

Regional variation in the impact of climate change: evidence that bottom-up regulation from plankton to seabirds is weak in parts of the Northeast Atlantic

Valentina Lauria^{1,5,*}, Martin J. Attrill², Andrew Brown³, Martin Edwards⁴,
Stephen C. Votier²

¹Marine Biology and Ecology Research Centre, Davy Building, and ²Marine Institute, Plymouth University, Drake Circus, Plymouth PL4 8AA, UK

³Natural England, Touthill Close, City Road, Peterborough PE1 1UA, UK

⁴Sir Alister Hardy Foundation for Ocean Science, The Laboratory, Citadel Hill, Plymouth PL1 2PB, UK

⁵*Present address:* Martin Ryan Institute, Department of Earth and Ocean Sciences, National University of Ireland, Galway, Ireland

ABSTRACT: Climate change has profoundly altered the structure and biodiversity of marine ecosystems worldwide, and for many upper-trophic-level predators changes in lower-trophic-level prey has been the main driver of this alteration. To better understand the nature of marine ecosystem response to global change requires detailed knowledge of predator–prey dynamics, but this is hampered by our poor understanding of spatial variation in the strength of trophic linkages. The aim of this study was to test for bottom-up effects across 4 trophic levels (phytoplankton, zooplankton, fish larvae and seabirds) over 17 yr, as well as testing for regional differences in 3 distinct marine ecosystems of the Northeast Atlantic: the Irish Sea, the Celtic Sea and the English Channel, where sea surface temperature has increased substantially in recent decades. Our results showed little evidence of bottom-up regulation from phytoplankton, zooplankton, fish larvae and seabirds, which is in contrast with the nearby North Sea, probably due to different oceanographic conditions. Despite this, we found a significant positive relationship between kittiwake productivity and the abundance of fish larvae at one colony in the Irish Sea. We speculate that during the period 1991 to 2007 these ecosystems were weakly regulated by climate change, and seabird populations in these regions might be more heavily influenced by other extrinsic factors. The spatial effects of climate change appear to vary across ecosystems, even within a relatively small geographic area. In this context, we urge complex multi-trophic-level studies to elucidate the effect of climate impacts on marine ecosystems.

KEY WORDS: Trophic linkages · Pelagic food web · Seabirds · Regional variability

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INTRODUCTION

Climate change has profoundly altered the structure and biodiversity of marine ecosystems worldwide, influencing ecological processes and consequently spatio-temporal patterns of species dis-

tribution and abundance (Beaugrand et al. 2009, Hoegh-Guldberg & Bruno 2010). These effects are exerted through variation in climate-influenced variables, such as sea surface temperature (SST), wind and currents. The responses are manifest by changes in the productivity of marine ecosystems from phyto-

*Email: valentina.lauria@nuigalway.ie

plankton to the dynamics of fish populations and up to apex predators (Cushing 1982, Frederiksen et al. 2006, Sandvik et al. 2008).

An increase in sea temperature can influence regional vertical stratification and associated nutrient availability (Sathyendranath et al. 2001), which may affect plankton productivity and distribution (Beaugrand et al. 2002, Richardson & Schoeman 2004). Increasing SST has also been shown to directly impact mid-trophic-level fish, in particular affecting their spawning and recruitment during the first year of life (Drinkwater & Myers 1987, Ottersen et al. 2004). Typically, apex predators such as seabirds are more likely to be indirectly affected by increases in SST, manifest via bottom-up regulation, where changes in the availability of key prey (lower trophic levels; Schneider 1990) can have dramatic consequences for demographics (Frederiksen et al. 2006), although there are also examples of climatic conditions having direct effects (Frederiksen et al. 2008).

The response of marine ecosystems to climate change apparently differs at a range of spatio-temporal scales (Richardson & Schoeman 2004, Brander 2010, Overland et al. 2010), but such variation is incompletely understood and inhibits our ability to predict the impacts of change. For example, while there is clear evidence of differences in climate change impacts on marine ecosystems worldwide (Hoegh-Guldberg & Bruno 2010), within the Northeast Atlantic clear spatial heterogeneity in the strength of climate change impacts has been recorded at much smaller scales (200 to 2000 km; McGinty et al. 2011). Moreover, while the importance of spatial variation in climate impacts has been highlighted for plankton (Llope et al. 2012), the extent to which climate change impacts on other trophic levels remains far less well understood (but see Frederiksen et al. 2007).

Beaugrand et al. (2008) suggested that marine ecosystems near critical thermal boundaries are highly vulnerable to changing temperatures, which may lead to abrupt ecosystem shifts across multiple trophic levels. Although regional response to climate change has been shown in the lower and mid-trophic levels (abundance and distribution) in the Northeast Atlantic (Toresen & Østvedt 2000, Beaugrand et al. 2002, Richardson & Schoeman 2004, McGinty et al. 2011), very little is known about the effect of climate change on multiple trophic levels at the regional scale. In the North Sea, a strong bottom-up effect was found across 4 trophic levels, highlighting the key role of juvenile pelagic fish stages (fish larvae) and

their relevance for upper-trophic-level predators such as seabirds (Frederiksen et al. 2006). However, recent work has revealed that in the nearby Celtic Sea, there is only weak evidence of trophic linkages and bottom-up effects influencing seabird demographics (Lauria et al. 2012), underlining the need for more research examining regional variation in response to climate change across multiple trophic levels.

