Ecological Applications, 18(3), 2008, pp. 701–710

DIFFERENTIAL EFFECTS OF A LOCAL INDUSTRIAL SAND LANCE FISHERY ON SEABIRD BREEDING PERFORMANCE

MORTEN FREDERIKSEN,[1,4] HENRIK JENSEN,[2] FRANCIS DAUNT,[1,5] RODERICK A. MAVOR,[3] AND SARAH WANLESS[1]

[1]*Centre for Ecology and Hydrology, Hill of Brathens, Banchory AB31 4BW United Kingdom*
[2]*Danish Institute for Fisheries Research, Charlottenlund Castle, DK-2920 Charlottenlund, Denmark*
[3]*Joint Nature Conservation Committee, Dunnet House, 7 Thistle Place, Aberdeen AB10 1UZ United Kingdom*

Abstract. Fisheries management across the world is moving toward an ecosystem-based approach, implying that fishery effects on nontarget species should be taken into account. However, such effects are often not well understood, partly because they can be difficult to distinguish from impacts of environmental fluctuations. We evaluated the effects of an industrial sand lance (*Ammodytes marinus*) fishery off the North Sea coast of the United Kingdom, which has been opened and closed in a quasi-experimental fashion, on sand-lance-dependent breeding seabirds. Controlling for environmental variation (sea surface temperature, abundance of larval sand lance, and size of adult sand lance), we found that, when the fishery was operating, breeding productivity in the intensively studied seabird colony on the Isle of May was significantly depressed for one surface-feeding seabird species, the Black-legged Kittiwake (*Rissa tridactyla*), but not for four diving species. Analyzing Kittiwake data from 12 colonies inside and outside the closure zone in a replicated before–after control–impact design, we again found that breeding productivity was significantly depressed in the closure zone when the fishery was active, whereas no effect was found in the control zone. Furthermore, Kittiwake breeding productivity was negatively correlated with fishery effort during the fishery period in the closure zone, but not in the control zone. The contrasting findings in the two zones could be related to environmental differences or to the fact that only one study colony in the control zone was exposed to high fishery effort within the typical foraging range of Kittiwakes during the breeding season. The strong impact on Kittiwakes, but not on diving species, could result from (1) inherently high sensitivity to reduced prey availability, (2) changes in the vertical distribution of sand lance at lower densities, (3) sand lance showing avoidance behavior to fishery vessels, or a combination of some or all of these factors. These findings indicate that local fishery closures can benefit sensitive predators and should be considered as a tool for future ecosystem-based fisheries management.

Key words: Ammodytes marinus; *BACI design; Black-legged Kittiwake; ecosystem-based management; fishery closure; industrial fishery;* Rissa tridactyla; *sand lance; seabirds.*

INTRODUCTION

In the past, management of marine fisheries has mostly been carried out on a single-stock basis, with the aim of achieving a stock-specific target such as maximum sustainable yield. This strategy has had mixed success with some spectacular failures (Pauly and Maclean 2003) and, in recent years, the emphasis has shifted toward so-called ecosystem-based management (Barange 2005, Jennings 2005). This implies that direct and indirect impacts on other components of marine ecosystems should be understood and taken into account in the fisheries management decision process. There are only a few examples where indirect fishery effects have been formally considered in fisheries management (e.g., Constable et al. 2000), partly because current understanding of ecosystem impacts of fisheries is limited. Highly visible top predators, including marine mammals and seabirds, are ecosystem components for which concerns about fishery impacts have been raised, and human fisheries affect them in many different ways. Consumption fisheries mainly affect these predators either through bycatch in active or passive fishing gear (Weimerskirch et al. 1997, Tuck et al. 2001), or indirectly through, e.g., extra food provisioning in the form of discards (Garthe et al. 1996) or changes in trophic structure, with the latter effects being either positive or negative (Sherman et al. 1981). Industrial fisheries for fishmeal and oil, on the other hand, have the potential to compete directly with seabirds and seals for the typically high-lipid, small, schooling pelagic fish on which many of these predators depend. Negative impacts of these fisheries on seabirds have been widely claimed, but few published studies convincingly demon-

Manuscript received 15 May 2007; revised 12 November 2007; accepted 14 November 2007. Corresponding Editor: K. B. Gido.

[4] Present address: National Environmental Research Institute, Department of Arctic Environment, University of Aarhus, Frederiksborgvej 399, DK-4000 Roskilde, Denmark. E-mail: mfr@dmu.dk

[5] Present address: Centre for Ecology and Hydrology, Bush Estate, Penicuik EH26 0QB United Kingdom.

strate such impacts (e.g., Duffy 1983). The difficulty of distinguishing conclusively between fishery impacts and the effects of concurrent environmental change in a generally nonexperimental situation is a major challenge in evaluating the effects of fishing on target stocks and other ecosystem components. However, specific fisheries may be opened and closed in a quasi-experimental manner, and in a minority of such cases, appropriate data on seabirds or other land-based predators and on environmental fluctuations are collected concurrently, allowing robust quantitative evaluation of potential impacts. Here, we evaluate the evidence in one such case, the industrial sand lance fishery in a region of the northwest North Sea.

Industrial fisheries for lesser sand lance (*Ammodytes marinus*, hereafter sand lance) in the North Sea started in the 1950s and gradually developed into the largest single-species fishery in the region, with landings exceeding 1 million Mg in some years (Furness 1999, International Council for the Exploration of the Sea 2007). However, the complex of sand banks off the Firth of Forth in southeast Scotland (Wee Bankie, Marr Bank, and other places) was not exploited by the sand lance fishery until 1990, when Danish vessels started to fish here. Landings then quickly grew to more than 100 000 Mg in 1993, a level that was considered to have negative effects on local sand lance stock size as well as on breeding productivity of local seabirds (Rindorf et al. 2000). In the late 1990s, concerns arose after several years of very poor breeding productivity of Black-legged Kittiwakes (*Rissa tridactyla*, hereafter Kittiwake) in the well-studied colony on the Isle of May and other colonies in the Firth of Forth area. This area supports large concentrations of breeding piscivorous seabirds (>200 000 breeding pairs [Daunt et al., *in press*]), most of which largely depend on sand lance during the breeding season, and the local sand lance aggregation appears to be separate from other North Sea aggregations (Proctor et al. 1998, Gallego et al. 2004). In order to avoid depletion of this aggregation and potential effects on top predators, a zone along the east coast of Scotland and northern England (approximately 21 000 km^2, Fig. 1), including the Wee Bankie, was therefore closed to the sand lance fishery from 2000 onward by the European Commission (Camphuysen 2005). A limited survey fishery by commercial fishing vessels has been maintained throughout the closure period (Wright et al. 2002, International Council for the Exploration of the Sea 2007). Simultaneous collection of both intensive and extensive data on seabird demography in the region since the 1980s allows an evaluation of the effect of the local sand lance fishery on breeding seabirds. Using detailed data from 1996–2003, Daunt et al. (*in press*) evaluated effects of closing the fishery in 2000 on foraging distribution, diet, food consumption, and breeding productivity of seabirds breeding in the Firth of Forth. Here, we use data from a longer time period (1986–2005) to evaluate effects of both the opening and the subsequent closure of the fishery. This paper has two main aims: (1) to test whether a fishery effect on seabird breeding performance was apparent when controlling for environmental variation and whether any potential fishery effect differed among a set of seabird species which vary in foraging behavior and consequently in predicted vulnerability to changes in prey abundance (Furness and Tasker 2000); and (2) to test whether a negative fishery effect on Kittiwake breeding productivity previously documented on the Isle of May (Frederiksen et al. 2004, Daunt et al., *in press*) was consistent on a regional scale, and whether temporal variation in Kittiwake breeding productivity was related to fishery effort or landings both inside and outside the closure zone.

