

Black-legged kittiwakes as indicators of environmental change in the North Sea: Evidence from long-term studies

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Abstract

Top predators, particularly seabirds, have repeatedly been suggested as indicators of marine ecosystem status. One region currently under pressure from human fisheries and climate change is the North Sea. Standardized seabird monitoring data have been collected on the Isle of May, an important seabird colony in the northwestern North Sea, over the last 10–20 years. Over this period oceanographic conditions have varied markedly, and between 1990 and 1999 a major industrial fishery for sandlance (*Ammodytes marinus*), the main prey of most seabird species, was prosecuted nearby. Sandlance fishing grounds close to seabird colonies down the east coast of the UK were closed in 2000 in an attempt to improve foraging opportunities for breeding seabirds, particularly black-legged kittiwakes (*Rissa tridactyla*). Initially this closure seemed to be beneficial for kittiwakes with breeding success recovering to pre-fishery levels. However, despite the ban continuing, kittiwakes and many other seabird species in the North Sea suffered severe breeding failures in 2004. In this paper, we test the predictive power of four previously established correlations between kittiwake breeding success and climatic/trophic variables to explain the observed breeding success at the Isle of May in 2004. During the breeding season, kittiwakes at this colony switch from feeding on 1+ group to 0 group sandlance, and results up until 2003 indicated that availability of both age classes had a positive effect on kittiwake breeding success. The low breeding success of kittiwakes in 2004 was consistent with the late appearance and small body size of 0 group sandlance, but at odds with the two variables likely to operate via 1 group availability (lagged winter sea surface temperature and larval sandlance cohort strength in 2003). The reason for the discrepancy is currently unknown, but analysis of 1 group sandlance body composition indicated that lipid content in 2004 was extremely low, and thus fish eaten by kittiwakes during pre-breeding and early incubation were likely to be of poor quality. Monitoring of reproductive success of kittiwakes, although useful, was clearly not sufficient to tease apart the complex causation underlying the 2004 event. Monitoring programs such as this, therefore, need to be complemented by detailed research to identify the mechanisms involved, and to attribute and predict the effects of natural and human-induced environmental change.

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1. Introduction

Many coastal shelf seas have a long history of human exploitation (Pauly and Maclean, 2003) and are also currently showing marked and rapid changes due to global warming (Edwards and Richardson, 2004). Given the economic and environmental value of such regions, evaluating their ecosystem status and performance is of high priority. Marine top predators have repeatedly been suggested as indicators of ecosystem state, with the most useful species generally regarded as those that are conspicuous and accessible, typically because they breed terrestrially, often in large traditional colonies (Croxall and Prince, 1979; Harris and Wanless, 1990; Montevecchi, 1993; Furness and Camphuysen, 1997; Sydeman et al., 2001). Many seabirds fall within this category, and during the breeding season their restricted foraging range associated with their colonial breeding habit means that biological attributes at a given colony, e.g. breeding population size, adult survival, timing of breeding, breeding success, attendance behavior, adult and chick body condition etc., can potentially be related to physical and trophic conditions within a defined ocean region. Breeding success is the most widely monitored parameter, being relatively straightforward to estimate although subject to variable effort/compensation by adults that can mask variation in food supply (Cairns, 1987). The differing life history characteristics of seabird species create a hierarchy in terms of sensitivity to changes in environmental conditions, such that species with small body size, high foraging costs, restricted feeding range and specialized diet are generally the most responsive (Cairns, 1987; Furness and Tasker, 2000).