The aims of the present study were 2-fold. First, we tested for trophic linkages across 4 trophic levels from phytoplankton to seabirds in waters of the Northeast Atlantic away from the North Sea, using a different approach to Lauria et al. (2012). Second, we investigated the extent to which these patterns varied among 3 different but adjacent areas off southwest Britain: the Irish Sea, the Celtic Sea and the English Channel. Each of these regions are important for pelagic fishes, mainly Atlantic herring *Clupea harengus* (hereafter herring) and sprat *Sprattus sprattus* (Hogan 2011), while other small pelagic fishes such as lesser sandeel *Ammodytes marinus* (hereafter sandeel) are less common (Trenkel et al. 2005). Furthermore, these productive ecosystems support an internationally important seabird community (Mitchell et al. 2004). We focused on a single seabird species, the black-legged kittiwake *Rissa tridactyla* (hereafter kittiwake), as it is found in all 3 of these areas and, because of their high foraging costs, these birds are highly sensitive to changes in the availability of prey (Frederiksen et al. 2005). Kittiwakes are widely distributed across the British Isles (8% of the world's population breed here; Mitchell et al. 2004), but the UK population declined by 25% between the periods 1985–1988 and 1998–2002 (JNCC 2012). This change in the North Sea is at least partly a response to climate-mediated changes in the availability of small forage fish that are their primary prey (Frederiksen et al. 2007). Frederiksen et al. (2005) showed that regional variation in kittiwake breeding success in the UK was related to variability in sandeel recruitment, but the extent of regional variation across multiple trophic levels is not known.

MATERIALS AND METHODS

Defining the regional ecosystems

Our study area is part of the Northeast Atlantic continental shelf, southwest of the UK (Fig. 1A). The main oceanographic features in this area are

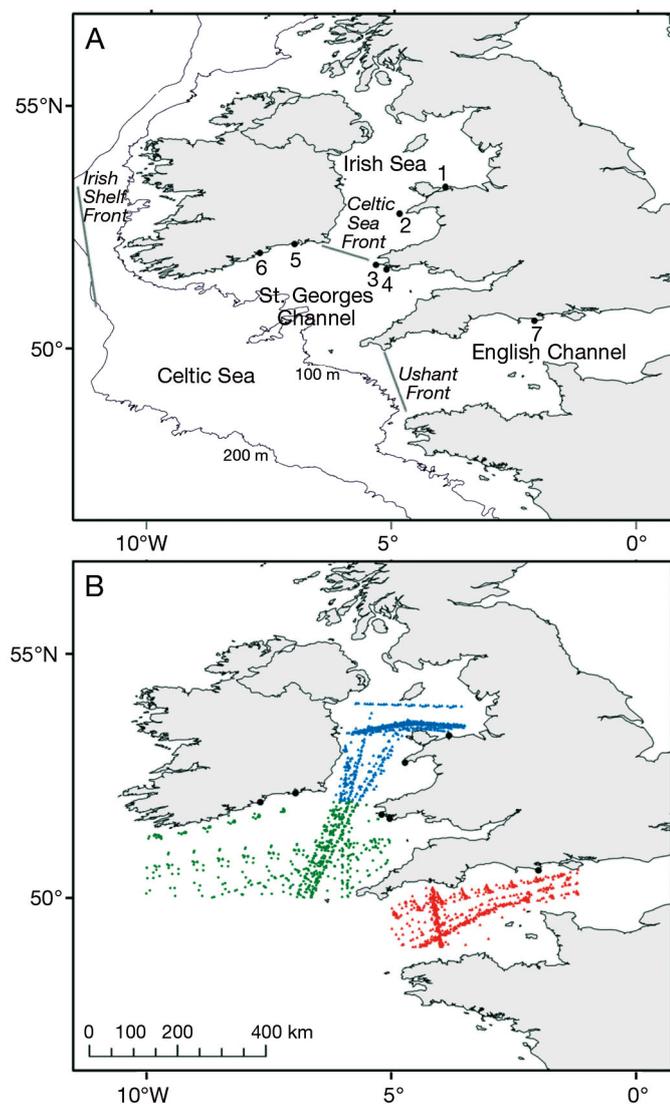


Fig. 1. (A) Study area, including frontal systems (adapted from OSPAR, 2002). The locations of kittiwake *Rissa tri-dactyla* colonies investigated are also presented. 1: Great Ormes Head, 2: Bardsey Island, 3: Skomer Island, 4: Elegug Stacks, 5: Dunmore East, 6: Ram Head, 7: Durlston Head. (B) Continuous Plankton Recorder sample locations (March to June) used for the Irish Sea (blue, 1991 to 2007) the Celtic Sea (green, 1991 to 2007) and the English Channel (red, 1991 to 2004)

persistent frontal systems, such as the year-round Irish Shelf front that occurs to the south and west of Ireland. This front marks the boundary between waters on the shelf (often mixed vertically by tide) and offshore North Atlantic waters. The turbulence caused by the front introduces nutrients from deeper waters to the surface, which fuels a spring phytoplankton bloom, especially diatoms (OSPAR 2002).