Methods

Study area

The closure zone for the sand lance fishery from 2000 extended from 55°30′ N to 58° N, and from 1° W to the coast of the United Kingdom (Fig. 1). The Isle of May is centrally located in this zone (56°11′ N, 2°33′ W). When testing the regional effect on Kittiwake breeding productivity, we used data from all regularly monitored colonies in the closure zone as well as in a control zone extending from 52° N to 55°30′ N and at least 75 km out from the United Kingdom's coast (Fig. 1), encompassing normal Kittiwake foraging range (Daunt et al. 2002). The exact configuration of the control zone was constrained by International Council for the Exploration of the Seas (ICES) statistical "squares" (0.5° latitude by 1° longitude), the smallest scale at which data on fishery effort and landings are available. The closure and control zones largely correspond to two of the sand lance aggregations identified in the North Sea (Proctor et al. 1998, Frederiksen et al. 2005). The southern limit of the closure zone also corresponds to the boundary between two clusters of Kittiwake colonies where temporal variation in breeding productivity was highly correlated within clusters, but uncorrelated between clusters (Frederiksen et al. 2005).

Fishery data

Sand lance spend most of their life buried in sandy sediments. Spawning occurs in midwinter (December–January), first-year (0-group) fish are available in the water column from metamorphosis in May–June until late summer, and older (1+ group) fish from April to June–July. They are short lived, and the spawning stock consists mainly of 1- and 2-group fish. The fishery occurs in April–June and mainly targets these age classes. Although the fishery in the closure zone took place from 1990 to 1999, we here define the fishery period as 1991–1998. This definition was adopted because sand lance fishery effort and landings in the area were very low in 1990 and 1999, comparable to the survey fishery in 2000–2005 (Fig. 2; Rindorf et al. 2000, Frederiksen et al. 2004, Greenstreet et al. 2006).

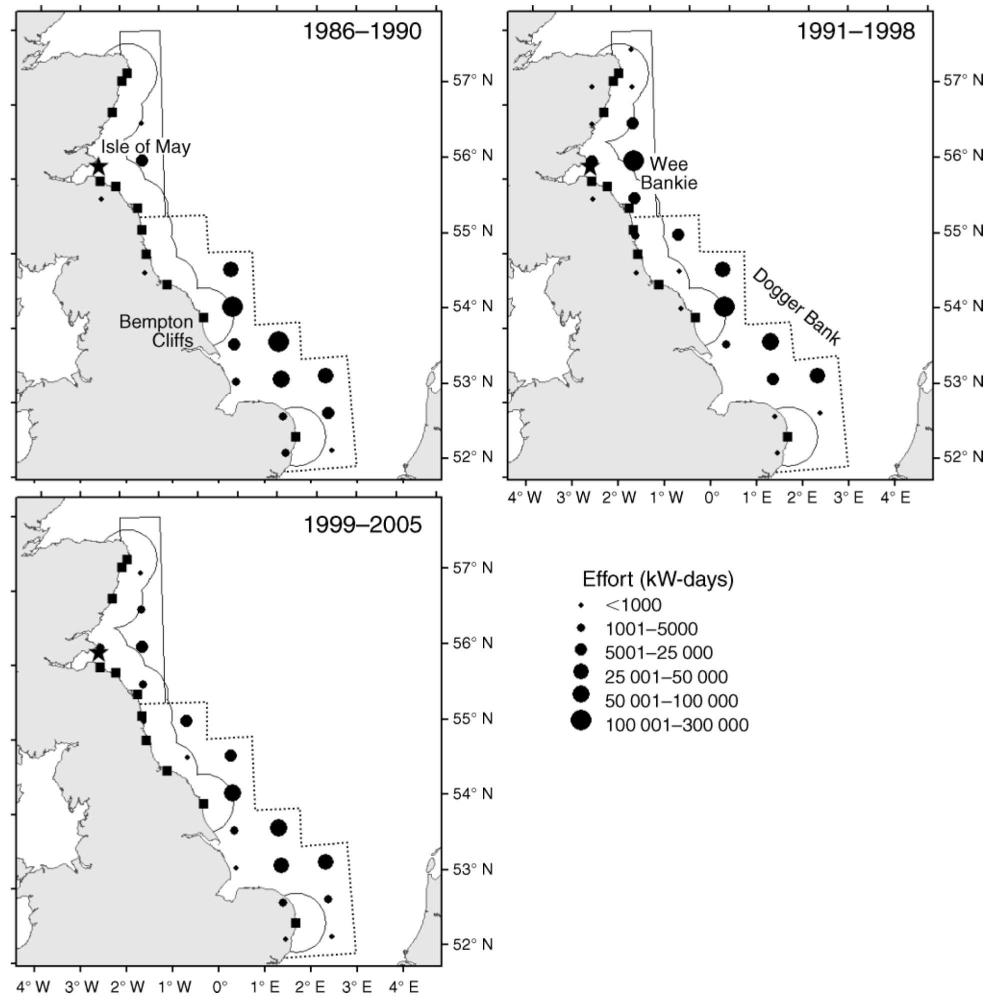

FIG. 1. Map of the study area off the east coast of the United Kingdom. The solid line indicates the sand lance fishery closure zone, and the dotted line indicates the control zone. Squares indicate the Black-legged Kittiwake colonies included in this study, and the star shows the location of the Isle of May. Mean Kittiwake foraging range (44.1 km; Daunt et al. 2006) is also indicated by circular outlines centered on each study colony. Solid circles of different sizes show effort (kW-days) of the industrial sand lance fishery. Effort is shown for each International Council for the Exploration of the Seas (ICES) statistical square, averaged over all years in three periods, before, during, and after the fishery operated in the closure zone. Symbols are located centrally in each ICES square, although some squares mostly consist of land.

