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From plankton to top predators: bottom-up control of a marine food web across four trophic levels

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Summary

1. Abundant mid-trophic pelagic fish often play a central role in marine ecosystems, both as links between zooplankton and top predators and as important fishery targets. In the North Sea, the lesser sandeel occupies this position, being the main prey of many bird, mammal and fish predators and the target of a major industrial fishery. However, since 2003, sandeel landings have decreased by > 50%, and many sandeel-dependent seabirds experienced breeding failures in 2004.

2. Despite the major economic implications, current understanding of the regulation of key constituents of this ecosystem is poor. Sandeel abundance may be regulated 'bottom-up' by food abundance, often thought to be under climatic control, or 'top-down' by natural or fishery predation. We tested predictions from these two hypotheses by combining unique long-term data sets (1973–2003) on seabird breeding productivity from the Isle of May, SE Scotland, and plankton and fish larvae from the Continuous Plankton Recorder survey. We also tested whether seabird breeding productivity was more tightly linked to sandeel biomass or quality (size) of individual fish.

3. The biomass of larval sandeels increased two- to threefold over the study period and was positively associated with proxies of the abundance of their plankton prey. Breeding productivity of four seabirds bringing multiple prey items to their offspring was positively related to sandeel larval biomass with a 1-year lag, indicating dependence on 1-year-old fish, but in one species bringing individual fish it was strongly associated with the size of adult sandeels.

4. These links are consistent with bottom-up ecosystem regulation and, with evidence from previous studies, indicate how climate-driven changes in plankton communities can affect top predators and potentially human fisheries through the dynamics of key mid-trophic fish. However, the failing recruitment to adult sandeel stocks and the exceptionally low seabird breeding productivity in 2004 were not associated with low sandeel larval biomass in 2003, so other mechanisms (e.g. predation, lack of suitable food after metamorphosis) must have been important in this case. Understanding ecosystem regulation is extremely important for predicting the fate of keystone species, such as sandeels, and their predators.

Key-words: *Ammodytes marinus*, ecosystem function, sandeel, seabirds, trophic structure.

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Introduction

Marine ecosystems are exposed to a wide range of anthropogenic impacts, most notably climate change and fishing. In the North Sea, one of the most heavily fished areas in the world, dramatic changes in abundance, community composition and phenology of plankton at lower trophic levels have been documented and linked to climate change (Edwards *et al*. 2002; Beaugrand 2004; Edwards & Richardson 2004). How climate-driven changes in plankton communities affect higher trophic levels (e.g. Beaugrand *et al*. 2003) will depend on how the structure

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and function of the ecosystem is regulated. Specifically, understanding the relative importance of top-down and bottom-up effects will be critical for predicting impacts on top predators. Top-down effects imply control through predation, including fishery, while bottom-up effects imply control through food abundance, often thought to be driven by climate or nutrient load.

Many marine ecosystems are dominated by a few abundant mid-trophic species, usually pelagic schooling fish, with higher diversity at lower and higher trophic levels (Rice 1995). Such species channel energy and nutrients from planktonic primary and secondary producers to top predators, and thus play an important role in regulating ecosystem dynamics. One of the species occupying this trophic position in the North Sea is the lesser sandeel (*Ammodytes marinus* Raitt; hereafter sandeel), which feeds on zooplankton (mainly copepods) (Reay 1986) and is a key prey of predatory fish, marine mammals and seabirds (Greenstreet, McMillan & Armstrong 1998; Høines & Bergstad 1999; Adlerstein & Welleman 2000; Furness 2002). In particular, the large breeding populations of seabirds in the NW North Sea (East coast of Scotland) depend extensively on sandeels (Wanless, Harris & Greenstreet 1998; Furness & Tasker 2000).

Since the 1970s, sandeels have been among the dominant mid-trophic pelagic fish in the North Sea. Because of their specific habitat requirements sandeels have a patchy distribution and exhibit strong population structure within the North Sea (Pedersen, Lewy & Wright 1999). Starting in the 1950s, a large industrial fishery for fishmeal and fishoil developed, which in the 1980s and 1990s was the largest single-species fishery in the region with landings in some years exceeding 1 million tonnes (Furness 1999). There are several indications that sandeels have been less abundant in the North Sea in the last few years than previously. In 2004 seabirds in this area experienced the worst breeding season on record, linked probably to a lack of suitable food, i.e. sandeels (Harris *et al*. 2004; Mavor *et al*. 2005). Similarly, in 2003 and 2004, landings from the industrial sandeel fishery were less than 50% of the average, indicating repeated recruitment failure since 2001 (ICES 2004). In July 2005 the fishery was suspended following greatly reduced landings, and only a limited fishery effort has been allowed initially in 2006 (Anonymous 2005).