This part of the continental shelf can be subdivided into 3 regions: the Irish Sea, Celtic Sea and English Channel. These were identified on the basis of seasonal fronts that tend to develop during spring: the Celtic Sea front (dividing the Celtic Sea from the Irish Sea) and the Ushant front (which develops from the coast of Brittany and extends to the western English Channel, dividing the Celtic Sea from the English Channel; ICES 2007) (Fig. 1A). The Celtic Sea front tends to develop in late spring at the confluence of cooler mixed waters of the Irish Sea and the warmer stratified waters of the Celtic Sea (OSPAR 2002), whereas the Ushant front is a seasonal tidal frontal system (Videau 1987) that separates the vertically mixed waters of the English Channel from the stratified waters of the Celtic Sea in spring (Holligan et al. 1984). Frontal systems are transition zones and are often effective barriers between very different ecosystems and water masses with different physical properties and nutrient availability (Durant et al. 2004). These represent changes associated with nutrient availability from deeper nutrient-rich waters supporting all members of the food web (Durant et al. 2004). Fronts are regions of enhanced plankton production (Holligan 1981), which leads to higher fish production (Mann & Lazier 1996), and consequently act to concentrate prey for apex predators, such as sharks and seabirds (Schneider 1990, Priede & Miller 2009).

Plankton data

The Continuous Plankton Recorder (CPR) survey is a plankton-monitoring programme that has been operated on a routine monthly basis since 1931 (see Richardson et al. 2006). A total of 2145 CPR samples, taken between 1991 and 2007, were used to investigate possible changes in the plankton community in the Irish Sea (52° to 55° N, 7° to 2° W), Celtic Sea (50° to 52° N, 10° to 5° W) and English Channel (49° to 51° N, 10° to 1° W) (Fig. 1B).

Each of these regions is considerably larger than the foraging range of kittiwake (~40 km; Ainley et al. 2003) but considering the need for sufficient numbers of CPR samples and uncertainty in estimates of seabird foraging range, we regarded the spatial scale as suitable. Furthermore, previous studies (e.g. Richardson et al. 2006) suggest that estimates of plankton abundance over larger areas are more robust at avoiding the problems of fine-scale variability in individual plankton samples (e.g. diel vertical migration, weather conditions); these

samples are concentrated or dispersed in patches. The abundance of diatoms and calanoid copepods was determined in each sample and spring means were calculated by averaging across samples taken in the period March to June. This period corresponds to larval metamorphosis of pelagic fish species such as herring and sprat (Russell 1976, ICES 2010). Calanoid copepod biomass was calculated by multiplying the abundance of each copepod species by its average mass estimated from an allometric relationship based on size (Richardson et al. 2006). Diatom abundance was used as a proxy for copepod food availability (Frederiksen et al. 2006), and a positive relationship between copepods and diatoms was assumed to represent a trophic linkage (bottom-up effect).

Fish larvae

Long-term abundance estimates derived from stock assessments (e.g. International Council for the Exploration of the Sea) on small pelagic fish (sandeel, sprat and herring) either do not exist in these regions or were not consistent for all 3 regions (e.g. herring is assessed in the Irish Sea and Celtic Sea, but there is no assessment in the English Channel). For this reason, we used fish larvae estimates of Clupeidae and Ammodytidae derived from the CPR samples.

Herring, sprat and sandeel spawn in winter, and larvae metamorphose into 0-group in spring (Russell 1976, Frederiksen et al. 2006, ICES 2010), so we calculated the mean of fish larval abundance in spring and early summer (March to June). Pelagic fish larvae feed on nauplii and calanoid copepods (Hunter 1980, Arrhenius 1996); however, because information on nauplii abundance was not available, we used both diatom abundance (which is a food proxy for nauplii) and copepod biomass as a proxy for fish larvae food (Frederiksen et al. 2006).

Seabirds

Data on kittiwake numbers and breeding success have been collected from colonies throughout Britain and Ireland since 1986 (Mavor et al. 2003), and reveal that declines have been steepest along the coast bordering the North Sea (by about 50% since the mid-1980s). By contrast, kittiwake populations in Wales seem relatively stable, although there has been a slight decline in recent years (JNCC 2012), whereas in southwest England, kittiwake popula-

tions have declined severely, including the recent abandonment of several colonies (A. Brown et al. unpubl. data). Kittiwake colonies in the British Isles tend to form geographical clusters, with colonies within a cluster sharing a similar pattern of annual fluctuations in breeding success (Furness et al. 1996). This spatial variation indicates that the factors responsible differ between regions (Furness et al. 1996, Frederiksen et al. 2007), suggesting that this species' productivity is likely to respond to climate change-mediated processes (such as changes in food availability) at the regional scale.

We thus extracted data on kittiwake breeding success from the Joint Nature Conservation Committee database (www.jncc.gov.uk/seabirds) for 7 breeding colonies in the southwest of Great Britain (Fig. 1A): 2 in the Irish Sea (Great Ormes Head 53° 20' N, 3° 51' W, mean sample size (number of pairs followed or nests observed) 245; Bardsey Island 52° 72' N, 4° 77' W, mean sample size 165; see Fig. 2C); 4 in the Celtic Sea (Skomer 51° 40' N, 05° 15' W, mean sample size 923; Elegug Stacks 51° 60' N, 04° 98' W, mean sample size 165; Dunmore East 51° 15' N, 06° 99' W, mean sample size 138; Ram Head 51° 15' N, 07° 70' W, mean sample size 420; see Fig. 3C,D); and 1 in the English Channel (Durlston Head 50° 54' N, 02° 02' W, mean sample size 61; see Fig. 4C). To compare variation in productivity among the colonies, data spanning the period from 1991 to 2007 were selected, with the exception of the colony in the English Channel where data after 2004 were not available. Therefore, all of our time series were within the 13 yr minimum required to determine a threshold of food abundance likely to impact on seabird breeding success (Cury et al. 2011). Kittiwakes feed on a range of prey including clupeids, sandeels and gadoids during the breeding season; however, inter-colony and interannual variation in diet is common. For instance, in the Irish Sea, kittiwakes rely mainly on clupeids during the breeding season (Chivers et al. 2012), but North Sea populations feed mainly on sandeels (Furness & Tasker 2000). Current and previous year spring means of pelagic fish larvae were used as proxies for food availability for kittiwakes to test whether availability of fish larvae could explain variation in kittiwake breeding success. Previous studies have shown fish larvae biomass (index calculated from the CPR fish larvae abundance and lengths) to be a reliable indicator of the availability of forage fish for seabirds in the North Sea (Frederiksen et al. 2006); however, in this study we used only fish larvae abundance because fish larvae lengths were not collected.