The sand lance fishery in the North Sea is operated predominantly by Danish vessels, particularly close to the coast of the United Kingdom in the closure and control zones. Data on the distribution of sand lance fishery effort and landings in the closure and control zones from 1986 to 2005 were extracted from Danish vessel logbooks at the Danish Institute for Fisheries Research. Mean vessel size increased over the study period, and there was a positive association between vessel size and catch rates (H. Jensen, *unpublished data*). Therefore, effort was measured for each vessel as the product of vessel size (engine power in kW) and the number of days spent in the area, and subsequently summed over all vessels. The resulting variable, with the unit kW-days, represents a partially standardized measure of effort. Catch per unit effort (CPUE) was estimated as the ratio between landings and effort.

Seabird data

Detailed long-term data on demography and foraging ecology of five seabird species have been collected since the early 1980s on the Isle of May by the Centre for Ecology and Hydrology, using highly standardized methods (Harris et al. 2005). Five species are studied in detail: European Shag (*Phalacrocorax aristotelis*), Black-legged Kittiwake (*Rissa tridactyla*), Common Murre (*Uria aalge*), Razorbill (*Alca torda*), and Atlantic Puffin (*Fratercula arctica*). Whereas all five species feed their chicks extensively on sand lance (Wanless et al. 1998, Rindorf et al. 2000, Lewis et al. 2001, Harris et al. 2005), they vary in their foraging behavior: Kittiwakes feed from the surface up to 50 km from the colony, European Shags mainly feed benthically close to land, while the remaining species dive throughout the water

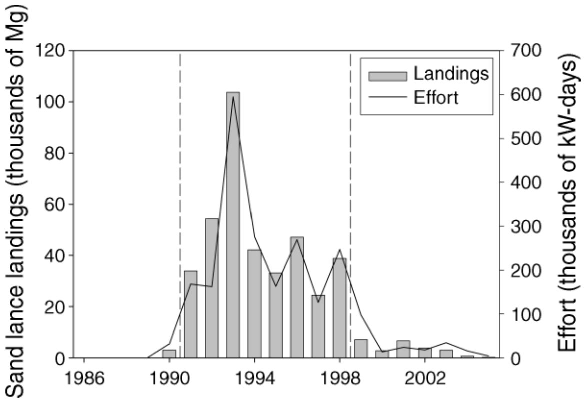

FIG. 2. Landings and effort of the industrial sand lance fishery in the closure zone off the east coast of the United Kingdom, 1986–2005, including the restricted-effort survey fishery in 2000–2005. The vertical dashed lines indicate the opening and closure of the fishery as defined here.

column at varying distances (generally <50 km) and predominantly offshore of the breeding colony (Camphuysen 2005). Because of their high foraging costs and restrictions associated with surface feeding, Kittiwakes are considered more sensitive to variation in prey abundance than the other species (order of sensitivity: Kittiwake > Atlantic Puffin > Razorbill > Common Murre > European Shag [Furness and Tasker 2000]). Most of the species feed mainly on 1+-group sand lance at least in the early part of the breeding season, but apart from European shag switch to 0-group fish during chick rearing. To measure breeding performance of Isle of May seabirds, we used mean breeding productivity (number of fledged chicks per occupied nest) of these five species, as well as the mean body mass of near-fledged Common Murre and Atlantic Puffin chicks. These data were available for all years (1986–2005).

As part of the UK Seabird Monitoring Programme coordinated by the Joint Nature Conservation Committee, breeding seabirds are monitored at a large number of colonies along the North Sea Coast. However, only for Kittiwakes was the coverage and quality of the available data sufficient to allow a replicated comparison between the closure and control zones. Data on Kittiwake breeding productivity (number of fledged chicks per occupied nest) were collected in 1986–2005 at 12 colonies (seven in the closure and five in the control zone), using standardized methods (Harris 1987, Walsh et al. 1995). Data were missing for 26 out of 240 colony-years (11%).

Statistical methods

Breeding performance of five seabird species on the Isle of May.—To estimate rigorously the effect of the fishery on Isle of May seabirds, we attempted to control for environmental variables, which might also affect demographic parameters. As environmental variables we included (1) local late winter (February–March) sea surface temperature lagged by one year (obtained from the German Bundesamt für Seeschifffahrt und Hydrographie; data *available online*)[6]; lagged winter sea surface temperature was negatively associated with Kittiwake breeding productivity on the Isle of May (Frederiksen et al. 2004), probably acting through sand lance recruitment (cf. Arnott and Ruxton 2002); (2) the mean length of 1-group sand lance collected from chick-feeding Atlantic Puffins, adjusted to 1 June (Wanless et al. 2004 and subsequent data and analyses), which was correlated with Common Murre breeding productivity on the Isle of May (Frederiksen et al. 2006); and (3) an index of the biomass of sand lance larvae (SBI) in the northwest North Sea, which was correlated with a generic measure of seabird breeding productivity on the Isle of May 1986–2003 with a one-year lag (Frederiksen et al. 2006). The sand lance index was based on data from the Continuous Plankton Recorder survey (Reid et al. 2003), which uses ships of opportunity to tow plankton samplers and has very good coverage in the North Sea. The effect of the fishery was modeled as a discrete on/off variable with no distinction between the (non-fishery) periods before and after the fishery operated. We used multiple regression to fit all possible models including one or more of the four predictor variables (fishery and three environmental variables). These 16 models (including a null model) were then ranked using Akaike's Information Criterion corrected for small sample size (AIC_c). The importance of each predictor was evaluated using evidence ratios, calculated by summing the Akaike weights (w_i) for all models where the effect appeared and dividing by the summed Akaike weights for models without the effect (Burnham and Anderson 2002). Akaike weights estimate the probability that the given model provides the best description of the data, given the set of models considered, and evidence ratios summarize this for individual effects, again conditional on the model set. Evidence ratios > 10 indicate moderately strong support for the effect (Lukacs et al. 2007). Model-averaged estimates and standard errors of the fishery effect were calculated using Akaike weights according to Burnham and Anderson (2004). The significance of the fishery effect was then evaluated with a t test with $20 - 5 = 15$ degrees of freedom. In contrast to traditional hypothesis testing, this approach is not conditional on one specific "best" model, and it provides a test of the fishery effect controlling for environmental effects and adjusting for model selection uncertainty (Burnham and Anderson 2004). As advocated by Stephens et al. (2005), we thus combined traditional hypothesis testing with model selection based on information theoretical measures, rather than relying on only one of these approaches. The lagged SBI was not fully available for 2005, so the full analyses were carried out with data from 1986–2004;

[6] ⟨http://www.bsh.de/en/Marine_data/Observations/Sea_surface_temperatures/anom.jsp⟩

TABLE 1. Estimated effect of an industrial sand lance fishery on breeding performance of five species of seabirds on the Isle of May, United Kingdom.

