species models indicate that predatory fish consume many times more than taken by the fishery, and predatory fish stocks, and therefore consumption, have varied considerably over the period of interest. The decrease in sandeel consumption as a consequence of depletion of stocks of mackerel and gadoids in particular has been larger than the increase in sandeel catch (Figure 6). Although the bioenergetics estimates of sandeel consumption have large associated confidence intervals, the conclusion that predatory fish take more sandeel than any of the other consumers seems to be robust. Similarly, the conclusion that stocks of the main predatory fish have declined in the North Sea is beyond dispute. The conclusion that overall predation on sandeel has declined remains somewhat tentative given the uncertainties in the calculations, but this result is consistent with the empirical data on sandeel stock size suggesting a slight increase in abundance (Figure 4). This may be one of the main reasons for the high breeding success and population growth of seabirds despite the growth of the sandeel fishery. If so, a future recovery of mackerel or gadoid stocks would be likely to severely compete with sandeel-dependent wildlife, as well as threatening the sustainability of the present industrial fishery. This conclusion is consistent with findings from studies of sandeel interactions with predatory fish and competitors in the northwest Atlantic (Fogarty *et al*., 1991; Nelson and Ross, 1991).

The North Sea case may be typical of seas worldwide where "fishing down the food web" (Pauly *et al*., 1998) has occurred. Also, for other marine food webs that have been studied in detail, the quantities of food fish consumed by predatory fish (even when these have been overexploited) typically greatly exceed the quantities taken by fisheries, or by marine mammals or seabirds. Bax (1991) reviewed patterns observed in six regions (Benguela, Georges Bank, Balsfjord, East Bering Sea, North Sea, and Barents Sea) and concluded that consumption of fish by predatory fish was from 5–56 t km^{-2}, while fisheries (of all types) took 1.4–6.1 t km^{-2}, marine mammals 0–5.4 t km^{-2}, and seabirds only 0–2 t km^{-2}. This general pattern suggests that depletion of predatory fish stocks often reduces mortality rates of food fish by more than is taken up by industrial fisheries and wildlife. Bogstad and Mehl (1997) and Gjøsæter (1997) reported that in the Barents Sea, increases in predation on capelin *Mallotus villosus* by a recovering cod stock caused collapses of the capelin stock, closure of the industrial fishery, and had devastating impacts on populations of seals and some seabirds (Barrett and Krasnov, 1996; Anker-Nilssen *et al*., 1997). If recovery of depleted predatory fish stocks has a great influence on the status quo in such marine ecosystems, changes in fisheries management that alter predatory fish abundance, and hence rates of predation on food-fish, may have a crucial influence on the food supply for seabirds and marine mammals, at least at the regional spatial scale.

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