Recent recruitment failures of sandeels and other pelagic fishes have been linked tentatively to observed climate-related changes in copepod communities (ICES 2006). Previous studies of recruitment in sandeels also indicate that it is affected by spawning stock size, winter temperatures and food abundance (Arnott & Ruxton 2002). A fuller understanding of how, e.g. climate change will affect the North Sea ecosystem, including top predators and human fisheries, thus requires considerable knowledge about trophic interactions involving sandeels. Specifically, it is critically important to know whether sandeel abundance is controlled mainly bottom-up by food availability or top-down by predation or fisheries. With this goal, we analysed data on four trophic levels (phytoplankton, zooplankton, sandeel larvae, seabirds) collected concurrently in the NW North Sea over a 30-year period. Industrial sandeel fisheries in this area started in 1990 and in the following years contributed 5–15% of the total North Sea landings; a closure zone was established in 2000 off the UK East coast following concerns about local seabird breeding success (Camphuysen 2005).

We investigated trophic interactions involving sandeels by combining two unique long-term data sets: studies of five seabird species on the Isle of May off SE Scotland (Harris *et al*. 2004), and the Continuous Plankton Recorder (CPR) survey (Reid *et al*. 2003). The Isle of May studies provide the most comprehensive long-term data set on seabird ecology in the North Sea, and the CPR is the only large-scale, long-term survey of plankton available. Ideally we would have used unbiased sandeel abundance estimates from fishery-independent surveys of the relevant area, but no such data exist for this, or indeed any, part of the North Sea over this time scale. In preference to relying on fishery-derived estimates of standing stock biomass at the North Sea scale (ICES 2004), we decided to use CPR data on fish larvae to derive an index of sandeel biomass relevant to the sandeel aggregation off East Scotland (Pedersen *et al*. 1999). While the CPR samples primarily phyto- and zooplankton, it also retains planktonic fish larvae. We extracted data on sandeel larvae from the NW North Sea and compared these with plankton and seabird data from the same area. This is the first time these standardized long-term data covering all trophic levels in the North Sea on a biologically meaningful spatial scale have been analysed together. Data from the CPR survey have been used previously to show that the abundance, distribution and community composition of phyto- and zooplankton in the North-east Atlantic and North Sea are controlled by climatic processes (Beaugrand *et al*. 2002; Beaugrand *et al*. 2003; Richardson & Schoeman 2004). Here, we use CPR and seabird data to distinguish among three general mechanisms that might control the structure and function of marine pelagic ecosystems (Cury, Shannon & Shin 2001; Worm & Myers 2003): strong bottom-up control, strong top-down control and weak trophic links. The predicted patterns of correlations between predators and prey under the various control mechanisms differ markedly: positive correlations would suggest strong bottom-up control, negative correlations strong top-down control and weak or no correlations between predators and prey would suggest weak trophic links or insufficient data (Worm & Myers 2003). While recognizing that significant correlations do not necessarily imply causality, consistently positive, negative or weak associations between measures of biomass or demographic performance at successive trophic levels would support the hypothesis under consideration.

Long-term studies of sandeels brought to the Isle of May colony by Atlantic puffins (*Fratercula arctica* L.) have shown a pronounced decline in the size of individual fish (Wanless *et al*. 2004), and low quality (size, energy content) of sandeels has been suggested as a contributing cause of seabird breeding failures in 2004 (Wanless *et al.* 2005). A secondary objective of our study was to investigate whether seabird reproductive success was more sensitive to variation in sandeel biomass or in the quality of individual fish prey, and whether seabird species differed in this regard. Among the five seabird species studied in detail on the Isle of May, four carry multiple prey items to their offspring, either in the stomach or in the bill, whereas the remaining species carries single fish in the bill. We tested whether variation in breeding productivity of each species was better explained by the CPR-based index of sandeel biomass or by the length of individual sandeels (Wanless *et al.* 2004).

Materials and methods

SEABIRD DATA

Data on five species of seabirds were collected on the Isle of May, SE Scotland (56°11′ N, 2°33′ W): Atlantic puffin and European shag (*Phalacrocorax aristotelis* L.) from 1973, common guillemot (*Uria aalge* Pont.) and razorbill (*Alca torda* L.) from 1982, and black-legged kittiwake (*Rissa tridactyla* L.) from 1986. This is the most comprehensive colony-based data set on seabird ecology in the North Sea, and arguably in Europe. Breeding productivity (number of fledged chicks per breeding pair) was estimated using standardized methods (Harris *et al.* 2004). For European shags, we used mean brood size at ringing (age approximately 3 weeks) as a proxy for breeding productivity to increase the number of years with data, as the two measures were highly correlated ($r = 0{\cdot}90$, $P < 0{\cdot}0001$, $n = 19$ years). To identify common patterns in breeding productivity, we calculated the first principal component of breeding productivity for the four multiple-prey loaders (see below) for 1986–2003; this accounted for 53% of the variation and was associated positively with breeding productivity for all species (loadings = 0·42–0·89).