Species	Parameter	Effect	SE	Evidence ratio	t_{14}	*P*
European Shag	breeding productivity	−0.023	0.063	0.242	−0.37	0.72
Black-legged Kittiwake	breeding productivity	−0.387	0.131	27.1	−2.97	0.010
Common Murre	breeding productivity	0.034	0.029	2.33	1.18	0.26
Common Murre	fledging mass	3.43	5.92	0.438	0.58	0.57
Razorbill	breeding productivity	0.024	0.032	0.844	0.74	0.47
Atlantic Puffin	breeding productivity	−0.0041	0.011	0.209	−0.37	0.72
Atlantic Puffin	fledging mass	0.84	1.84	0.270	0.46	0.65

Notes: Effects shown are averaged across 16 models including one or more of three environmental covariates, thus controlling for environmental variation and model selection uncertainty. The evidence ratio summarizes the support for a fishery effect and is calculated as the summed Akaike weight of all models including the fishery effect divided by the summed weight of models not including this effect. Values >10 indicate moderate to strong support. Units are chicks/nest for breeding productivity and grams for chick fledging mass.

conclusions did not change when the analysis was repeated using available data for 2005.

Kittiwake breeding productivity in the closure and control zones.—A rigorous nonexperimental assessment of the effect of any anthropogenic impact on the environment requires data from before and after the impact occurred, and from locations affected and unaffected by the impact. A before–after control–impact (BACI) design (Stewart-Oaten et al. 1986) is an appropriate framework for such assessments. In the basic version of this design, data from single locations affected and unaffected by the impact are collected on several occasions before and after the impact and analyzed in a two-way analysis of variance (ANOVA). A statistically significant interaction between period and location then indicates an effect of the impact. This design was elaborated by Underwood (1994) to include several control locations. We treated the presence or absence of a fishery in the closure zone as the impact, years as temporal replicates within each period and colonies as spatial replicates within each zone. Data were available for years both before the fishery started and after it was closed, allowing us to evaluate both the effect of the opening of the fishery and the subsequent closure. In the analysis, we assumed that effects operated without lags, i.e., came into force as soon as the fishery opened and ceased when it was closed. We used a nested two-way ANOVA, with zone (fishery and control) and period (before, during, and after the fishery) as main effects, and colony and year as nested effects, and with annual sample size (number of nests monitored) as a weighting factor. A significant interaction between zone and period would indicate an overall effect of the fishery on breeding productivity, controlling for any differences between zones and periods (Stewart-Oaten et al. 1986, Underwood 1994). In addition, we tested for interactions between zone and specific pairs of periods: zone × (before/during) tests for an effect of the opening of the fishery, zone × (during/after) tests for an effect of the closure, and zone × (before/after) tests whether the difference in breeding productivity between the zones remained the same before and after the fishery period.

In addition, we tested whether annual variation in Kittiwake breeding productivity in the closure and control zones was related to total annual fishery effort, landings or CPUE, including the survey fishery in 2000–2005. For this, we used a linear mixed model, with random colony (within zone) and year effects, weighted by annual sample size. All statistical analyses were carried out in SAS 9.1 (SAS Institute 2003).

RESULTS

Spatial and temporal distribution of the sand lance fishery

In the control zone, fishery effort was unequally distributed in space, with the highest concentration of effort on the western edge of the Dogger Bank (approximately 54°15′ N, 0°30′ E; Fig. 1). The spatial distribution was roughly constant throughout the study period, although the northernmost part was not exploited during the 1980s. Within the closure zone, fishery effort was concentrated in one ICES statistical square, largely corresponding to the Wee Bankie. During the 1990s, mean effort in this square was similar to the most heavily exploited parts of the control zone (Fig. 1). Both effort and landings in the closure zone rose quickly from 1990 and peaked in 1993, remaining high until 1998 (Fig. 2). Although the fishery was open and active in 1990 and 1999, effort and landings in these years were low and similar to the survey fishery in 2000–2005, in line with our definition of 1991–1998 as the fishery period.

Breeding performance of five seabird species on the Isle of May

Controlling for environmental variation, the only species showing a significant effect on breeding productivity during the fishery period was the Kittiwake (Table 1, Fig. 3A). On average, the number of Kittiwake chicks produced annually per nest was 0.32 when the fishery was active and 0.72 when no fishery was operating. Chick fledging mass was not affected by the fishery in the two species for which data were available (Fig. 3B).

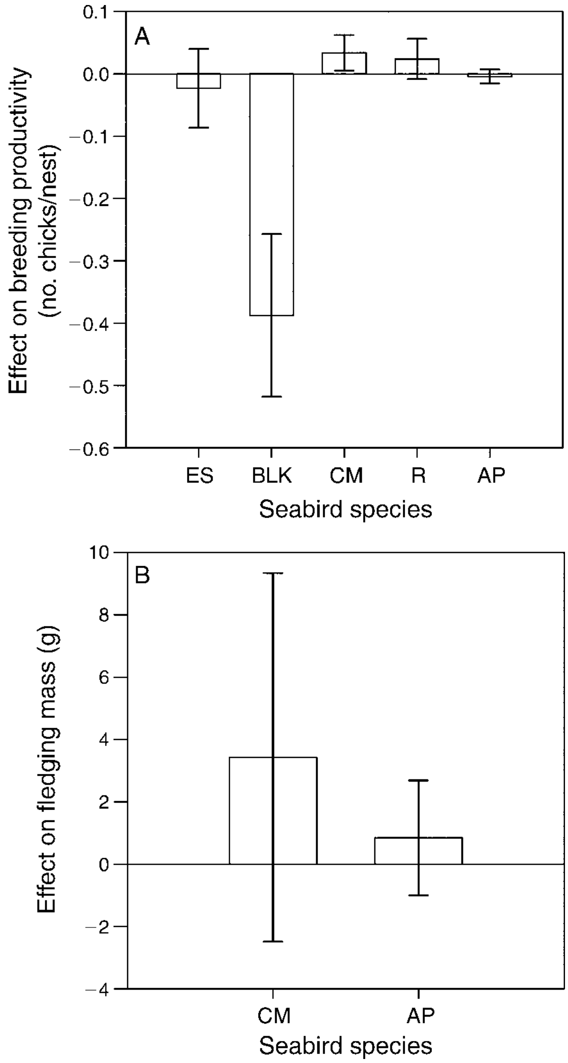

FIG. 3. Model-averaged effects (mean ± SE) of the sand lance fishery on (A) seabird breeding productivity, and (B) chick fledging mass on the Isle of May, 1986–2004. Abbreviated common names are: ES, European Shag; BLK, Black-legged Kittiwake; CM, Common Murre; R, Razorbill; AP, Atlantic Puffin.