Environmental data

For each of the 3 regions, we extracted local measures of SST. This spatial scale was preferred over large-scale climate variability indicators (such as the North Atlantic Oscillation Index) because of our interest in regional-scale differences between marine systems (Frederiksen et al. 2004a). Although SSTs have increased throughout the Northeast Atlantic in recent years, marked regional variation is apparent (Edwards et al. 2007). Winter SST (WSST December to March) was used to test for direct effects on plankton (diatom abundance and copepod biomass) and fish larvae abundance. As the recruitment probability for pelagic fish varies with temperature, in particular during their first year of life (Ottersen & Stenseth 2001), annual mean SST with a 1 yr lag (ASST-1) was used as a broad index to test the indirect climate effect on seabirds (kittiwake) via food limitation. Monthly SST data from 1991 to 2007 were derived from satellite images and collated from the PO.DAAC Ocean ESIP Tool (POET) at the Physical Oceanography Distributed Active Archive Center (PO. DAAC) (<http://poet.jpl.nasa.gov>) with a spatial resolution of 0.04° longitude \times 0.04° latitude.

Model construction and statistical analyses

For each region, correlations among explanatory variables were tested before model development (see Tables S1–S3 in the Supplement at www.int-res.com/articles/suppl/m488p011_supp.pdf). This allowed us to test for the potential confounding effect of collinearity (type I errors) between explanatory variables. To investigate the difference between regions, both explanatory and response variables were also tested for correlation (see Table S4 in the Supplement).

We tested successively for possible temporal trends in our data using linear regression. Multiple regres-

sion models were used to identify the main predictors (environmental conditions, food availability) for each of our 4 trophic levels (diatoms, copepods, fish larvae and seabirds). When the dependent variable was not normally distributed, data were $\log_{10}(x)$ transformed. Kittiwake productivity (breeding success) was expressed as the number of fledged chicks per breeding pair per year, weighted by the number of pairs sampled.

Starting from the full model, the most parsimonious model for each trophic level was selected on the basis of the lowest Akaike's information criterion (AIC), corrected for small sample size (AIC_c)—a measure that selects the model with the best balance between bias and precision and avoids problems of, for example, multiple testing and collinearity among explanatory variables. To evaluate the robustness of the significant relationships in the best model, a number of single-variable models were run to examine the effects of explanatory variables in the absence of others. The variables used for the model construction are shown in Table 1.

A set of candidate models was compared using differences in AIC_c between the top-ranked and current model (ΔAIC_c), and by calculating the AIC_c weight (the scaled likelihood that each model is the best description of the data; Burnham & Anderson 2002). Competing models were selected when their AIC_c was within 2 of the lowest, as they were considered to have equivalent support from the data (Burnham & Anderson 2002), and these are presented in Tables S5 and S6 in the Supplement. Model goodness of fit was compared using the deviance and coefficient of determination (R^2). Covariates were considered statistically significant when the p-value was <0.05 . Model residuals were evaluated to check for non-normality, heteroscedasticity and autocorrelation of errors. All modelling was carried out using R version 2.14.1 (R Development Core Team 2011).

Table 1. Response variables and predictors used for the multiple regression models. For each response variable the full model is also given. WSST: winter sea surface temperature; ASST-1: 1 yr lagged annual sea surface temperature; kittiwake BS: breeding success expressed as the number of fledged chicks per breeding pair per year, weighted for sample size; fish larvae/fish larvae lag: current/previous year spring means of pelagic fish larval abundance

Response variable	Climate effect	Food availability	Full model
Diatom abundance	WSST	–	Diatom ~ WSST + year
Copepod biomass	WSST	Diatom	Copepods ~ WSST + diatom + year
Fish larval abundance	WSST	Diatom; copepods	Fish larvae ~ WSST + diatom + copepods + year
Kittiwake BS	ASST-1	Fish larvae; fish larvae lag	Kittiwake ~ ASST-1 + fish larvae + larvae lag + year

RESULTS

Correlation between covariates

Preliminary explanatory analyses for each region showed evidence of covariation in environmental conditions, with WSST and ASST co-varying by region and increasing significantly over time (Tables S1–S4 in the Supplement).

Environmental variables

WSST and ASST (Figs. 2A, 3A and 4A) increased significantly over time in all the regions (Irish Sea WSST: $p < 0.001$, slope = 0.095 ± 0.022 [SE]; ASST: $p < 0.001$, slope = 0.077 ± 0.014 ; Celtic Sea WSST: $p = 0.004$, slope = 0.059 ± 0.017 ; ASST: $p < 0.001$, slope = 0.070 ± 0.012 ; English Channel WSST: $p < 0.02$, slope = 0.075 ± 0.028 ; ASST: $p < 0.001$, slope = 0.073 ± 0.016). The Irish Sea waters were cooler than the other 2 regions with a mean temperature of 7.99°C for WSST and an ASST of 10.97°C . In contrast, the Celtic Sea and English Channel SST averages were similar (Celtic Sea: 9.86°C WSST and 12.61°C ASST; English Channel 9.72°C WSST and 12.63°C ASST).

