Responses of seabirds to depletion of fish stocks

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REVIEW

Responses of seabirds to depletion of food fish stocks

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Abstract Life history theory predicts that seabirds will respond to reduction in food abundance by changes in behaviour or breeding effort, buffering adult survival. Empirical data show some support for this but also sometimes indicate a trade-off in which survival of breeding seabirds may be reduced by food shortage. The sensitivity of seabird adult survival rates may be a feature of the detailed ecology of particular species and may be affected by ecological conditions such as the possibilities for prey switching. Fishery managers may set a lower limit biomass to protect fish stock recruitment, often at about 20% of predicted unfished stock biomass. It is unclear whether this threshold would also protect the needs of seabirds dependent on the fish stock. Time series of seabird breeding success and fish stock biomass may indicate minimum densities of food required. These are orders of magnitude more than the consumption by seabird populations. The critical prey density may also vary tremendously among seabird species and is clearly a function of the detailed ecology of each species. It is possible to predict which species will be most sensitive to reduced food supply. Sensitive species may be sentinels of the ''health'' of the marine ecosystem. For example, in Shetland and elsewhere in the North Sea, breeding success of kittiwakes *Rissa tridactyla* is particularly sensitive to abundance and quality of sandeels *Ammodytes* spp. However, seabird communities may be affected by a variety of interactions prompted by changes in fisheries; maintaining food fish levels may not alone be sufficient where communities have altered in composition over decades of fishing, as in the North Sea, and where predator–prey impacts induced by changes in fishery management may disrupt seabird communities.

Keywords Seabird · Fisheries · Stock depletion · Ecosystem-based management

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Introduction

Stocks of food fish, such as sandeels *Ammodytes* spp. (Camphuysen 2005), capelin *Mallotus villosus* (Hjermann et al. 2004), and sprats *Sprattus sprattus* (Österblom et al. 2006) are increasingly being harvested by industrial fisheries to provide the fish meal required for manufacture of aquafeeds (Boyd et al. 2006). The rapid growth of aquaculture, especially farming of carnivorous fish and crustaceans (such as salmonids and tiger prawns), has greatly increased the demand for fish meal (Jennings et al. 2001). However, these fish stocks often support large populations of seabirds and other wildlife. There is concern among conservation bodies that the harvesting of food fish may harm wildlife and may also affect the entire marine food web, including commercially important predators, such as cod *Gadus morhua* and other valuable fish (Furness 2002; Frederiksen et al. 2004, 2007; Camphuysen 2005; Greenstreet 2006; Hunt and McKinnell 2006).

Seabirds are long-lived animals with a low reproductive output. Life history theory predicts that seabirds should buffer their adult survival rates against fluctuations in their food supply (Boyd et al. 2006), and since food fish are short-lived animals with high but also variable recruitment rates (Jennings et al. 2001; Browman and Stergiou 2004), it is inevitable that seabirds will experience large changes in the abundance of the food fish on which they depend. They must, therefore, have evolved the ability to cope with variation in food abundance. The literature indicates that, as predicted, seabird breeding success does show a close correlation with food fish abundance (Furness and Tasker 2000; Rindorf et al. 2000; Davis et al. 2005; Frederiksen et al. 2005), whereas breeding numbers and adult survival may not track these short-term fluctuations (Boyd et al. 2006). Nevertheless, several recent studies do show a trade-off between adult survival rate and reproductive performance, as a result of adults increasing investment when food supply declines and so incurring costs (e.g., Davis et al. 2005). However, variation in breeding success is much greater, and easier to measure, and so is likely to provide a much clearer signal of food shortage (Furness 2002; Mitchell et al. 2004; Mavor et al. 2006).

Furness and Tasker (2000) reviewed the ecological characteristics of seabirds in the North Sea and ranked species from highly sensitive (e.g. terns, kittiwake *Rissa tridactyla*, Arctic skua *Stercorarius parasiticus*) to insensitive (e.g. northern gannet *Morus bassanus*) to reductions in sandeel abundance. They argued that the most sensitive seabirds would be small seabirds with high foraging costs, little ability to dive below the sea surface, little ''spare'' time in their daily activity budget, short foraging range from the breeding site, and little ability to switch diet. This prediction was supported by empirical data from studies at Shetland (Furness and Tasker 2000).