Sandeels are the most important prey item during the breeding season for all seabirds included in the study. Among the seabird species studied, one (common guillemot) carries single prey to the colony and feeds mainly on 1 + group (i.e. ≥ 1 year old) sandeels. Our expectation was therefore that the size of individual fish would be more important than total sandeel biomass in determining breeding productivity for this species. The other four species carry multiple prey items, either in the bill (razorbill, Atlantic puffin) or in the stomach (European shag, black-legged kittiwake). Shags feed typically on 1 + group sandeels throughout the year (Harris & Wanless 1991), whereas the other species shift from 1 + group early in the breeding season to 0 group later (Lewis *et al.* 2001b; Wanless *et al.* 2004; Wilson, Daunt & Wanless 2004; unpublished data). We expected that their breeding productivity would be related to sandeel availability, as measured by larval biomass in the same or the previous year.

PLANKTON AND FISH DATA

The CPR survey is the longest-running, large-scale, marine biological survey in the world. The CPR is a near-surface (10 m) plankton sampler towed voluntarily each month behind commercial ships on their normal routes of passage. Methods of analysis for ~400 phyto- and zooplankton taxa have remained almost unchanged since 1958 (Reid *et al.* 2003). We used 8595 CPR samples collected from an area bounded by 54° N–59° N and 2° W–2° E between 1973 and 2003 (Fig. 1). This area corresponds reasonably well with sandeel population structure. Rather than constituting one large stock, sandeels in the North Sea are divided into several distinct aggregations (Pedersen *et al.* 1999), and one of these occurs off East Scotland (Frederiksen *et al.* 2005). There are adjacent aggregations around the Orkney Islands and in the central North Sea, and it is possible that the study area used here overlaps slightly with both. However, the East Scotland aggregation occupies most of the study area, and the spatial distribution of samples with sandeel larvae indicates that most larvae belong to this aggregation (Fig. 1). The study area is considerably larger than the foraging range of Isle of May seabirds (Fig. 1), but given sandeel population structure and the need for sufficient numbers of CPR samples we regard this area as suitable. Breeding productivity in seven black-legged kittiwake colonies within the study area was highly correlated among years, whereas correlations were low with other UK regions (Frederiksen *et al.* 2005).

Sandeel larvae feed mainly on copepod eggs and nauplii (Economou 1991), which are not well sampled by the CPR, so we used the abundance of diatoms (the main food of nauplii) and adult copepod biomass during larval development as proxies for food availability for sandeel larvae. Several sources of evidence support the use of these proxies: when phytoplankton is abundant, copepod egg production is high (Hirst & Bunker 2003), and diatoms are the preferred food source of many copepods (Irigoien *et al.* 2002). Sandeels spawn in winter, eggs hatch in February or March and around May larvae metamorphose into 0 group (i.e. first-year) fish, which are likely to be less well sampled by the CPR. We therefore estimated a sandeel biomass index (SBI) standardized to 1 May, and used diatom abundance and copepod biomass for January–April as predictors of sandeel larval biomass. Fish larvae in CPR samples are not identified routinely to species level, being recorded instead as 'young fish'. However, CPR samples allow identification of 42 species or higher taxa of fish (Coombs 1980), and sandeels are the most common ichthyoplankton captured. For this study, CPR samples from January to July 1973–2003 where young fish had been recorded were obtained from the archive. Sandeel larvae were identified, counted and measured to the nearest mm. All sandeel larvae during these months were assumed to be *A. marinus*, except larvae < 10 mm in May–July (Hart 1974).