One of the regions currently under intense pressure from both fisheries and climate change is the North Sea, a small, shallow, semi-enclosed shelf sea between Britain and continental Europe, fed by water influxes at its northern and southern ends and strongly influenced by tidal forces (Otto et al., 1990). It is highly productive and shows strong seasonality with a pronounced spring phytoplankton bloom (Edwards et al., 2002). The North Sea supports breeding populations of about 20 seabird species, most of these populations being of international importance (Mitchell et al., 2004). Most of the breeding colonies are on mainland cliffs or offshore islands down its western (i.e. UK) coast, with the main seabird breeding season being between April and August. The species show a variety of breeding and foraging strategies, but the majority are piscivorous, with the lesser sandlance (*Ammodytes marinus*) being the main prey item (Furness and Tasker, 2000). Sandlance also form the prey of many other mammalian and fish predators in the North Sea (Harwood and Croxall, 1988; Daan et al., 1990; Greenstreet et al., 1998; Santos et al., 2004), and are themselves important consumers of zooplankton (Reay, 1986). They thus form a key link between secondary producers and upper trophic levels. Human fisheries also target mid-trophic species, and up until 2002 the industrial fishery for sandlance was the largest single-species fishery in the North Sea, with annual catches of 0.5–1.0 m t (ICES, 2004). Given this situation, the focus of seabird monitoring schemes has been to assess top-down effects due to removals of sandlance by the industrial fishery. However, changes in lower trophic levels in the North Sea in terms of plankton abundance, community composition and phenology have become increasingly apparent and these have largely been attributed to changes in ocean climate (Edwards et al., 2002; Edwards and Richardson, 2004). Climate-driven changes in distribution, abundance and condition of North Sea demersal fish have also been reported (e.g. Beaugrand et al., 2003; Perry et al., 2005). Thus the emphasis of seabird monitoring programs has progressively shifted towards the detection and attribution of changes due to both fisheries and climate (e.g. Frederiksen et al., 2004).

In the UK Seabird Monitoring Programme, particular attention has recently been given to black-legged kittiwakes (*Rissa tridactyla*), because the breeding population in the North Sea has been declining since the early 1990s, and the species is also regarded as being particularly sensitive to reductions in sandlance availability (Furness and Tasker, 2000). Intensive diet sampling of kittiwakes indicates that whilst sandlance are the dominant prey, there is a consistent switch in the age class taken, with 1+ group taken early in the season and 0 group taken from late May/early June onwards (Lewis et al., 2001). This dietary change accords well with age-related temporal differences in sandlance behavior in this area. The 1+ group is present in the water column from late spring to early summer, and 0 group metamorphoses in late May/early June and remains active in the water column until later in the summer (Winslade, 1974; Reeves, 1994; S.P.R. Greenstreet, pers. comm.).

The main seabird monitoring site in the North Sea is on the Isle of May off the southeast coast of Scotland (Fig. 1). Standardized demographic, phenology and diet data have been collected there annually since the