Fisheries reduce the biomass of harvested stocks (Jennings et al. 2001). A well-managed fishery generally has a target of reducing the stock to a biomass of B_{MSY}, the biomass of fish that generates the long-term maximum sustainable yield (MSY). This biomass is often around 40–50% of the biomass that would be present in the absence of fishing (Jennings et al. 2001). Many fish stocks are over-fished, and the biomass is below B_{MSY} (Pauly et al. 2003). Often, a lower limit is set (B_{lim}), where fishing should cease if the stock biomass falls below this limit reference point, in order to allow rebuilding of the stock before the abundance of spawning fish has been reduced to a level where future recruitment is jeopardised. B_{lim} is frequently set at 0.5 B_{MSY}, i.e., at a level of around 20–25% of the estimated biomass that would be present in the absence of fishing of this stock (Jennings et al. 2001). However, it is entirely unclear whether a stock that has been reduced close to B_{lim} is still adequate to sustain healthy populations of top predators, including seabirds. The aim of this paper is to explore this question by looking at a long time-series of data on seabird breeding success in relation to large changes in the abundance of a food fish stock on which they feed while breeding.

Seabirds breeding in Shetland feed predominantly on sandeels (Furness 2002), and there is a time series of data on breeding success of seabirds at Foula, Shetland, since the early 1970s. The sandeels around Shetland form a small, discrete, stock, separate from the sandeel stock(s) in the rest of the North Sea (Wright 1996; Pedersen et al. 1999). The biomass of this stock has been estimated since the start of an industrial fishery at Shetland in the early 1970s [International Council for the Exploration of the Sea (ICES) 2002; Cook 2004]. Large reductions in sandeel abundance in the late 1980s, and since 2000, provide a valuable test of the impact of reduced food abundance on dependent seabirds, as the sandeel abundance in the poor years fell to well below 20% of the abundance that had been present in the 1970s, and, indeed, the fishery was closed due to low spawning stock abundance in 1990, and although subsequently reopened, has never returned to the high harvest levels taken in the late 1970s and early 1980s (ICES 2002).

Methods

From 1976 to 1984 the total stock biomass of sandeels at Shetland was estimated by virtual population analysis (VPA) from the industrial fishery landings and was reported in the annual ICES ''Report of the Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak''. From 1984, a fishery-independent assessment of sandeel abundance at Shetland was also performed by, or under contract to, FRS Marine Laboratory, Aberdeen, by standardised trawling on sandeel grounds at Shetland in early summer and by the counting of numbers of sandeels of each age class caught. The survey data were used to refine the VPA. In 1990 the commercial fishery for sandeels at Shetland was closed, and when it reopened it was restricted to such a low level that sandeel stock assessment was based entirely on the survey data. Cook (2004) presented survey data and used these to estimate age-specific mortality rates of Shetland sandeels. These survey data, updated to 2004 by R.M. Cook (in literature) were used to scale-up to the total stock biomass by regressing VPA total stock biomass on survey catch for the years in which both were measured (1984–1994).

Breeding success of kittiwakes, Arctic terns *Sterna paradisaea*, Arctic skuas and great skuas *Stercorarius skua* was measured each year from 1976 to 2004 at Foula, Shetland, using standard methods recommended by the Joint Nature Conservation Committee (JNCC) and The Seabird Group (Walsh et al. 1995; Mavor et al. 2006). The time series of breeding success data for each of the four species was regressed on sandeel total stock biomass, fitting linear and logarithmic regressions.