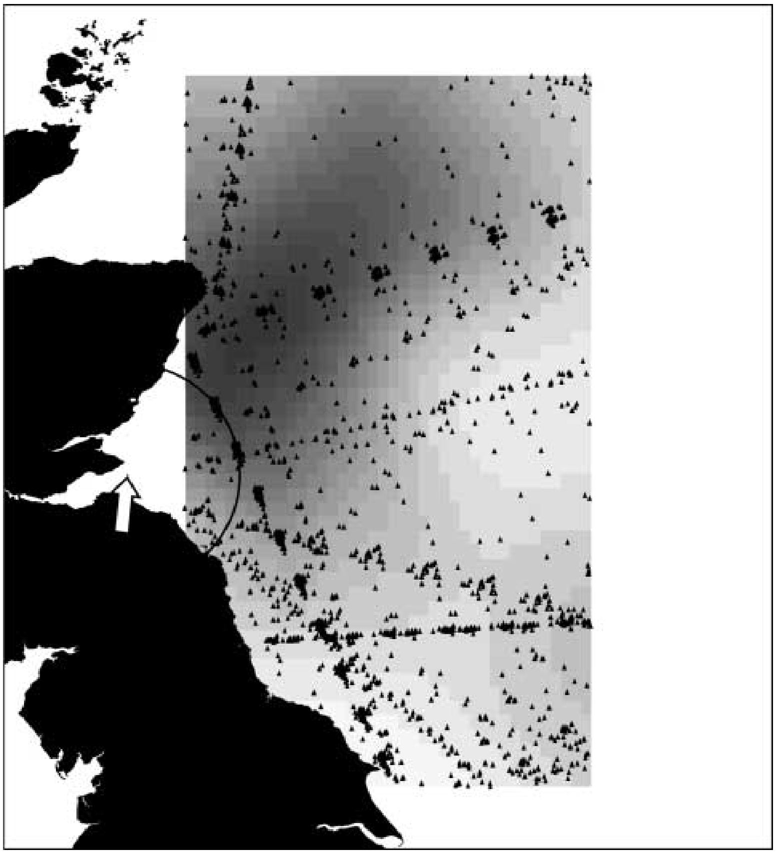

Fig. 1. Map of the study area, showing the location of all CPR samples 1973–2003. Darker shading indicates higher probability of occurrence of sandeel larvae, estimated by fitting a two-dimensional spline function to presence/absence data from April and May. The arrow indicates the Isle of May, and the solid line the approximate maximum foraging range of seabirds breeding there (Camphuysen 2005).

ESTIMATING ABUNDANCE AND BIOMASS

Annual mean abundances of diatoms and copepods were calculated by averaging across the months January–April. Copepod biomass was calculated by multiplying abundance of each copepod taxon by its average mass estimated from an allometric relationship based on size (Richardson *et al.* 2006). An index of biomass of sandeel larvae was estimated in a two-step process using generalized linear mixed models in SAS 8·2 (SAS Institute Inc. 2001). Occurrence of sandeel larvae over the season was clearly unimodal, presumably reflecting gradual hatching early in the season making larvae available for the CPR, and gradual metamorphosis reducing catchability later. The probability of a sample containing sandeel larvae was therefore modelled as a quadratic function of date, with a binomial error and a logit link function. The mass of each sandeel was estimated (Munk & Nielsen 1994), and these were summed for all larvae in a sample. Summed mass in positive samples increased approximately exponentially over the season, reflecting allometric growth and increasing aggregation of larvae. The mass of sandeels in a positive sample was therefore modelled as a linear function of date, with a gamma error and a log link function. To accommodate the tendency for consecutive samples within a tow to be similar, a within-tow first-order autocorrelation term was included. Models also included random intercepts and growth rates for each year. An annual sandeel biomass index (SBI) was finally calculated, using predicted values for 1 May, as the product of the probability of a sample containing sandeel larvae and the summed mass of larvae in a positive sample. As the catchability of larvae by the CPR is unknown, we present the SBI as a unitless number.

TROPHIC RELATIONSHIPS

Mean 1 group sandeel length on 1 June was estimated by measuring fish obtained from Isle of May Atlantic puffins carrying food for their young, the only available long-term data set on sandeel size for this area (for details, see Wanless *et al.* 2004). A potential problem of using data on food delivered to chicks is that adults may sample prey non-randomly and thus provide biased estimates of fish size. However, in this case calibration studies showed a 1 : 1 relationship of mean length between fish collected from puffins and from dedicated survey cruises on the same dates in the same area (Wanless *et al.* 2004). Furthermore, mean length of 0 group sandeels in CPR samples was correlated with mean length of 0 group fish obtained from puffins ($r = 0{\cdot}59$, $P = 0{\cdot}0039$; after linear de-trending $r = 0{\cdot}45$, $P = 0{\cdot}038$), although CPR sandeels were smaller, presumably because larger fish were better able to avoid capture (Fig. 2).