Kittiwake breeding productivity in the closure and control zones

The overall interaction between period and zone was highly significant (Fig. 4A; $F_{2,181} = 5.19$, $P = 0.0065$). Breeding productivity in the closure zone declined relative to the control zone when the fishery was opened (relative decline = 0.268 chicks/nest, zone × (before/during) interaction, $F_{1,181} = 7.92$, $P = 0.0054$), and increased relative to the control zone when the fishery was closed (relative recovery = 0.204 chicks/nest, zone × (during/after) interaction ($F_{1,181} = 5.91$, $P = 0.0160$). Both interaction terms remained significant at the 5% level with the sequential Bonferroni adjustment. The zone × (before/after) interaction was not significant ($F_{1,181} = 0.38$, $P = 0.54$), indicating that the relative "quality" of the environment in the two zones was the same before and after the fishery period. Defining the fishery period as 1990–1999 instead of 1991–1998 resulted in even more significant zone × period interactions (overall interaction, $F_{2,181} = 16.98$, $P < 0.0001$; zone × (before/during) interaction, $F_{1,181} = 26.11$, $P < 0.0001$; zone × (during/after) interaction, $F_{1,181} = 15.63$, $P = 0.0001$). Breeding productivity was lower inside the closure zone than outside throughout the 1990s except in 1997 (Fig. 4B), i.e., also in the two years not defined here as fishery years (1990 and 1999). The test for a fishery effect would have been more significant if we had defined these two years as fishery years, making our test conservative (see *Discussion*).

There was a highly significant interaction between effort and zone ($F_{1,200} = 15.58$, $P < 0.0001$), with a negative relationship between fishery effort and breeding productivity in the closure zone and no relationship in the control zone (Fig. 4C). Landings were negatively related to breeding productivity, with a marginally significant interaction (landings × zone interaction, $F_{1,198} = 3.71$, $P = 0.056$; landings main effect without interaction, $F_{1,197} = 18.07$, $P < 0.0001$). In contrast, CPUE had no relationship with breeding productivity (CPUE × zone interaction, $F_{1,186} = 0$, $P = 0.99$; CPUE main effect without interaction: $F_{1,119} = 1.20$, $P = 0.28$).

DISCUSSION

We found clear evidence that the breeding productivity of Kittiwakes at local colonies was reduced during the period when the sand lance fishery was active in the Wee Bankie area (Figs. 3A, 4A, B). This confirms and extends the findings of Frederiksen et al. (2004), who found that breeding productivity as well as adult survival of Isle of May Kittiwakes were reduced when the fishery was operating. Here, we document that the reduction in breeding productivity occurred throughout the area likely to be affected by the Wee Bankie fishery. Furthermore, the statistical relationship between breeding productivity, fishery and sea surface temperature was very similar for the seven colonies in the closure zone (Frederiksen et al. 2008). The reduced Kittiwake breeding productivity during the fishery years was thus a general phenomenon occurring throughout the closure zone.

Based on data from 1996–2003, Daunt et al. (*in press*) found a significant recovery in Kittiwake breeding productivity at the Isle of May following the closure of the Wee Bankie fishery in 2000. Our results support this, at least relative to the decline observed at the same time in the control zone (Fig. 4A). When the fishery period was defined as 1990–1999 instead of 1991–1998, the evidence for a recovery in breeding productivity following closure of the fishery was even stronger. Frederiksen et al. (2004) concluded that the low breeding productivity at the Isle of May in 1990 and 1999 was more likely linked to exceptionally warm

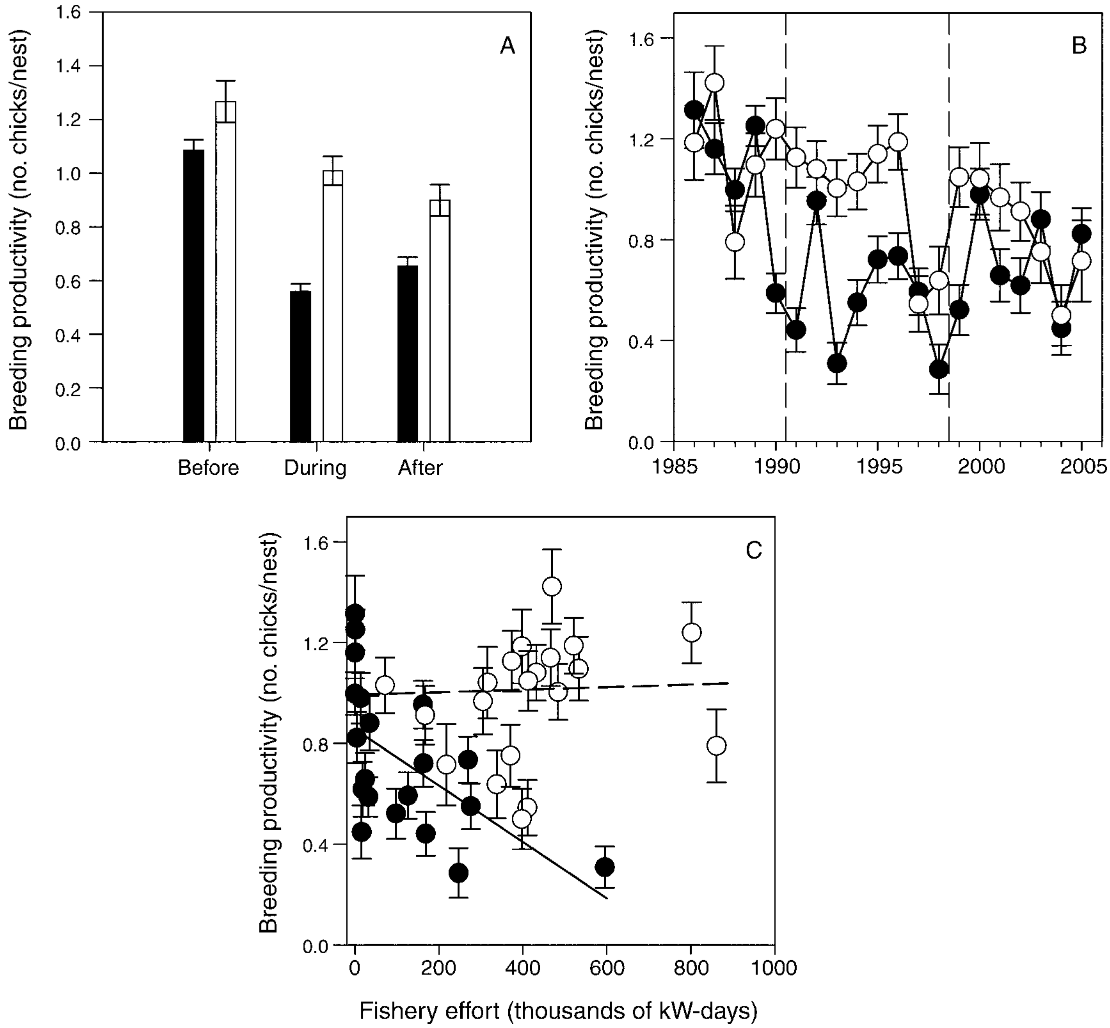

FIG. 4. Kittiwake breeding productivity in the closure (solid bars and symbols) and control (open bars and symbols) zones. (A) Mean productivity before, during, and after the fishery years. (B) Annual mean productivity. The vertical dashed lines indicate the opening and closure of the fishery as defined here. (C) The relationships between productivity and fishery effort in the two zones. Symbols indicate annual mean values, whereas the regression lines in (C) are derived from a linear mixed model using individual colony means. See Table 1. Error bars indicate ±1 SE.

winters in 1988–1989 and 1997–1998 than to the very limited fishery occurring in those years. Nevertheless, these two winters were also very warm in the control zone, where breeding productivity was normal in 1990 and 1999 (Fig. 4B). This highlights the importance of defining control and impact periods appropriately in environmental impact studies, particularly in situations where ecological effects of both the putative impact and other drivers are complex and involve potential lags. Based on the extended study period, we believe that the definition of the fishery period we have used here (1991–1998) is the most robust, but emphasize that our conclusions regarding fishery impacts are likely to be slightly conservative.