Phytoplankton

Diatom abundance fluctuated over time in all regions, with no clear linear trend (Figs. 2B, 3B & 4B). SST did not explain diatom variability in any of the regions. Our most parsimonious model included the intercept only for the Irish Sea and English Channel (Table 2); for the Celtic Sea, the best model selected for diatom abundance included only year, although this was not statistically significant ($p = 0.09$).

Zooplankton

Copepod biomass fluctuated over time in all 3 regions, with no

clear linear trend (Figs. 2B, 3B & 4B). In the Irish Sea, our most parsimonious model explaining changes in copepod biomass included diatom abundance, although this was not statistically significant (Table 2). In the Celtic Sea and English Channel, our most parsimonious model included the intercept only (Table 2).

Fish larvae

Fish larval abundance fluctuated over time, with no clear linear trend (Figs. 2B, 3B & 4B). Neither WSST nor diatom abundance nor copepod biomass explained a significant amount of the variation in fish larval abundance in the Irish Sea (Table 2). In the Celtic Sea, the best-supported model included diatom abundance, although this relationship was not statistically significant ($p = 0.09$) (Table 2). In the English Channel, variation in fish larval abundance was best explained by a weak positive relationship

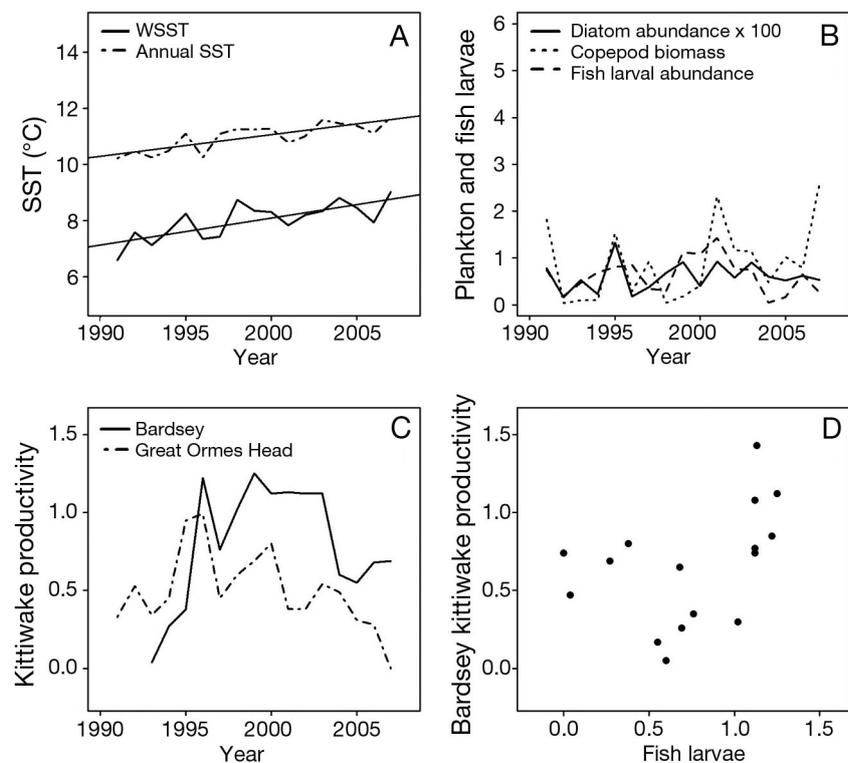


Fig. 2. Variables used for Irish Sea model construction. (A) Sea surface temperature (SST, $^\circ\text{C}$): WSST: winter sea surface temperature. (B) Plankton and fish larvae: diatom abundance (cell count m^{-3} of filtered water), copepod biomass (mg wet weight m^{-3} of filtered water), and fish larval abundance. (C) Black-legged kittiwake productivity (number of fledged chicks per breeding pair, weighted for sample size). (D) Correlation between kittiwake productivity at Bardsey and fish larvae abundance in the Irish Sea. A straight line indicates presence of temporal trends

with diatom abundance ($p = 0.04$, slope = $0.395 \times 10^{-7} \pm 0.171 \times 10^{-7}$; Table 2).

Seabirds

In the Irish Sea, kittiwake productivity at Bardsey (mean 0.80 ± 0.38 , range 0 to 1.25) was significantly positively correlated with fish larvae ($p = 0.02$) and year ($p = 0.02$), whereas at Great Ormes Head (mean 0.51 ± 0.26 , range 0 to 0.99), the most parsimonious model included the intercept only (Table 2).

In the Celtic Sea, variation in kittiwake productivity at Skomer (mean 0.68 ± 0.23 , range 0.21 to 1.01), Elegug Stack (mean 0.25 ± 0.24 , range 0 to 0.82) and Ram Head (mean 0.44 ± 0.27 , range 0.05 to 0.93) was not explained by any of our covariates (Table 2). Kittiwake productivity at Dunmore East (mean 0.73 ± 0.23 , range 0.41 to 1.09) increased over time ($p = 0.012$, slope = 0.026 ± 0.009), but was not significantly correlated with any covariates (Table 2).

In the English Channel, variation in kittiwake productivity at Durlston Head (mean 0.70 ± 0.32 , range 0.18 to 1.29) was not explained by our covariates (Table 2).