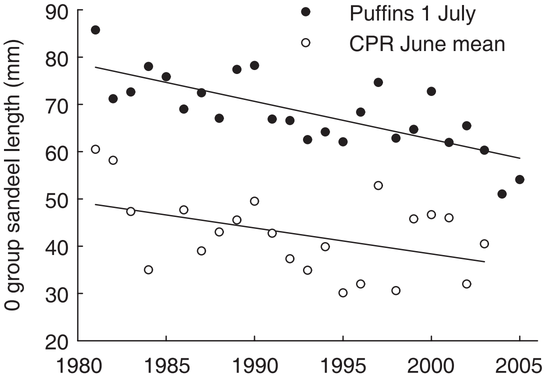

Fig. 2. Annual mean length 1981–2005 of 0 group sandeels obtained from Atlantic puffins on the Isle of May, standardized to 1 July (Wanless *et al.* 2004; updated), and from CPR samples in the study area in June (this study), with regression lines.

Multiple regression was used to identify factors affecting sandeel biomass (SBI) and seabird breeding productivity. To account for spurious correlations caused by similar trends over time, a continuous linear time effect was always included among the candidate explanatory variables. For seabirds, previously identified correlates were included (Frederiksen *et al.* 2004a,b) (Table 1), as well as SBI and 1 group sandeel size. Relationships between, e.g. food abundance and predator breeding productivity are expected to be asymptotic, reflecting predator functional response. Asymptotic (e.g. logistic) models use one extra parameter for each predictor, and because of our limited number of data points we did not consider such models. As an approximation, we tested whether relationships were improved by log-transforming the SBI. In all cases, model selection and significance levels were practically unchanged (results not shown). The most appropriate model was selected using Akaike's information criterion, and summed Akaike weights were used to evaluate the evidence for each predictor in the model set (Burnham & Anderson 1998).

POTENTIAL BIASES

It is well known that the CPR under-samples plankton absolute numbers (Richardson *et al.* 2006), but a more important issue is whether it does so in a consistent and predictable manner. Although no device measures the abundance of plankton perfectly (Wiebe & Benfield 2003), there is increasing evidence from comparisons with other net samplers (Clark, Frid & Batten 2001; John *et al.* 2002; Richardson *et al.* 2004) and satellite data (Batten *et al.* 2003; Raitsos *et al.* 2005) that the CPR is a reliable and consistent semiquantitative index of phyto- and zooplankton abundance capturing real seasonal and interannual changes (Richardson *et al.* 2006). Although using such a large area in this study meant possibly including sandeel larvae from more than one of the separate aggregations in the North Sea (Pedersen *et al.* 1999), annual estimates of plankton abundance over an area this size are more robust because they subsume the considerable fine-scale variability in individual samples associated with diel vertical migration and weather conditions that can concentrate or disperse patches (Richardson et al. 2006).

Results

Diatom abundance and copepod biomass fluctuated from year to year (Fig. 3a) without significant linear trends over time ($r = 0{\cdot}28$ and 0·13, $P = 0{\cdot}14$ and 0·51, respectively). Although annual estimates were uncorrelated ($r = 0{\cdot}024$, $P = 0{\cdot}90$), diatom abundance and copepod biomass showed similar decadal patterns, being low in the 1970s and 1990s and high in the 1980s and since 1999. The SBI was strongly positively associated with diatom abundance, copepod biomass and time (Fig. 3b–d), and the selected multiple regression model included these three covariates (Fig. 3e, $R^2 = 64{\cdot}1\%$, model $P < 0{\cdot}0001$, type III $P = 0{\cdot}0004$, 0·003 and 0·013, respectively). The biomass of sandeel larvae on 1 May was thus associated with food availability during the larval period, although the increasing trend over time seemed

Table 1. Strength of evidence for predictors of seabird breeding productivity. The table indicates which predictors were included in candidate multiple regression models for each species, and the strength of support for each relationship. A blank cell indicates that the predictor was not included for that species. Values shown are summed Akaike weights for all possible multiple regression models including each of the predictors. Values range from 0 to 1, and high values indicate strong support for a given predictor. Predictors included in the selected model for each species are shown in bold type, and for these, type III *P*-values are given. R^2 for the selected model is also given

Predictor	Shag	Kittiwake	Guillemot	Razorbill	Puffin
Time (linear trend)	0·25	0·26	0·46	0·30	**0·88 *P* = 0·0029**
1 group size	0·35		**0·61 *P* = 0·011**	0·36	
SBI		0·12		0·25	0·30
SBI lagged	**0·52 *P* = 0·081**	**0·56 *P* = 0·075**	0·20	0·25	**0·60 *P* = 0·063**
Breeding phenology	**1·00 *P* = 0·0004**				
Lagged sea surface temperature		**0·99 *P* = 0·0004**			
Sandeel fishery presence		**0·97 *P* = 0·0031**			
Model R^2	53·7%	77·7%	28·1%	–	30·5%
n (years)	29	18	22	22	28