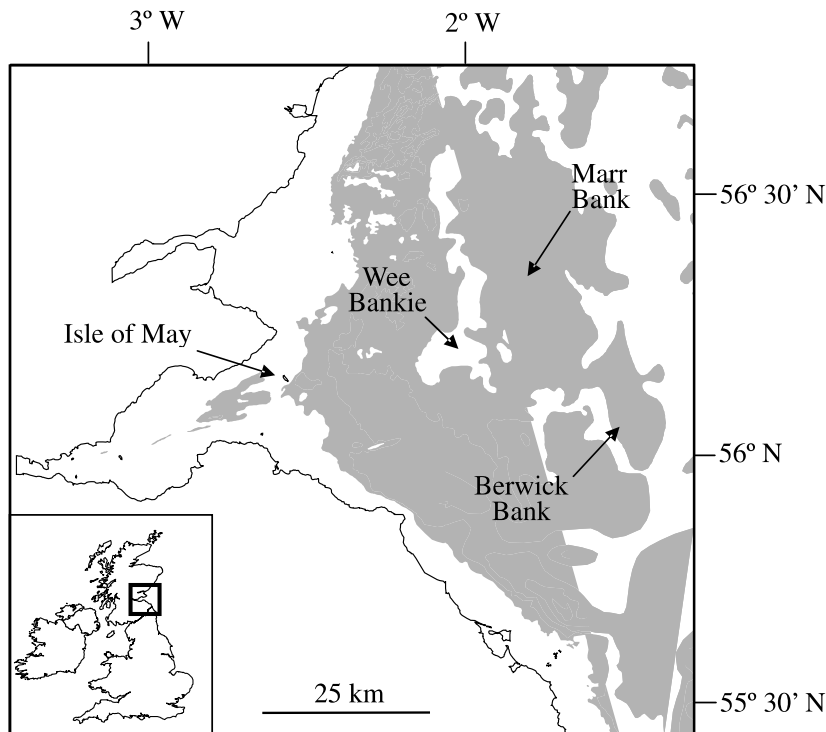


Fig. 1. Map of the study area, showing the Scottish coastline (black line) and bathymetry (white < 40 m; grey > 40 m). The Isle of May and principal offshore sandbank complexes of Wee Bankie, Marr Bank and Berwick Bank are also shown.

1970s and 1980s. Breeding success of kittiwakes on the Isle of May has been monitored annually since 1986 using standardized methods (Harris, 1987). These productivity estimates have been compared to a range of climate and trophic variables and have provided correlative evidence that kittiwake performance is significantly associated with winter sea surface temperature (Frederiksen et al., 2004), larval sandlance biomass (Frederiksen et al., 2006), as well as phenology and condition of 0 group sandlance (Lewis et al., 2001, updated)). For the first two variables, the strongest relationships were obtained using a one-year lag, suggesting that the effect operated through conditions affecting the availability of 1 group fish.

When kittiwake monitoring was initiated, no sandlance fishery was operating close to the Isle of May. In 1990, an industrial fishery targeting 1+ group sandlance opened on the Wee Bankie and associated banks 40–60 km from the colony and thus well within the foraging ranges of many of the seabirds, including kittiwakes. The fishery was prosecuted throughout the 1990s. However, owing to pressure from conservationists and fishery biologists about adverse effects on predators and reductions in sandlance abundance, the fishery along the east coast of Britain was closed in 2000, and the ban remained in effect through 2004. Thus, the seabird monitoring program on the Isle of May spanned a period with, and without, a local sandlance fishery, enabling the potentially additive effects of human exploitation to be assessed. Accordingly, the fishery was included as a factor in the analysis involving winter sea surface temperature, because it was assumed that any effect on kittiwake success would be indirect and operate via sandlance availability. Accounting for the negative relationship with sea surface temperature, breeding success was highly significantly depressed during the fishery years, although the mechanism involved was unclear (Frederiksen et al., 2004).

All the relationships were established using data collected prior to 2004. The 2004 season attracted enormous attention in the UK and international media, with catastrophic failures being reported at many seabird colonies, particularly those in the northern North Sea (Proffitt, 2004). Since the sandlance fishery was either closed (off the east coast of Britain) or minimal (Orkney and Shetland), the failures could not be attributed directly to fishing. Instead, climate change was widely reported to be the cause of the seabird breeding failure. (Royal Commission on Environmental Pollution, 2004; RSPB, 2004; BBC, 2005). There was, however, little

critical evaluation of these claims and, crucially, no rigorous assessment of how data from 2004 fitted into the previously established relationships. The aim of this paper is, therefore, to test the predictive power of the previously observed correlations by evaluating whether they successfully predicted breeding success in 2004. In this way, we attempt to identify how that year differed from previous ones and thus determine whether the observed low breeding success was due to unusual events or could be predicted from established relationships with environmental variables.

2. Methods

The examples used here all come from long-term studies carried out at the black-legged kittiwake colony on the Isle of May (56° 11'N, 2° 33'W).

2.1. Kittiwake monitoring data

Long-term data on kittiwake return rate (proportion of color-banded breeding adults seen in one year recorded alive in the following season), first egg date, mean clutch size (in well-constructed nests after the main laying period is over and including those without eggs), mean mass of a sample of adult birds in June, mean proportions of broods of one and two chicks unattended at midday, and the proportion of the diet (by biomass) composed of sandlance, were collected using standardized methods in most years. The main variable used for monitoring was breeding success. Between 1986 and 2004, annual data on the number of chicks fledged/active nest were collected in 15 plots dispersed through the colony to provide a representative sample of the main habitats (for methods, see [Harris and Wanless \(1997\)](#)).