Kittiwake breeding productivity remained mostly high in the control zone (Fig. 4B), although colonies in this area did experience bad years in 1997 and 1998. There was also a strong negative relationship between fishery effort and breeding productivity in the closure zone, but not in the control zone (Fig. 4C). The entire control zone was open to the sand lance fishery throughout the study period, raising the question of why no fishery effects were found, and why Kittiwakes generally did better there. However, only parts of the control zone were affected by sand lance fisheries within seabird foraging range (Fig. 1). Whereas all but the two northernmost study colonies in the closure zone were within normal Kittiwake foraging range (mean 44.1 km [Daunt et al. 2006]) of the Wee Bankie fishery, possibly only at one study colony in the control zone (Bempton Cliffs; Fig. 1) did intensive sand lance fisheries take place within this range. Frederiksen et al. (2005) found that Kittiwake breeding productivity was correlated among colonies within each zone, but not between the two zones, and inferred that birds in each zone depended on separate sand lance aggregations with non-synchronous dynamics. This pattern potentially indicates a violation of the fundamental assumption of the BACI approach, i.e., that there is no systematic change (unrelated to the impact being assessed) in the relatively quality of the control and impact zones over the study period. However, the nonsignificant zone × (before/after) interaction found here suggests that the difference in sand lance dynamics could be partly due to different fishing pressure in the two zones, although the mechanism remains unclear. Winter mean sea surface temperatures are about 0.4°C lower in the control zone than in the closure zone (despite the control zone being more southerly; M. Frederiksen, *unpublished data*), which would favor sand lance recruitment (Arnott and Ruxton 2002) and thus breeding Kittiwakes. Sand lance from the Wee Bankie aggregation grow more slowly and mature later than those in other parts of the North Sea (Boulcott et al. 2007), supporting the hypothesis of underlying environmental differences between the two zones. At the same time, the extremely poor breeding productivity noted for Kittiwakes as well as other seabird species at the Isle of May and elsewhere in 2004 (Proffitt 2004, Mavor et al. 2006), which has been tentatively linked to poor food quality (Wanless et al. 2005), was apparent in both the closure and control zones (Fig. 4B), indicating that some large-scale environmental processes were common to the two zones.

No effects on breeding performance were found for the four diving species monitored on the Isle of May (Fig. 3). At least three candidate explanations are consistent with ecological theory, all centering on the limited access surface-feeding Kittiwakes have to the prey resource. Firstly, any reductions in sand lance abundance may have been sufficiently small that diving seabirds were able to compensate and feed their chicks as normal (cf. Daunt et al., *in press*). This pattern is likely if functional responses are nonlinear over the relevant range, in which case a given proportional reduction in prey abundance would have a proportionally stronger effect at the lower absolute abundance levels experienced by surface feeders (cf. Cairns 1987). Second, a general reduction in sand lance abundance may lead to vertical redistribution if certain vertical zones are more optimal to sand lance because of a more favorable balance between food intake rates and predation risk (Daunt et al. 2006). Under such an ideal free distribution scenario, high densities may only occur near the surface when overall abundance is high. Finally, sand lance schools may actively seek out deeper waters in response to the presence or activity of fishery vessels. Such avoidance behavior has been recorded for other pelagic schooling fish (Soria et al. 1996, Vabø et al. 2002, Jørgensen et al. 2004). Although the relationship with fishery effort (Fig. 4C) was consistent with the occurrence of avoidance behavior, it is perhaps unlikely that any response would be sufficiently large scale and long lasting to notably affect availability to surface-feeding seabirds.

The effectiveness of marine protected areas (MPAs) as tools for fisheries management and ecosystem conservation, and whether the two aims can be combined, has been much debated, particularly in the case of fishery closures as opposed to stricter non-use MPAs (Hastings and Botsford 2003, Roberts et al. 2005). Temporary or permanent fishery closures can be regarded as MPAs, although only some types of exploitation are excluded. Fishery closures are probably more likely to be effective in the short term when the target species is relatively sedentary and has a short life cycle, criteria exemplified by lesser sand lance. Predators dependent on such species are also expected to benefit from closures. This study provides evidence that the closure of the industrial fishery in the Wee Bankie area has benefited one species of breeding seabird, the Black-legged Kittiwake. There is some independent evidence to confirm this. Following earlier declines of ~50%, Kittiwake breeding numbers have stabilized since 2004 at the Isle of May as well as other colonies in the closure zone (Mavor et al. 2006; Harris et al., *in press*), consistent with recruitment to the breeding population approximately at age 4 of the large cohort of chicks fledged in 2000 (Fig. 4B). Fishery-related reductions in the availability of "forage fish" prey have been implicated in recent declines of marine mammals and seabirds, although establishing the relative importance of this and other potential causes has been problematic, e.g., in Steller sea lions (*Eumetopias jubatus*) in Alaska (Cornick et al. 2006, Trites et al. 2007). Our results indicate that closing a particular fishery can sometimes have a positive effect on the demography of highly sensitive seabird species, such as the Black-legged Kittiwake in this study. However, unrelated environmental changes have since caused dramatic declines in prey quality and seabird breeding productivity in 2004 (Fig. 4B, see also Wanless et al. 2005) and 2006–2007 (S. Wanless and F. Daunt, *unpublished data*), highlighting the complex and dynamic conditions currently found in this part of the North Sea.