DISCUSSION

Our study showed little evidence of bottom-up regulation in 3 different Northeast Atlantic ecosystems over a 17 yr period. Moreover, there was little evidence for strong regional differences in the nature of these links across 3 regions in the Northeast Atlantic (Irish Sea, Celtic Sea and English Channel), although there was a significant positive correlation between kittiwake breeding success and fish larval abundance at one Irish Sea colony (Bardsey), as well as a sig-

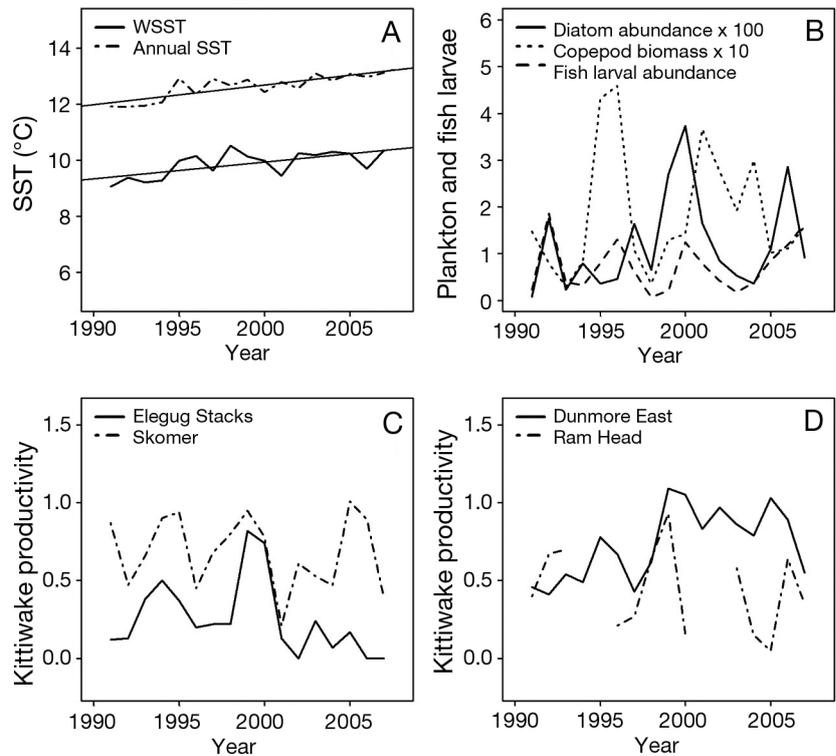


Fig. 3. Variables used for Celtic Sea model construction. (A) Sea surface temperature (SST, °C): WSST: winter sea surface temperature. (B) Plankton and fish larvae: diatom abundance (cell count), copepod biomass (mg wet weight), and fish larval abundance. (C,D) Black-legged kittiwake productivity (number of fledged chicks per breeding pair, weighted for sample size). A straight line indicates presence of temporal trends

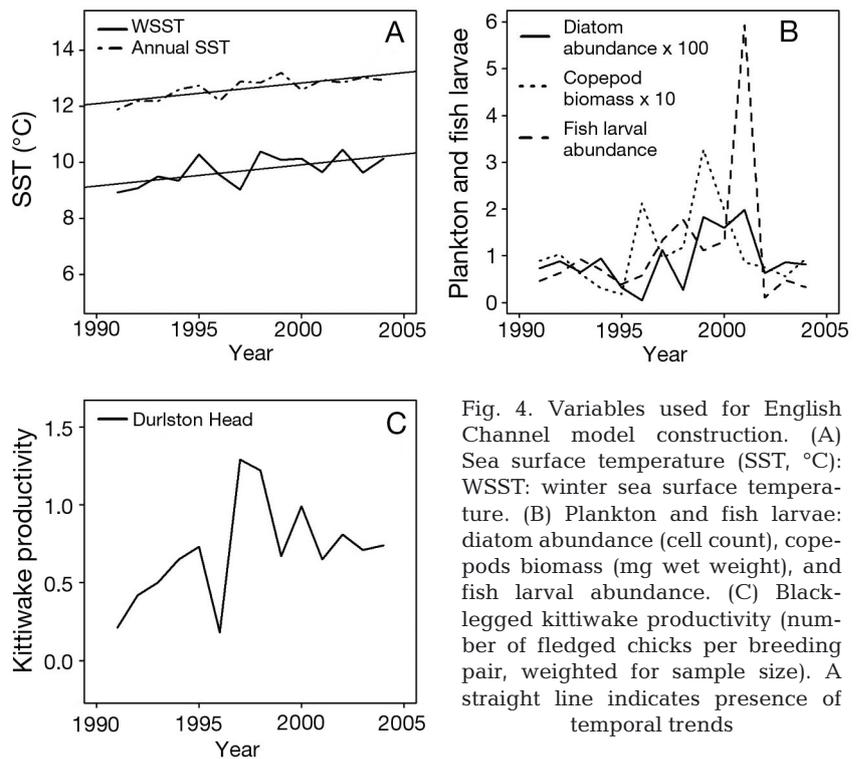


Fig. 4. Variables used for English Channel model construction. (A) Sea surface temperature (SST, °C): WSST: winter sea surface temperature. (B) Plankton and fish larvae: diatom abundance (cell count), copepods biomass (mg wet weight), and fish larval abundance. (C) Black-legged kittiwake productivity (number of fledged chicks per breeding pair, weighted for sample size). A straight line indicates presence of temporal trends

nificant relationship between fish larvae and diatom abundance in the English Channel. The possible implications of these findings for our

understanding of trophic regulatory mechanisms, particularly in light of changing climate, are discussed below.