Arctic skuas in Shetland feed almost exclusively on sandeels, although they obtain these by stealing them from terns, kittiwakes and auks, and so the link between their breeding success and sandeel stock size is indirect (Furness 1987; Pennington et al. 2004; Davis et al. 2005). The amount of sandeels eaten by Arctic skuas at Shetland each summer was estimated by tabulating data from the literature on Arctic skua numbers in Shetland, the duration of their stay in the region each summer, the daily energy requirement of an Arctic skua [field metabolic rate (FMR) estimated from a general regression model of FMR on seabird body mass], food utilisation efficiency of Arctic skuas eating sandeels, and the average calorific value of Shetland sandeels. These data, and the literature sources, are listed in Table 1. These data were then used to compare the quantity of sandeels eaten by Arctic skuas with the total stock biomass they require to be present in Shetland in order to sustain good breeding success (estimated from the regression of Arctic skua breeding success on sandeel stock biomass).

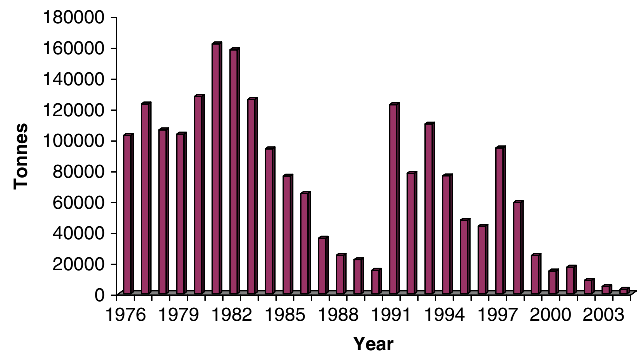

Fig. 1 Estimated biomass (tonnes) of the Shetland stock of sandeels *Ammodytes marinus*.. Data from 1976 to 1994 were estimated by virtual population analysis and reported in the report of the working group on the assessment of demersal stocks in the North Sea and Skagerrak, June 2001. ICES CM 2002/ACFM:01, International Council for the Exploration of the Sea, Copenhagen. Data from 1995 onwards were from survey catch data (Cook 2004; R.M. Cook, personal communication), scaled-up to total stock biomass based on the regression of VPA biomass estimate on Shetland sandeel survey catch for the years when both were measured (1984–1994)

Results

The estimated total biomass of sandeels in the Shetland stock (Fig. 1) fell from around 120,000 tonnes in 1976–1984 to below 30,000 tonnes in 1988–1990, then recovered due to high recruitment in 1991, the season after the fishery was closed. The stock biomass fluctuated between 40,000 tonnes and 120,000 tonnes during the 1990s but then fell rapidly from 1999 onwards. Although data are less reliable for the most recent years (R.M. Cook, personal communication), it is clear that sandeel abundance at Shetland since 2000 has been as low as at any time since stock assessment began in the early 1970s (Fig. 1).

Breeding success of kittiwakes at Foula from 1976 to 2004 shows a strong correlation with sandeel total stock biomass ($r = 0.797$, $P < 0.01$, Fig. 2). The data are well fitted by a logarithmic relationship, where breeding success is zero at very low sandeel abundance, increases rapidly with increasing sandeel abundance at low abundances, but shows little further increase in breeding success from moderate to high sandeel stock biomass (Fig. 2). Arctic tern breeding success shows a strong correlation with sandeel stock biomass ($r = 0.724$, $P < 0.01$, Fig. 3), but, in this case, a linear relationship is a better fit than a logarithmic one, suggesting that Arctic tern breeding success continued to increase over the entire range of sandeel abundances experienced at Shetland. Arctic skua breeding success shows a similar relationship to sandeel stock biomass ($r = 0.844$, $P < 0.01$, Fig. 4) as that shown by the kittiwake. Great skua breeding success shows a similar logarithmic relationship, but with the low breeding success only at very small sandeel stock biomass, and a higher level of variation not explained by the regression ($r = 0.647$, $P < 0.01$, Fig. 5).