2.2. Winter sea surface temperature

Following [Frederiksen et al. \(2004\)](#), winter sea surface temperature (WSST) for the waters around the Isle of May in February/March each year between 1986 and 2004 were taken from the German Bundesamt für Seeschifffahrt und Hydrographie, <http://www.bsh.de>.

2.3. Larval sandlance biomass

To estimate an index of larval sandlance biomass (sandlance recruitment index, SRI), fish larvae were extracted from archived Continuous Plankton Recorder samples from the NW North Sea (CPR; [Reid et al., 2003](#)), identified to species and measured. Generalized linear mixed models were used to predict for any given date: (1) the probability of occurrence of sandlance larvae in a sample and (2) the mean summed mass of larvae in a positive sample. The results were combined to estimate the mean mass of sandlance larvae in a CPR sample, standardized to 1 May, and this was used as a larval sandlance index. Details of the method are given in [Frederiksen et al. \(2006\)](#).

2.4. Phenology and body length of 0 group sandlance

Information on the timing of appearance of 0 group sandlance and their body length at a given date was derived from regurgitations of food loads obtained from kittiwakes during routine handling for banding (118–264 food samples/season). Otoliths (fish ear bones) and other hard prey remains were extracted from the regurgitates and identified using keys in [Härkönen \(1986\)](#) and [Watt et al. \(1997\)](#). Sandlance otoliths were measured along the maximum otolith diameter, and the age class of the fish determined from otolith macrostructure using counts of annuli ([ICES, 1995](#)). The lengths of sandlance taken by kittiwakes were estimated using year-specific fish length/otolith length relationships derived from intact fish brought in by Atlantic puffins (*Fratercula arctica*) on the Isle of May to provision their chicks. Estimates of mean sandlance lengths on

15 June in each year were predicted from these year-specific relationships and the date of first appearance of 0 group fish was recorded. A more detailed description of these methods is given in Lewis et al. (2001).

Predicted values and standard errors for breeding success in 2004 were derived from all four established relationships using data up to and including 2003, and compared to observed breeding success in 2004 using *z* tests.

3. Results

Comparisons of monitoring data for kittiwakes on the Isle of May in 2004 with mean values for previous years indicate that return rate of adults was similar to the long term mean, but all the other measures pointed to 2004 being a poor season with breeding starting late, below average values for clutch size, adult weight and breeding success, high levels of brood neglect (unattended nests with chicks) and a low proportion of sandlance in the diet (Table 1).

The relationships between kittiwake breeding success and lagged winter sea surface temperature, lagged larval sandlance biomass and 0 group sandlance phenology and body length derived from all available data up to, and including, 2003 are shown in Fig. 2. Also indicated is the observed value for 2004. Comparisons of climate and trophic values for 2004 with those for previous years indicated that winter sea temperature and appearance date of 0 group fell well within the observed range. In contrast, estimated larval sandlance biomass in the previous spring was well above the long-term average, while the mean length of 0 group was among the lowest ever recorded. Substituting these values into the previously established relationships to give predicted values for kittiwake breeding success in 2004 indicated that the observed success of 0.29 (se 0.06) chicks/nest was lower than expected from sea temperature and dramatically lower than expected from larval sandlance biomass. In contrast, predicted values derived from appearance date and body length of 0 group sandlance provided reasonable agreement with the observed breeding success (Table 2; Fig. 2).

4. Discussion

Breeding success of black-legged kittiwakes in the UK, particularly at colonies along the North Sea coast, has been advocated as a reliable and sensitive indicator of the state of the marine ecosystem for those predators that are reliant on sandlance (Furness and Tasker, 2000). Breeding success at a given colony is therefore considered to reflect some measure of sandlance availability during the period that birds are associated with the colony, and this assumption is supported by a clear regional clustering of kittiwake breeding success corresponding to the known spatial structuring in sandlance populations (Frederiksen et al., 2005).