Conclusions

Our results demonstrate that MPAs, in this case a fishery closure, can benefit short-lived pelagic fish stocks and their avian predators. However, such positive effects require that the regulations of the MPA exclude or restrict human activities with negative impacts on the critical resource. In the Dutch Wadden Sea, dredging for edible cockles (*Cerastoderma edule*) was allowed until 2004 despite the high protection status of the area under national and EU legislation as well as international conventions. The result was declines in recruitment and quality of cockles, and subsequently in a specialist avian predator, the Red Knot (*Calidris canutus islandica*; van Gils et al. 2006). For mixed-use MPAs to contribute to effective ecosystem-based management, it is thus necessary that regulations are designed at the outset taking into account the requirements of e.g., natural predators. Furthermore, a network of MPAs is much more likely to achieve conservation aims than single reserves, particularly for highly mobile top predators. As a parallel in terrestrial systems, a recent large-scale analysis has demonstrated that the European Union's Bird Directive with its associated network of Special Protected Areas has delivered substantial conservation benefits: population trends were more positive for highly protected species after the Directive was implemented, and more positive within the EU than outside (Donald et al. 2007). At the World Summit on Sustainable Development in 2002, agreement was reached on establishing a global network of MPAs by 2012 (Sherman 2006). Designing this network and drafting regulations for fisheries and other exploitative activities will be a major challenge for marine scientists and managers in the coming years. It will be critically important to take advantage of the experience gained from existing reserves, whether successful or not, as well as relevant long-term ecological data sets.

Acknowledgments

We are grateful to everyone who contributed Kittiwake data to the UK Seabird Monitoring Programme, which is coordinated by the Joint Nature Conservation Committee (JNCC) in partnership with the statutory country conservation agencies and other conservation organizations in the United Kingdom and the Republic of Ireland. We also thank M. P. Harris and other colleagues for their contributions to the long-term seabird study on the Isle of May, which is funded by the Natural Environment Research Council and JNCC. Continuous Plankton Recorder data were supplied by the Sir Alister Hardy Foundation for Ocean Science. This research was supported by the European Commission through the FP6 Specific Targeted Research Project "PROTECT" (SSP8-CT-2004-513670). Thanks also to two anonymous referees for constructive comments on a previous draft.

Literature Cited

Arnott, S. A., and G. D. Ruxton. 2002. Sandeel recruitment in the North Sea: demographic, climatic and trophic effects. Marine Ecology Progress Series 238:199–210.

Barange, M. 2005. Science for sustainable marine bioresources. A report for NERC, DEFRA and SEERAD. GLOBEC International Project Office, Plymouth, UK.

Boulcott, P., P. J. Wright, F. M. Gibb, H. Jensen, and I. M. Gibb. 2007. Regional variation in maturation of sandeels in the North Sea. ICES Journal of Marine Science 64:369–376.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. A practical information-theoretic approach. Second edition. Springer, New York, New York, USA.

Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociological Methods and Research 33:261–304.

Cairns, D. K. 1987. Seabirds as indicators of marine food supplies. Biological Oceanography 5:261–271.

Camphuysen, C. J., editor. 2005. Understanding marine foodweb processes: an ecosystem approach to sustainable sandeel fisheries in the North Sea. IMPRESS final report. Royal Netherlands Institute for Sea Research, Texel, The Netherlands.

Constable, A. J., W. K. de la Mare, D. J. Agnew, I. Everson, and D. Miller. 2000. Managing fisheries to conserve the Antarctic marine ecosystem: practical implementation of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR). ICES Journal of Marine Science 57: 778–791.

Cornick, L. A., W. Neill, and W. E. Grant. 2006. Assessing competition between Steller sea lions and the commercial groundfishery in Alaska: a bioenergetics modelling approach. Ecological Modelling 199:107–114.

Daunt, F., S. Benvenuti, M. P. Harris, L. Dall'Antonia, D. A. Elston, and S. Wanless. 2002. Foraging strategies of the Black-legged Kittiwake *Rissa tridactyla* at a North Sea colony: evidence for a maximum foraging range. Marine Ecology Progress Series 245:239–247.

Daunt, F., S. Wanless, S. P. R. Greenstreet, H. Jensen, K. C. Hamer, and M. P. Harris. *In press*. The impact of fishery closure on seabird food consumption, distribution and productivity in the northwestern North Sea. Canadian Journal of Fisheries and Aquatic Sciences.

Daunt, F., S. Wanless, G. Peters, S. Benvenuti, J. Sharples, D. Grémillet, and B. Scott. 2006. Impacts of oceanography on the foraging dynamics of seabirds in the North Sea. Pages 177–190 *in* I. L. Boyd, S. Wanless, and C. J. Camphuysen, editors. Top predators in marine ecosystems: their role in monitoring and management. Cambridge University Press, Cambridge, UK.

Donald, P. F., F. J. Sanderson, I. J. Burfield, S. M. Bierman, R. D. Gregory, and Z. Waliczky. 2007. International conservation policy delivers benefits for birds in Europe. Science 317:810–813.

Duffy, D. C. 1983. Environmental uncertainty and commercial fishing: effects on Peruvian guano birds. Biological Conservation 26:227–238.

Frederiksen, M., M. Edwards, A. J. Richardson, N. C. Halliday, and S. Wanless. 2006. From plankton to top predators: bottom-up control of a marine food web across four trophic levels. Journal of Animal Ecology 75:1259–1268.

Frederiksen, M., R. A. Mavor, and S. Wanless. 2008. Seabirds as environmental indicators: the advantages of combining data sets. Marine Ecology Progress Series 352:205–211.

Frederiksen, M., S. Wanless, M. P. Harris, P. Rothery, and L. J. Wilson. 2004. The role of industrial fisheries and oceanographic change in the decline of North Sea Black-legged Kittiwakes. Journal of Applied Ecology 41:1129–1139.

Frederiksen, M., P. J. Wright, M. Heubeck, M. P. Harris, R. A. Mavor, and S. Wanless. 2005. Regional patterns of Kittiwake *Rissa tridactyla* breeding success are related to variability in sandeel recruitment. Marine Ecology Progress Series 300: 201–211.

Furness, R. W. 1999. Does harvesting a million metric tons of sand lance per year from the North Sea threaten seabird populations? Pages 407–424 *in* Ecosystem approaches for fisheries management. Alaska Sea Grant College Program. AK-SG-99-01. University of Alaska, Fairbanks, Alaska, USA.

Furness, R. W., and M. L. Tasker. 2000. 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. Marine Ecology Progress Series 202:253–264.

Gallego, A., M. R. Heath, and B. Cook. 2004. The origin and destination of sandeel larvae sampled in the northern North Sea: bio-physical modelling simulation results. ICES CM 2004/P:09, International Council for the Exploration of the Sea, Copenhagen, Denmark.

Garthe, S., K. Camphuysen, and R. W. Furness. 1996. Amounts of discards by commercial fisheries and their significance as food for seabirds in the North Sea. Marine Ecology Progress Series 136:1–11.

Greenstreet, S. P. R., E. Armstrong, H. Mosegaard, H. Jensen, I. M. Gibb, H. M. Fraser, B. E. Scott, G. J. Holland, and J. Sharples. 2006. Variation in the abundance of sandeels *Ammodytes marinus* off southeast Scotland: an evaluation of area-closure fisheries management and stock abundance assessment methods. ICES Journal of Marine Science 63: 1530–1550.