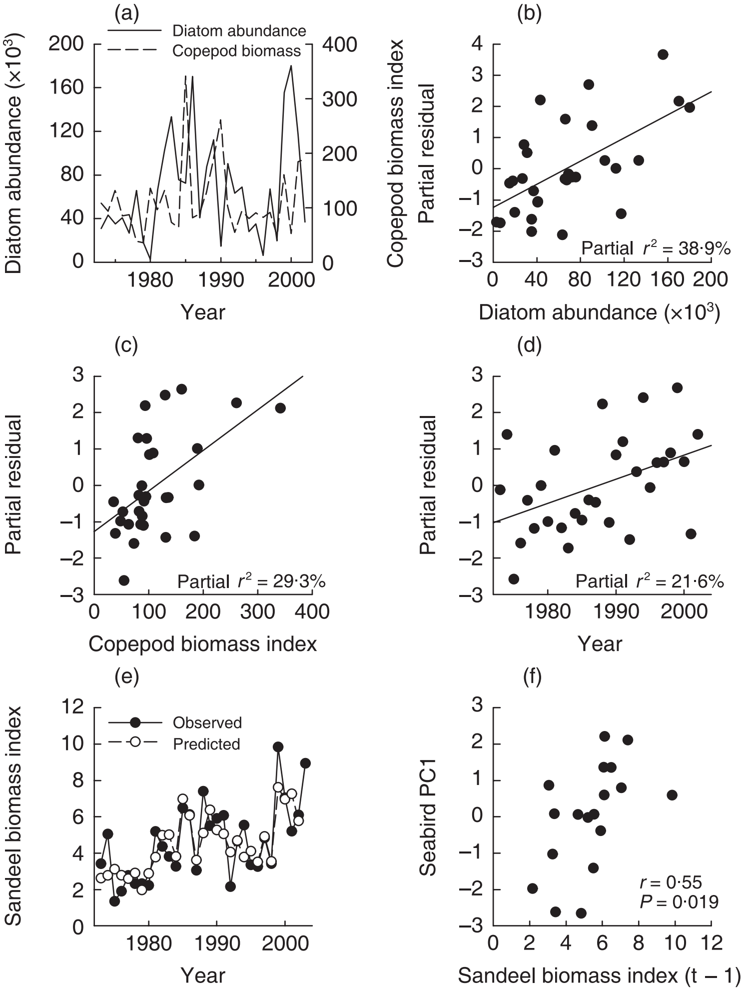

Fig. 3. The sandeel biomass index and factors associated with it. (a) Diatom abundance and copepod biomass in the NW North Sea from 1973 to 2002. (b–d) Partial residual plots for the multiple regression of sandeel biomass index (1 May) against (b) diatom abundance and (c) copepod biomass in January–April, and (d) time. (e) Observed and predicted values for the sandeel biomass index 1973–2003. Predicted values were based on the observed relationships with diatom abundance, copepod biomass and time. Note the high observed value in 2003. (f) The first principal component of seabird breeding productivity 1986–2003 (for four multiple-prey loaders) plotted against the sandeel biomass index in the previous year. Note that 2004 breeding productivity is not included.

to have other, currently unknown, causes. As plankton abundance is thought to be influenced strongly by climate (Richardson & Schoeman 2004; Hays, Richardson & Robinson 2005), the initial strength of a sandeel year class may be affected indirectly by climate.

The first principal component of breeding productivity in the four multiple-prey loading seabirds was correlated positively with the SBI in the previous year ($r = 0{\cdot}55$, $P = 0{\cdot}019$; Fig. 3f), but not in the same year ($r = -0{\cdot}19$, $P = 0{\cdot}46$). This result was confirmed at the species level, where the lagged SBI was included as a predictor in the selected multiple regression models for three of the four species (Fig. 4), whereas the index for the same year was never included (Table 1). For the razorbill, we did not identify any predictor of breeding productivity. Common guillemot breeding productivity was associated with the mean size of 1 group sandeels standardized to 1 June in the current year (Fig. 4) rather than with SBI in the previous year (Table 1). Our predictions about the seabird–sandeel interaction were thus largely confirmed: seabird breeding productivity was associated positively with the body size or biomass of sandeels, with biomass being important for multiple-prey loaders (except razorbill) and size for the single-prey loader. Furthermore, SBI in the previous year was more important than in the same year for European shag, black-legged kittiwake and Atlantic puffin, despite the latter two species feeding their chicks mainly on 0 group sandeels.