Table 1 Estimated quantity of sandeels eaten by the Arctic skua population of Shetland in the period 1980–2000

Arctic skua population of Shetland was ca. 5,000 birds including non-breeders (Mitchel et al. 2004)
These birds are present in Shetland for ca. 90 days per year (Pennington et al. 2004)
Arctic skua field metabolic rate (FMR) is ca. 750 kJ/day (Ellis and Gabrielsen 2002)
Arctic skua food utilisation efficiency is ca. 80% (Hilton et al. 2000)
The population, while at Shetland, needs $5{,}000 \times 90 \times 750 \times 1.25 = 4.2 \times 10^8$ kJ
4.2×10^8 kJ is approximately 65 tonnes of sandeels
Breeding success is poor if Shetland sandeel stock biomass is below 30,000 tonnes (Fig. 4)

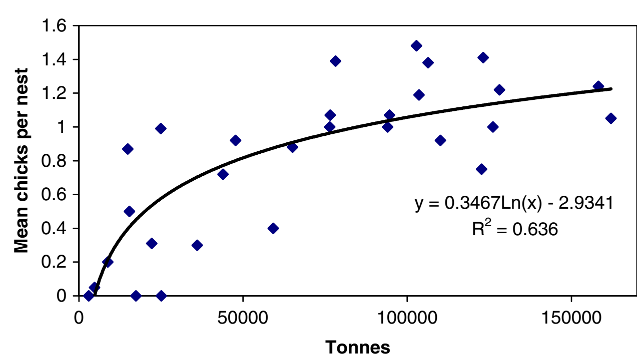

Fig. 2 Breeding success of kittiwakes *Rissa tridactyla* at Foula, Shetland, from 1976 to 2004 in relation to the estimated biomass of sandeels in the Shetland area

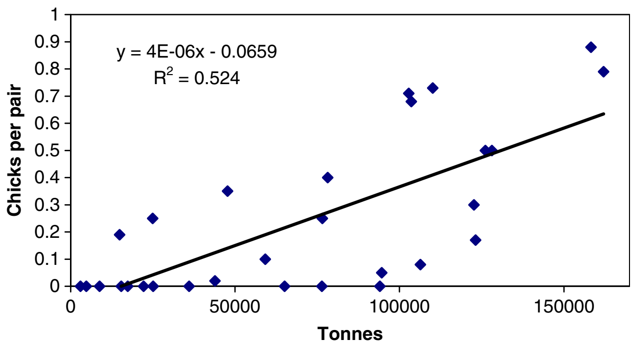

Fig. 3 Breeding success of Arctic terns *Sterna paradisaea* at Foula, Shetland, from 1976 to 2004 in relation to the estimated biomass of sandeels in the Shetland area

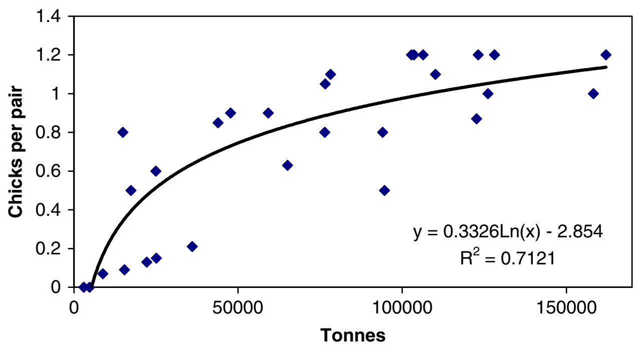

Fig. 4 Breeding success of Arctic skuas *Stercorarius parasiticus* at Foula, Shetland, from 1976 to 2004 in relation to the estimated biomass of sandeels in the Shetland area

We can estimate the amount of sandeels consumed by Arctic skuas from data on the numbers and energy requirements of these birds. The annual consumption of sandeels by Arctic skuas at Shetland in the period 1980–2000 is estimated to have been around 65 tonnes per year (Table 1). This contrasts strongly with the observation from Fig. 4 that Arctic skua breeding success at Shetland fell to less than half of the level seen in years of high sandeel abundance when sandeel stock biomass was below about 30,000 tonnes. The data indicate that Arctic skuas require a sandeel stock biomass about 460-times greater than the amount that they consume, in order to be able to gain energy at a rate sufficient to sustain a good level of breeding success.