Harris, M. P. 1987. A low-input method of monitoring Kittiwake *Rissa tridactyla* breeding success. Biological Conservation 41:1–10.

Harris, M. P., M. Newell, F. Daunt, and S. Wanless. *In press*. Isle of May seabird studies in 2005. JNCC Report. JNCC/CEH, Peterborough/Banchory, UK.

Harris, M. P., S. Wanless, S. Murray, and E. Mackley. 2005. Isle of May seabird studies in 2004. JNCC Report No. 375, JNCC/CEH, Peterborough/Banchory, UK.

Hastings, A., and L. W. Botsford. 2003. Comparing designs of marine reserves for fisheries and for biodiversity. Ecological Applications 13:S65–S70.

International Council for the Exploration of the Sea (ICES). 2007. Report of the Working Group on the assessment of demersal stocks in the North Sea and Skagerrak. ICES CM 2007/ACFM:35. International Council for the Exploration of the Sea, Copenhagen, Denmark.

Jennings, S. 2005. Indicators to support an ecosystem approach to fisheries. Fish and Fisheries 6:212–232.

Jørgensen, R., N. O. Handegard, H. Gjøsæter, and A. Slotte. 2004. Possible vessel avoidance behaviour of capelin in a feeding area and on a spawning ground. Fisheries Research 69:251–261.

Lewis, S., S. Wanless, P. J. Wright, M. P. Harris, J. Bull, and D. A. Elston. 2001. Diet and breeding performance of Black-legged Kittiwakes *Rissa tridactyla* at a North Sea colony. Marine Ecology Progress Series 221:277–284.

Lukacs, P. M., W. L. Thompson, W. L. Kendall, W. R. Gould, P. F. Doherty, K. P. Burnham, and D. R. Anderson. 2007. Concern regarding a call for pluralism of information theory and hypothesis testing. Journal of Applied Ecology 44:456–460.

Mavor, R. A., M. Parsons, M. Heubeck, and S. Schmitt. 2006. Seabird numbers and breeding success in Britain and Ireland, 2005. UK Nature Conservation Report No. 30. Joint Nature Conservation Committee, Peterborough, UK.

Pauly, D., and J. Maclean. 2003. In a perfect ocean: the state of fisheries and ecosystems in the North Atlantic Ocean. Island Press, Washington, D.C., USA.

Proctor, R., P. J. Wright, and A. Everitt. 1998. Modelling the transport of larval sandeels on the north west European shelf. Fisheries Oceanography 7:347–354.

Proffitt, F. 2004. Reproductive failure threatens bird colonies on North Sea coast. Science 305:1090.

Reid, P. C., J. M. Colebrook, J. B. L. Matthews, and J. Aiken. and Continuous Plankton Recorder Team. 2003. The Continuous Plankton Recorder: concepts and history, from plankton indicator to undulating recorders. Progress in Oceanography 58:117–173.

Rindorf, A., S. Wanless, and M. P. Harris. 2000. Effects of sandeel availability on the reproductive output of seabirds. Marine Ecology Progress Series 202:241–252.

Roberts, C. M., J. P. Hawkins, and F. R. Gell. 2005. The role of marine reserves in achieving sustainable fisheries. Philosophical Transactions of the Royal Society of London B 360:123–132.

SAS Institute. 2003. SAS/STAT user's guide, version 9. SAS Institute, Inc., Cary, North Carolina, USA.

Sherman, K. 2006. The large marine ecosystem network approach to WSSD targets. Ocean and Coastal Management 49:640–648.

Sherman, K., C. Jones, L. Sullivan, W. Smith, P. Berrien, and L. Ejsymont. 1981. Congruent shifts in sand eel abundance in western and eastern North Atlantic ecosystems. Nature 291: 486–489.

Soria, M., P. Freon, and F. Gerlotto. 1996. Analysis of vessel influence on spatial behaviour of fish schools using a multi-beam sonar and consequences for biomass estimates by echo-sounder. ICES Journal of Marine Science 53:453–458.

Stephens, P. A., S. W. Buskirk, and G. D. Hayward. and C. Martínez del Rio. 2005. Information theory and hypothesis testing: a call for pluralism. Journal of Applied Ecology 42:4–12.

Stewart-Oaten, A., W. W. Murdoch, and K. R. Parker. 1986. Environmental impact assessment: "pseudoreplication" in time? Ecology 67:929–940.

Trites, A. W., et al. 2007. Bottom-up forcing and the decline of Steller sea lions (*Eumetopias jubatas*) in Alaska: assessing the ocean climate hypothesis. Fisheries Oceanography 16:46–67.

Tuck, G. N., T. Polacheck, J. P. Croxall, and H. Weimerskirch. 2001. Modelling the impact of fishery by-catches on albatross populations. Journal of Applied Ecology 38:1182–1196.

Underwood, A. J. 1994. On beyond BACI: sampling designs that might reliably detect environmental disturbances. Ecological Applications 4:3–15.

Vabø, R., K. Olsen, and I. Huse. 2002. The effect of vessel avoidance of wintering Norwegian spring spawning herring. Fisheries Research 58:59–77.

van Gils, J. A., T. Piersma, A. Dekinga, B. Spaans, and C. Kraan. 2006. Shellfish dredging pushes a flexible avian top predator out of a marine protected area. PLoS Biology 4: 2399–2404.

Walsh, P. M., D. J. Halley, M. P. Harris, A. del Nevo, I. M. W. Sim, and M. L. Tasker. 1995. Seabird monitoring handbook for Britain and Ireland. JNCC/RSPB/ITE/Seabird Group, Peterborough, UK.

Wanless, S., M. P. Harris, and S. P. R. Greenstreet. 1998. Summer sandeel consumption by seabirds breeding in the Firth of Forth, south-east Scotland. ICES Journal of Marine Science 55:1141–1151.

Wanless, S., M. P. Harris, P. Redman, and J. Speakman. 2005. Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. Marine Ecology Progress Series 294:1–8.

Wanless, S., P. J. Wright, M. P. Harris, and D. A. Elston. 2004. Evidence for decrease in size of lesser sandeels *Ammodytes marinus* in a North Sea aggregation over a 30-yr period. Marine Ecology Progress Series 279:237–246.

Weimerskirch, H., N. Brothers, and P. Jouventin. 1997. Population dynamics of Wandering Albatross *Diomedea exulans* and Amsterdam Albatross *D. amsterdamensis* in the Indian Ocean and their relationships with long-line fisheries: conservation implications. Biological Conservation 79:257–270.

Wright, P. J., H. Jensen, H. Mosegaard, J. Dalskov, and S. Wanless. 2002. European Commission's annual report on the impact of the Northeast sandeel fishery closure and status report on the monitoring fishery in 2000 and 2001. Report to EC DG XIV. Scientific, Technical, and Economic Committee for Fisheries, Bruxelles, Belgium.