Table 2. Model selection to estimate factors influencing each trophic level for the 3 regions. Only the best supported models are shown. AIC_c weight: corrected Akaike's information criterion weights, values range from 0 to 1, high values indicating strong support for a given predictor; R²: adjusted coefficient. Significant relationships are highlighted in **bold**; variables that are not statistically significant but feature in the best model are also presented

Model selected	AIC _c weight	N (years)	Deviance	R ²	p-value	Slope (±SE)
IRISH SEA						
PRIMARY PRODUCERS						
Diatom abundance						
Intercept only	0.47	17	1.04		<0.001	4.717 (±0.06)
PRIMARY CONSUMERS						
Copepod biomass						
Diatom	0.31	17	8.14	0.16	0.062	0.121 10 ⁻⁶ (±6.05 10 ⁻⁶)
Fish larval abundance						
Intercept only	0.26	17	2.29		<0.001	0.626 (±0.091)
APEX PREDATORS						
Kittiwake productivity						
Bardsey						
Fish larvae + year	0.28	16	1.39	0.38	Fish larvae: 0.022 Year: 0.018	0.604 (±0.233) 0.048 (±0.017)
Great Ormes Head						
Intercept only	0.20	17	1.00		<0.001	0.500 (±0.060)
CELTIC SEA						
PRIMARY PRODUCERS						
Diatom abundance						
Year	0.42	17	2.45	0.12	0.098	0.035 (±0.020)
PRIMARY CONSUMERS						
Copepod biomass						
Intercept only	0.44	17	1.83		<0.001	1.115 (±0.082)
Fish larval abundance						
Diatom	0.29	17	3.93	0.12	0.97	0.526 (±0.297)
APEX PREDATORS						
Kittiwake productivity						
Skomer						
Intercept only	0.24	17	0.88		<0.001	0.682 (±0.056)
Elegug Stacks						
Intercept only	0.20	17	0.096		<0.001	0.091 (±0.018)
Dunmore East						
Fish larvae lag + year	0.38	17	0.434	0.41	Fish larvae lag: 0.07 Year: 0.008	-0.172 (±0.089) 0.026 (±0.008)
Ram Head						
Intercept only	0.35	13	0.860		<0.001	0.442 (±0.074)
ENGLISH CHANNEL						
PRIMARY PRODUCERS						
Diatom abundance						
Intercept only	0.59	14	2.18	0.12	<0.001	4.834 (±0.109)
PRIMARY CONSUMERS						
Copepod biomass						
Intercept only	0.48	14	1.38		<0.001	0.942 (±0.087)
Fish larval abundance						
Diatom	0.43	14	1.48	0.25	0.004	0.395 10 ⁻⁷ (±0.171 10 ⁻⁷)
APEX PREDATORS						
Kittiwake productivity						
Durlston Head						
Intercept only	0.28	14	1.35		<0.001	0.697 (±0.086)

Regional variation in the impacts of climate change on plankton and fish

Richardson & Schoeman (2004) showed an increase in phytoplankton abundance between 1958 and 2002 in the cooler regions of the Northeast Atlantic (north of 55°N) and a decrease in warmer regions (south of 50°N) in response to an increase in mean ASST, related to differences in vertical mixing and nutrient availability. In the North Sea, phytoplankton biomass increased during the mid-1980s in response to increasing SST (Beaugrand & Reid 2003). In contrast, we found no relationship between diatom abundance in the Irish Sea, Celtic Sea or English Channel (Figs. 2B, 3B and 4B) and SST over our more recent and shorter timeframe. This weak linkage between primary producers and water temperature may be linked to different oceanographic conditions (i.e. water vertical mixing). For example, over the study period, diatom abundance did not increase in the Irish Sea and western English Channel waters, which are mixed during the summer (Holligan et al. 1984, OSPAR 2002), whereas diatom abundance increased significantly in the Celtic Sea, which tends to be stratified (OSPAR 2002) (Fig. 3B). Alternatively, the shorter timeframe of our study may be outside a period of major change.

We found that zooplankton (calanoid copepods) biomass in our study area was not strongly influenced by WSST (Table 2). This contrasts with the North Sea where pseudo-temperate calanoid copepod abundance (e.g. *Calanus helgolandicus*) is positively correlated with SST (Beaugrand et al. 2002). The lack of a strong climate signal in our study areas (Table 2) suggests that there was little change over the period 1991 to 2007; it may be that longer time-series data sets (over 4 decades) are necessary to detect climate impacts on plankton (Beaugrand et al. 2009). Alternatively, these ecosystems (Irish Sea, Celtic Sea and English Channel) are not at critical thermal boundaries, unlike other regions in the Northeast Atlantic such as the North Sea (Beaugrand et al. 2008). If this is indeed the case, it suggests a greater resilience to the deleterious impacts of climate change in waters off southwestern Britain. Despite strong regional differences in the responses of zooplankton to changes in SST across the Northeast Atlantic (Llope et al. 2012, McGinty et al. 2011), we found no evidence of such variation at this much smaller scale.

In our 3 marine systems, the abundance of fish larvae showed marked interannual variability during 1991 to 2007, but this variability was not corre-

lated with changes in WSST (Table 2). In the North Sea, changing water temperatures are strongly linked with changes in the biology of fish, such as sandeel *Ammodytes marinus* recruitment (Arnott & Ruxton 2002). This absence of a climate signal in our systems may relate to the rather short duration of our study (17 yr), although Arnott & Ruxton (2002) were able to detect a climatic effect during the 16 yr period (1983 to 1999). An alternative explanation for our findings may be that juvenile fish abundance in these regions is influenced by other ecological mechanisms, such as the effect of changing frontal systems on primary production, which consequently affect foraging and distribution of fish (Olson 2002). A more detailed analysis is needed to better understand how extrinsic and intrinsic factors influence fish populations in the Celtic Sea, including testing for the impacts on depth distribution (Dulvy et al. 2008).