The poor breeding success of North Sea seabirds in 2004 occurred in the absence of a commercial sandlance fishery off the east coast of Britain, the area where most breeding seabirds would have fed (Camphuysen,

Table 1

Breeding parameters of black-legged kittiwakes on the Isle of May in 2004 compared to data collected in an identical manner in previous years

	2004		Previous years		
	<i>n</i>	Mean	<i>n</i>	Mean	95% CI
Return rate (adults seen in <i>t</i> – 1 and <i>t</i>)	143	0.82	17	0.79	0.76–0.83
First egg date	^a	22 May	23	8 May	6–12 May
Clutch-size (eggs)	427	1.65	15	1.7	1.5–1.9
Breeding success (chicks fledged nest ^{–1})	476	0.29	19	0.59	0.39–0.79
Adult mass (g)	362	365	15	374	366–382
% broods of one chick unattended	28 days	31	17	9	5–14
% broods of two chicks unattended	28 days	48	17	27	18–37
% sandlance in diet by mass (diet samples)	120	79	17	83	76–89

Sample size (*n*) in 2004 indicates the number of records from which the mean was estimated, for previous years *n* indicates the number of years between 1981 and 2003 for which mean values were available. Values in bold indicate where the 2004 value fell outside the 95% CI for previous years.

^a Based on whole colony checks of c. 3000 nests.