Discussion

We show here that over a 3-year period the biomass of sandeel larvae was associated positively with plankton abundance during their growth period, and seabird breeding productivity was higher when sandeel larval biomass had been high in the previous year. These positive associations indicate that bottom-up processes are important in regulating ecosystem dynamics in this area, although this result does not imply that top-down processes play no part. Bottom-up control of zooplankton

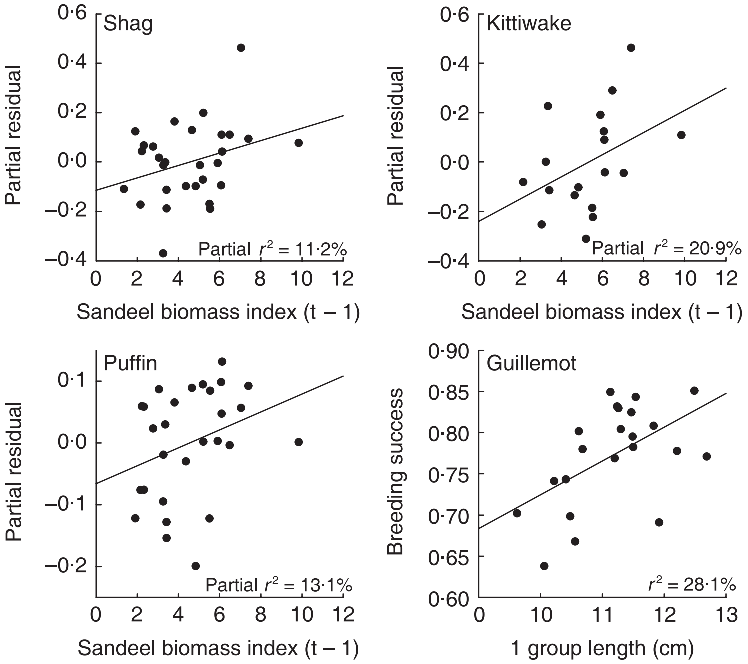

Fig. 4. Relationships between seabird breeding productivity and sandeel size or biomass. For shag, kittiwake and puffin, partial residuals from multiple regressions including sandeel biomass index in the previous year are shown. Other predictors included in the selected models were, respectively, breeding phenology (Frederiksen *et al.* 2004a), presence of a sandeel fishery and sea surface temperature in the previous winter (Frederiksen *et al.* 2004b), and time (Table 1). For guillemot, only the size of 1 group sandeels (Wanless *et al.* 2004) was included in the selected model.

abundance (Richardson & Schoeman 2004), fish recruitment (Beaugrand *et al.* 2003) and fishery yield (Ware & Thomson 2005), as well as seabird breeding productivity (Aebischer, Coulson & Colebrook 1990) has been inferred previously in the North Sea and elsewhere. However, to our knowledge this is the first study showing consistent trends across four trophic levels in a marine ecosystem. While this pattern appears to be consistent in our study area in the NW North Sea, it may not be a general phenomenon, and indeed the relative importance of top-down and bottom-up control may vary even within the North Sea. Abiotic factors (e.g. tides, currents and annual temperature cycle) vary extensively between different regions, and this could affect the amount and timing of primary and secondary production, which in turn could affect the potential for bottom-up control. Spatial variation in the presence or absence of key species could also be important. As an example, adult herring (*Clupea harengus* L.), while being almost absent in our study area, are very abundant further north around Shetland and could have strong effects on ecosystem processes, both as predators and prey (Furness 2004; ICES 2004).

In cases where bottom-up control dominates ecosystem processes, this has far-reaching implications for the dynamics of seabirds and other marine top predators. When bottom-up control is dominant, top predator populations are unlikely to be regulated through density-dependent prey depletion (cf. Birt *et al.* 1987), because prey abundance will be controlled by production at lower trophic levels. Instead, their foraging success, breeding productivity and ultimately population size are likely to track spatial and temporal variation in prey abundance (e.g. Frederiksen *et al.* 2005), although interference among seabirds and/or disturbance of prey may still lead to density-dependent reductions in prey availability around large colonies (Lewis *et al.* 2001a). Under this scenario, seabirds can be reliable, and often cost-effective, indicators of marine environmental conditions (Montevecchi 1993); the same applies to any organisms at any trophic level for which long-term monitoring is feasible, such as plankton (Brander, Dickson & Edwards 2003; Beaugrand 2005). Dominant bottom-up control is also consistent with the many recent studies showing climate impacts on seabird demography, in the North Sea and elsewhere (e.g. Jenouvrier, Barbraud & Weimerskirch 2003; Frederiksen *et al.* 2004b; Grosbois & Thompson 2005; Sandvik *et al.* 2005). Indeed, most of these studies have assumed explicitly or implicitly that climate affects seabirds indirectly through their prey; this assumption in itself implies that bottom-up control is important.