Regional patterns and trophic coupling across 4 trophic levels

Recent work has shown marked spatial variation in the nature of top-down or bottom-up regulation between primary producers and consumers in marine systems (Shurin et al. 2002, Borer et al. 2005, Llope et al. 2012). During the period 1991 to 2007 in the Irish Sea, Celtic Sea and English Channel, we found little evidence to suggest strong linkages across 4 trophic levels in terms of food availability (Table 2). At low trophic levels, some regional differences emerged. We found trophic coupling between fish larvae and diatom abundance in the English Channel, but no significant relationship between these lower trophic levels in the Irish Sea and Celtic Sea.

At the highest trophic level, our results showed that, at 6 colonies in the Celtic Sea and English Channel, kittiwake breeding success was not influenced by our measure of food availability (CPR-derived fish larval abundance; Table 2), yet there was a significant positive relationship at 1 colony in the Irish Sea (Bardsey; Table 2). While it is possible that fish larvae from CPR samples may not be an accurate reflection of kittiwake food availability, previous research in the North Sea suggests that this is not the case (Frederiksen et al. 2004, 2006). Therefore, the lack of a relationship between kittiwake productivity and our index of prey availability in parts of the Irish Sea, Celtic Sea and English Channel suggests other ecological mechanisms such as predation (Votier et al. 2008b), competition with fisheries

(Frederiksen et al. 2004a) or direct weather effects (Frederiksen et al. 2008) may be driving the strong interannual variation observed in kittiwake breeding success.

Frederiksen et al. (2005) suggested that patchiness and non-synchronous dynamics in prey populations, in response to spatio-temporal variation in the physical environment, would lead to regional variation in kittiwake breeding success. However, the scale of these impacts is poorly known. Within regions, changes in prey availability or disturbance effects (e.g. density dependence, predation) could have differential impacts on population dynamics. Our results showed that kittiwake productivity in 2 neighbouring colonies in the Irish Sea (Bardsey and Great Ormes Head) apparently responded differently to changes in our index of prey availability (Table 2). In particular, it seemed that the recent decline at Great Ormes Head was not influenced by changes in fish larval abundance, suggesting that either there is no bottom-up effect or this food proxy is not suitable to explain the variation of kittiwake productivity in this colony. The latter option seems unlikely given that this proxy generated a signal at nearby Bardsey. Furthermore, the Celtic Sea colonies showed similar trends, which were seemingly not explained by resource limitations, suggesting that, in this case, the local-scale factors influencing kittiwake productivity might be similar. We previously suggested that kittiwake productivity at Skomer is not influenced by changes in food availability (herring 0- and 1-group) (Lauria et al. 2012), which is consistent with the results of the current study. Regional studies across multiple trophic levels may constitute a valuable approach in informing seabird conservation policy and more research should focus on this type of multi-trophic-level research.

CONCLUSIONS

This study enhances our understanding of the range of variation in the nature and strength of trophic-coupling mechanisms in the Northeast Atlantic during a period of intense warming. Detailed knowledge to date has concerned the North Sea (where some strong effects have been observed), but our study has significantly extended our understanding of trophic coupling in other sea areas, where the effects appear much less readily discernible. It focuses, in particular, on kittiwake—a widespread and abundant seabird species, which the UK supports in internationally important numbers. In the North

Atlantic, changes in oceanographic conditions are expected to have large impacts on high-latitude ecosystems (Hátún et al. 2005). Recent large-scale studies over 4 decades (Hátún et al. 2009) have shown that important changes in the lower trophic levels of marine ecosystems in the Northeast Atlantic are strongly associated with regime shifts that can have knock-up effects in abundance or productivity of apex predators (Irons et al. 2008, Hátún et al. 2009). Other studies, at smaller scales, have suggested a negative impact of climate change on seabirds in the Northeast Atlantic (Votier et al. 2005, 2008a, Riou et al. 2011) and, in particular, the North Sea (Aebischer et al. 1990, Frederiksen et al. 2006).

The apparent lack of strong bottom-up effects in the Irish Sea, Celtic Sea and English Channel pelagic food webs, as detected in our study, is consistent with the recent findings of a study of the demographics of 4 seabird species in a single colony (Lauria et al. 2012), but in contrast with evidence of bottom-up regulation in the North Sea (Frederiksen et al. 2006). Our study thus draws attention to considerable spatial variation, and highlights the importance of spatial differences in the effects of climate change (i.e. McGinty et al. 2011). In contrast, we found no evidence of variation at small regional scales (McGinty et al. 2011).

While some regions in the North Atlantic (i.e. North Sea) seem to be more vulnerable to climate change and a clear 'regime shift' has been observed (Beaugrand et al. 2008), this effect appears to be rather weak elsewhere (i.e. Celtic Sea; Henderson 2007, Beaugrand et al. 2009, Lauria et al. 2012). We cannot completely exclude the role of bottom-up regulation because of the time scale involved (17 yr), although recent work suggests that a minimum of 13 yr is required to detect changes in seabird breeding success as a function of changes in prey abundance (Cury et al. 2011). However, it is clear that further investigations are required to understand changes in the demographics of top predators taking account of other potential confounding effects, such as those relating to the direct effects of climate (Frederiksen et al. 2008) and the complex impacts of fisheries (Frederiksen et al. 2004a).

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