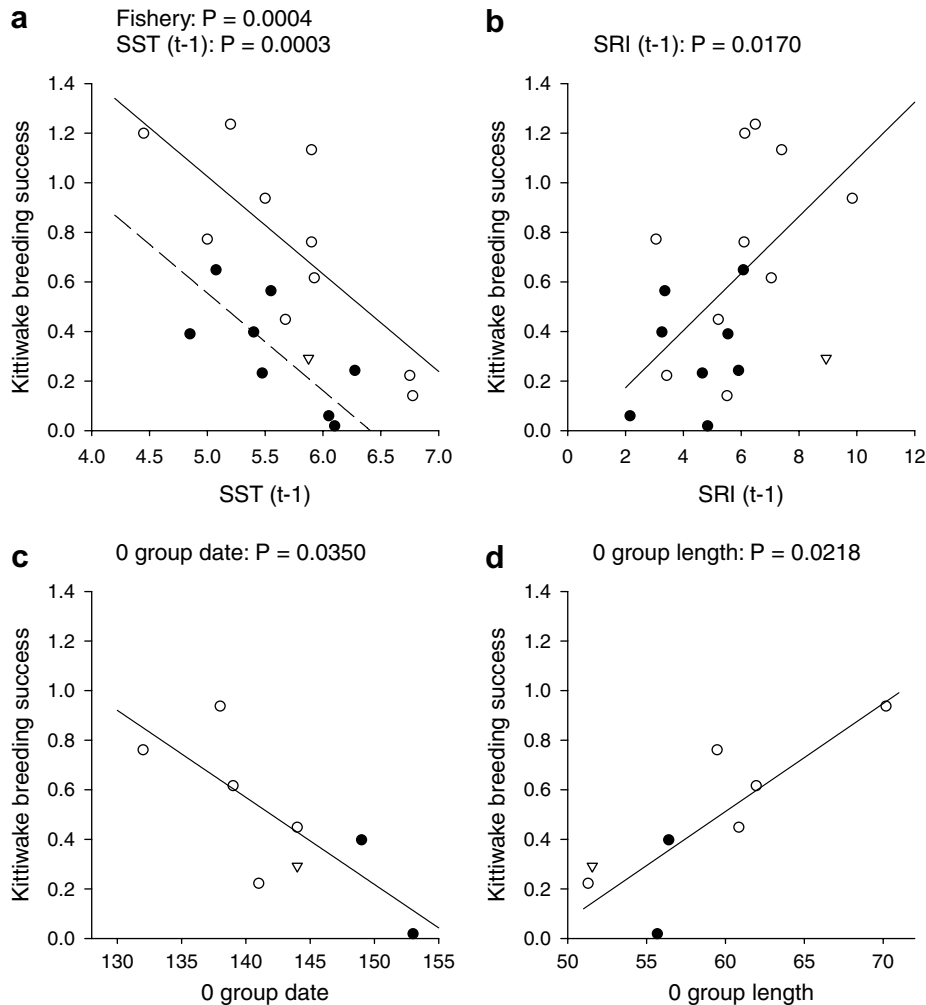


Fig. 2. Relationships between black-legged kittiwake breeding success on the Isle of May and: (a) winter sea surface temperature in the previous year, (b) larval sandlance biomass in the previous year, (c) date of first appearance of 0 group sandlance and (d) mean length of 0 group sandlance for all available years up to 2003. Years when the local sandlance fishery was and was not operating are shown by filled and open circles respectively. In (a), the presence of the fishery is also included as a predictor; P values are shown for both predictors, and parallel regression lines for years with and without a fishery. The observed value in 2004, which was not used to derive the relationships, is indicated by an inverted triangle.

Table 2

Predicted values (and standard errors) of black-legged kittiwake breeding success in 2004 derived from previously established relationships, and comparisons with the observed value of 0.29 chicks fledged nest⁻¹

	Sea surface temperature and fishery	Larval sandlance biomass	Date of appearance of 0 group sandlance	Length of 0 group sandlance
Years	1986–2003	1986–2003	1997–2003	1997–2003
Predicted value (chicks fledged nest ⁻¹)	0.68 (0.07)	0.97 (0.17)	0.43 (0.08)	0.14 (0.13)
P between observed & predicted values	3.6×10^{-8}	9.7×10^{-5}	0.105	0.245
R^2 of relationship without 2004	0.718	0.304	0.622	0.684
R^2 of relationship including 2004	0.672	0.186	0.617	0.676

2005). Landings of sandlance from fishing grounds in the central and eastern North Sea were well below the long term average (ICES, 2004), implying a widespread problem in some aspect of sandlance availability both to seabirds and the fishery. In terms of sea surface temperature in the winter of the previous year, the climate

correlate of Isle of May kittiwake breeding success, 2004 was not an unusual year and predicted success in the absence of the fishery was 0.68 fledged chicks/nest, 2.3 times the value actually recorded. The observed breeding success was in fact much closer to that predicted if a local fishery had been operating (Fig. 2). One interpretation of this could be that some other top-down process came into play in 2004. Further north in the North Sea, the resurgence in herring (*Clupea harengus*) abundance has been suggested as having a negative impact on sandlance stocks through increased predation (Furness, 2004). Such an effect is unlikely to be important around the Isle of May as few adult herring occur in the area (ICES, 2004). However, the possibility of new top-down processes starting to play a role clearly needs to be borne in mind.

It was notable that the two variables likely to operate via availability of 1 group sandlance, i.e. lagged winter sea surface temperature and larval sandlance biomass in 2003, both performed poorly in terms of predicting kittiwake breeding success in 2004. In contrast, the two variables associated with 0 group, i.e. date of appearance in kittiwake diet and body length, performed much better. Values for 1 group variables indicated that conditions should have been generally favorable for kittiwake breeding in 2004, whereas date of appearance of 0 group and particularly 0 group length, pointed to conditions being poor. We had no direct estimate of 1 group availability for 2004, but our results suggest some problem for the fish over the winter or during the spring. Monitoring of 1 group sandlance brought in by Atlantic puffins and common murre (*Uria aalge*) for their chicks in 2004 indicated that they formed a very small proportion of the diet, with sprats (*Sprattus sprattus*) being the main prey (Wanless et al., 2005). Moreover, nutrient analyses of these fish revealed that their lipid content was extremely low and energy values were less than 25% of expected (Wanless et al., 2005). It is thus probable that availability of 1 group sandlance for kittiwakes during April and May 2004 (when 1 group form the majority of the diet (Lewis et al., 2001, updated) was also low, and those fish that were eaten were of lower energy value than normal. Both these effects could potentially have contributed to the poor agreement between observed and expected breeding success. Analyses of 0 group sandlance indicated that lipid levels in this age class also were low and would further compound the adverse effects resulting from their small size (Wanless et al., 2005).