Our results also confirmed the expectation that breeding productivity of multiple-prey loaders was linked to prey biomass, whereas the single-prey loading common guillemot was more sensitive to changes in the size and thus energy content of individual fish (Table 1). Productivity as well as fledging mass of common guillemots on the Isle of May has declined gradually since the 1980s (Harris *et al.* 2005), and our results indicate that this long-term trend is likely to have been caused at least partly by the decreasing size of adult sandeels in the region (Wanless *et al.* 2004). Common guillemots have been regarded as comparatively insensitive to changes in prey availability, as they can access prey throughout the water column and are able to increase parental foraging effort when prey becomes scarce (Furness & Tasker 2000). However, we show here that they are very sensitive to changes in prey quality, which is unsurprising given that adults have to carry single fish from fishing grounds up to 25 km or more from the colony back to their offspring (Camphuysen 2005). In the Baltic Sea, abundance and size of sprat (*Sprattus sprattus* L.) are correlated negatively, and this has led to a counterintuitive negative relationship between sprat abundance and fledging mass of common guillemot chicks, which here are fed mainly on sprat (Österblom *et al*. 2006). Among multiple-prey loaders, the greater importance of 1 + group sandeels in determining breeding productivity even of species feeding their chicks mainly on 0 group fish, as evidenced by the lagged SBI being selected rather than the same year's value (Table 1), has been suggested previously for kittiwakes (Frederiksen *et al*. 2004b), but not for puffins. The most probable explanation is that the body condition of breeding adults is critical for successful breeding (cf. Pinaud & Weimerskirch 2002), and that body condition reflects the availability of 1 + group sandeels early in the season. Which aspect of prey availability is critical is thus likely to differ among seabird species according to their life history and foraging ecology, and we should expect species to respond in different ways to changes in prey abundance, biomass, age structure, three-dimensional distribution and quality. However, in years when prey quality is extremely low, such as 2004 (see below), all species depending on this prey are likely to suffer.

The long-term increase in the biomass of sandeel larvae (Fig. 3e) is likely to have contributed to the parallel increases in breeding populations of several seabird species in this area (Mitchell *et al*. 2004), although recovery from past human exploitation and persecution may also have been important. However, the failing sandeel recruitment in 2002–04 (ICES 2006) and the widespread food-related seabird breeding failures observed in 2004 (Proffitt 2004) were not consistent with predictions based on sandeel larval biomass. In addition to the long-term increase, sandeel larvae were particularly abundant in spring 2003 (Fig. 3e), and under exclusive bottom-up control we would have expected high sandeel recruitment and a good breeding season in 2004, rather than the widespread failures that occurred. This suggests that a strong 2003 years class of sandeel larvae was severely reduced before the 2004 breeding season. Either bottom-up or top-down mechanisms could have been responsible. Sandeels and sprats in seabird chick diet on the Isle of May were exceptionally small and low in energy value in 2004, due possibly to lack of suitable plankton food (Wanless *et al*. 2005). Copepods are known to show large variation in lipid content (e.g. Miller, Crain & Morgan 2000), and such variation is likely to have strong implications for their nutritional quality for sandeels. Predation from record-high herring stocks (ICES 2004) has also been suggested as a cause of the lack of sandeels (Furness 2004). A combination of bottom-up (lack of food after metamorphosis) and top-down (predation) effects could thus have been responsible for the low recruitment of sandeels and consequent poor breeding productivity of North Sea seabirds in 2004. Simultaneous or alternate operation of bottom-up and top-down mechanisms has been suggested in other marine ecosystems (Hunt *et al*. 2002), with profound implications for ecosystem regulation.

With evidence from previous studies (Beaugrand *et al*. 2002; Edwards & Richardson 2004), our results provide a mechanism for how climate-driven changes in plankton phenology, abundance or species composition can affect top predators in a marine shelf ecosystem, potentially including not only seabirds and marine mammals, but also human fisheries. Understanding this bottom-up control is critical for predicting how important mid-trophic fish, such as sandeels, and the predators that depend on them will be affected by future climate change and other anthropogenic pressures. Under recent scenarios for climate change, sea surface temperatures in the NW North Sea are expected to increase by 1·5–3 °C by the late 21st century (Hulme *et al*. 2002), and ocean currents may also change. This is likely to lead to fundamental changes in the ecosystem, propagating upwards from phytoplankton to higher trophic levels. However, top-down control from changing fish populations, probably related to human fisheries, may also affect ecosystems strongly. The combined effect of the simultaneous pressures of climate change and fisheries is difficult to predict, but there is little doubt that seabirds and other marine top predators will be exposed to dramatic changes in the coming decades.

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