Discussion

The total stock biomass of sandeels at Shetland in the late 1980s and after 2000 has been at a level that is about 5–15% of the biomass present through the late 1970s and early 1980s, when the stock sustained an industrial fishery

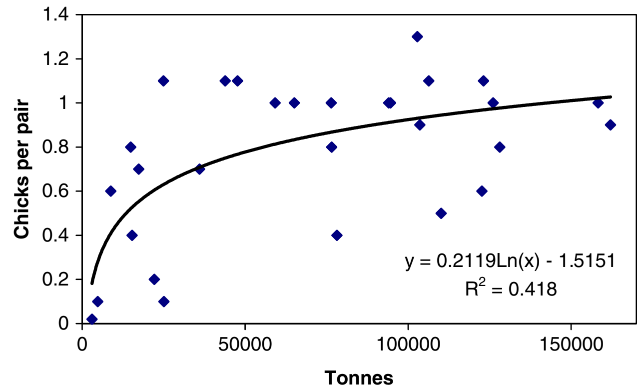

Fig. 5 Breeding success of great skuas *Stercorarius skua* at Foula, Shetland, from 1976 to 2004 in relation to the estimated biomass of sandeels in the Shetland area

(Fig. 1). There is much uncertainty as to the cause of the recruitment failure and stock decline that occurred in the late 1980s, but it is clear that the decline since 2000 has not been a direct consequence of fishing mortality on Shetland sandeels, since the level of directed fishing on Shetland sandeels after 1990 has been negligible. Most commentators have attributed the recent decline of sandeel stocks in Shetland and elsewhere in the North Sea to global warming (Royal Commission on Environmental Pollution 2004; but see also Frederiksen et al. 2007). Arnott and Ruxton (2002) demonstrated that North Sea sandeels tend to show poor recruitment in years when the sea temperature is high, so there is a plausible mechanism for a climate-driven effect. There is also evidence of bottom-up effects through climate-driven changes in zooplankton (Frederiksen et al. 2004). However, although Poloczanska et al. (2004) found autocorrelation of recruitment of sandeels at Shetland, and attributed this to some environmental factor, they did not find any relationship that they could identify, such as with the North Atlantic oscillation or sea temperature. Furthermore, Frederiksen et al. (2007) suggested that changes in sandeel abundance might be, at least in part, attributable to top–down effects of predation by herring *Clupea harengus* rather than just to bottom-up effects of climate. Thus, the Shetland case study does provide a strong example of the responses of seabirds to very considerable changes in their food fish abundance, possibly caused by altered abundances of key predators, such as herring, as well as bottom-up factors such as climate.

Breeding numbers of some seabird species at Shetland have decreased in recent years, and this can be, at least in part, attributed to the low abundances of sandeels; but, in many species, the changes in breeding numbers may reflect short-term non-breeding during years of low sandeel abundance rather than changes in the adult population size (Mavor et al. 2006). An important finding is that, in some cases, reductions in breeding numbers may be closely linked to changes in predation rates on adult seabirds as well as to responses of the adults to sandeel abundance. Not only has low abundance of sandeels at Shetland reduced kittiwake breeding success, and so potentially reduced numbers of recruits that can join the population in future, but declines in survival rates of adult kittiwakes in Shetland are closely correlated with the productivity and diet of great skuas as well as with sandeel abundance (Oro and Furness 2002; Votier et al. 2004). Changes in adult survival rates of seabirds may have a particularly strong influence on population dynamics. Some of the variation in breeding success of kittiwakes that is not ''explained'' by sandeel abundance may be due to these variations in predation rates, as depredations of breeding adults will cause some further breeding failures within colonies.

Breeding success of some species of seabirds at Shetland decreased very considerably in years of low abundance of sandeels. This was true of kittiwakes, Arctic terns, Arctic skuas and great skuas (Figs. 2, 3, 4, 5). However, the detail of the relationship differed among these species, with Arctic tern apparently gaining benefit from increases in sandeel abundance even at the highest recorded levels of sandeel stock biomass, where, for the other species, the breeding success had effectively reached an upper plateau. In contrast, some seabirds, such as northern gannet, show no detectable correlation in breeding success with sandeel stock biomass at Shetland but have maintained high breeding success in all years from 1986 to 2005 (Mavor et al. 2006). Such variation among seabird species was predicted by Furness and Tasker (2000), who identified gannets as likely to be insensitive to variations in sandeel abundance as they can switch from eating sandeels to eating adult herring and mackerel *Scomber scombrus* or fishery discards. There may, of course, be a cost to generalist seabirds of switching prey, since it is reasonable to assume that their preferred prey provides the best energy gain. However, such prey switching may not be costly if it comes about as a result of one food fish species increasing in abundance when another declines. In the case of gannets at Shetland it is likely that adult herring and mackerel provide a very suitable high-energy alternative to sandeels.