The low quality, in terms of size and lipid content, of sandlance recorded in 2004 (Harris et al., 2005; Wanless et al., 2005) is indicative of exceptionally poor feeding conditions for sandlance and hence of changes in lower trophic levels. Detailed data on zooplankton abundance, phenology and species composition are not yet available for 2004, but results up to 2003 indicate that major changes are already taking place in the North Sea in terms of the abundance, phenology and community composition (Edwards et al., 2002; Edwards and Richardson, 2004), all probably in response to changes in ocean climate (Beaugrand, 2004; Richardson and Schoeman, 2004). For example, the abundance of *Calanus* copepods, the most important secondary producers, has declined over recent decades, and there has been a major shift in dominant species from the large, spring-peaking *C. finmarchicus* to the smaller, summer-peaking *C. helgolandicus* (Edwards et al., 2002; Hays et al., 2005). Changes in kittiwake breeding are therefore likely to be expressions of these mid-trophic level changes at the top end of the food web.

The closure of sandlance fishing grounds down the east coast of the UK in 2000 was introduced with the aim of increasing sandlance abundance and consequently improving feeding conditions for seabirds, particularly kittiwakes. Initial signs were encouraging, with kittiwake breeding success immediately returning to pre-fishery levels for any given set of environmental conditions, suggesting that adverse effects of the fishery were potentially reversible (Frederiksen et al., 2004). However, the situation in 2004, when no fishery was operating close to the colony, clearly gives cause for concern. The extent of the problem escalated further in 2005 when real time monitoring of sandlance stocks at a North Sea scale indicated that abundance was well below the agreed threshold set for commercial fishing. The reason for this widespread decline is currently unknown and probably complex, potentially involving top-down processes associated with natural predators and/or sustained pressure from fisheries, bottom-up processes associated with climatic/environmental change, and interactive effects between these drivers. While the underlying cause(s) remains unclear, the findings triggered the closure of the whole North Sea sandlance fishery from 15 July 2005 onwards (Anonymous, 2005). The shift in North Sea fishery catches, from high-trophic level species to mid-trophic level species such as sandlance, is part of a global trend termed 'fishing down the food web' (Pauly et al., 1998). The closure, even if only temporary, of an important mid-trophic level fishery is indicative of major ecosystem changes and also has potentially serious economic and social implications for the area.

The seabird breeding failures at North Sea colonies in 2004 attracted intense media interest, but many of the claims that climate change was responsible were unsubstantiated. Our examination of the evidence provided by four previously established relationships derived from monitoring of kittiwake breeding success and trophic/climate variables, indicates that low success in 2004 was consistent with the late appearance and small body size of 0 group sandlance, but was at odds with winter sea surface temperature and expected strength of the 1 group cohort based on larval biomass in 2003. The reason for the discrepancy is currently unknown, but it seems likely that the exceptionally low lipid content of sandlance played a crucial role. Clearly, routine assessment of the nutritional content of seabird prey would be a valuable addition to any monitoring program. Evaluation of the findings from the existing scheme thus indicate that the 2004 event had a complex causation and that, while monitoring kittiwake reproductive success was useful, data from a single species with a specialized feeding method and a correlative approach were not sufficient to identify the mechanism(s) involved. This highlights the urgent need for more detailed research that integrates monitoring, targeted data collection (including experiments) and modeling. We must quantify trophic interactions better and come to understand the impacts of environmental influences and the contexts in which they occur. This will improve the quality of advice available to fishery managers, conservationists and policy makers.

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