The breeding success of Arctic skuas at Foula shows a strong correlation with breeding success of Arctic skuas in other colonies on Shetland monitored during 1986–2005. Computing the amount of sandeels eaten by Arctic skuas throughout Shetland shows that this total is only a tiny fraction of the required sandeel stock biomass to sustain successful breeding by Arctic skuas. This ratio of the biomass consumed in relation to the biomass required in the environment provides some index of the ability of the species to find food. It is interesting to compare the very high ratio for Arctic skuas (ca. 460-times) with the equivalent statistic for oystercatchers *Haematopus ostralegus* wintering on the Wadden Sea, where these birds require only about four-times the biomass of mussels *Mytilus edulis* and other molluscs that they will consume in order to allow overwinter survival (Ens 2006; Zwarts et al. 1996), and for common guillemots *Uria aalge* in the Barents Sea, where a population estimated to consume 70,000 tonnes of capelin per year (Mehlum and Gabrielsen 1995) fared well until 1985 but suffered 90% mortality in winter 1985–1986, when the Barents Sea capelin stock fell from 6 million tonnes in 1980 to 500,000 tonnes in 1985 (Barrett and Krasnov 1996), a level approximately seven-times the amount previously consumed each year by this population. Arctic skuas and oystercatchers may be towards opposite extremes in terms of the critical prey densities they require. Oystercatchers can literally feed on their food, whereas Arctic skuas have to invest a lot of time and energy in searching out birds carrying fish and in energetically expensive chasing behaviour that also has a low rate of success (Furness 1987).

Kittiwake breeding success has been shown to be highly responsive to sandeel abundance, not only in Shetland, but also elsewhere. Frederiksen et al. (2004) showed strong effects of sandeel fishing locally on the breeding success of kittiwakes at the Isle of May, independent of other environmental factors related to oceanographic change. These clear responses of kittiwakes make this an obvious species of interest as a biomonitor of the North Sea sandeel stocks, in areas of the North Sea. Frederiksen et al. (2005) showed that kittiwake breeding success appears to relate to local sandeel dynamics in regions of the North Sea and so may provide insights into the geographical substructure of the North Sea sandeel stock(s).

The decline in breeding success of Arctic terns even as the Shetland sandeel stock biomass fell from very high to moderate levels (Fig. 3) suggests that it is difficult to identify an ''adequate'' sandeel biomass that will sustain all top predator populations. However, kittiwakes and Arctic skuas show a strongly non-linear response to sandeel abundance, with breeding failures predominantly at very low sandeel abundance. Thus, these ''sensitive'' species (as defined by Furness and Tasker 2000) may indicate that a B_{lim} for seabirds at Shetland might be estimated at a total stock biomass of ca. 30,000 tonnes (see Figs. 2, 3, 4, 5). Such a biomass would apparently be adequate to allow successful breeding by even the more sensitive seabird species on Shetland. However, given the strong predation impact of great skuas on smaller seabirds on Shetland, even such an approach may not in itself be adequate to ensure that seabird populations remain stable (Oro and Furness 2002; Votier et al. 2004), and it will be necessary to consider impacts of other fisheries (such as discarding rates from the whitefish trawl fishery) on the seabird community. Furthermore, this estimated B_{lim} cannot be applied to other locations on the assumption that results in Shetland could be generalised to other areas and seabird communities. It would be necessary to use empirical data to estimate critical biomass of food fish for seabirds in any given location of interest, although, in the context of sandeel stocks, it seems likely that the species of seabirds identified as sensitive indicators at Shetland would also be appropriate species on which to focus attention in other regions.

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