



# Phenological trends and trophic mismatch across multiple levels of a North Sea pelagic food web

Sarah Burthe<sup>1,\*</sup>, Francis Daunt<sup>1</sup>, Adam Butler<sup>2</sup>, David A. Elston<sup>3</sup>,  
Morten Frederiksen<sup>1,4</sup>, David Johns<sup>5</sup>, Mark Newell<sup>1</sup>, Stephen J. Thackeray<sup>6</sup>,  
Sarah Wanless<sup>1</sup>

<sup>1</sup>Centre for Ecology & Hydrology, Bush Estate, Penicuik, Midlothian EH26 0QB, UK

<sup>2</sup>Biomathematics and Statistics Scotland, The Kings Buildings, Edinburgh EH9 3JZ, UK

<sup>3</sup>Biomathematics and Statistics Scotland, Craigiebuckler, Aberdeen AB15 8QH, UK

<sup>4</sup>Dept. of Bioscience, Aarhus University, Frederiksborgvej 399, 4000 Roskilde, Denmark

<sup>5</sup>Sir Alister Hardy Foundation for Ocean Science, The Laboratory, Citadel Hill, Plymouth PL1 2PB, UK

<sup>6</sup>Centre for Ecology & Hydrology, Lancaster Environment Centre, Bailrigg, Lancaster LA1 4AP, UK

**ABSTRACT:** Differential phenological responses to climate among species are predicted to disrupt trophic interactions, but datasets to evaluate this are scarce. We compared phenological trends for species from 4 levels of a North Sea food web over 24 yr when sea surface temperature (SST) increased significantly. We found little consistency in phenological trends between adjacent trophic levels, no significant relationships with SST, and no significant pairwise correlations between predator and prey phenologies, suggesting that trophic mismatching is occurring. Finer resolution data on timing of peak energy demand (mid-chick-rearing) for 5 seabird species at a major North Sea colony were compared to modelled daily changes in length of 0-group (young of the year) lesser sandeels *Ammodytes marinus*. The date at which sandeels reached a given threshold length became significantly later during the study. Although the phenology of all the species except shags also became later, these changes were insufficient to keep pace with sandeel length, and thus mean length (and energy value) of 0-group sandeels at mid-chick-rearing showed net declines. The magnitude of declines in energy value varied among the seabirds, being more marked in species showing no phenological response (shag, 4.80 kJ) and in later breeding species feeding on larger sandeels (kittiwake, 2.46 kJ) where, due to the relationship between sandeel length and energy value being non-linear, small reductions in length result in relatively large reductions in energy. However, despite the decline in energy value of 0-group sandeels during chick-rearing, there was no evidence of any adverse effect on breeding success for any of the seabird species. Trophic mismatch appears to be prevalent within the North Sea pelagic food web, suggesting that ecosystem functioning may be disrupted.

**KEY WORDS:** Timing of breeding · Climate change · Prey size · *Ammodytes marinus* · Winter NAO · Long-term studies · Zooplankton · Phytoplankton

Resale or republication not permitted without written consent of the publisher

## INTRODUCTION

Phenology (the timing of seasonally recurring biological events) plays a crucial role in linking organisms to their biotic and abiotic environments (Forrest & Miller-Rushing 2010). Recent climate warming has

significantly altered the phenology of a wide range of taxa across ecosystems (Thackeray et al. 2010), but responses frequently vary among species, potentially disrupting the synchronisation of key ecological interactions (Visser & Both 2005). In particular, failure of a predator to overlap the period of peak resource de-

\*Email: sburthe@ceh.ac.uk

mand (typically breeding) with peak prey availability may lead to 'trophic mismatch,' and such decoupling may alter food web structure and ecosystems (Cushing 1990, Edwards & Richardson 2004). A recent review found that trophic mismatch was widespread, with predator phenology shifting too little or too much in response to that of prey (Visser & Both 2005).

Marine systems are vulnerable to trophic mismatch because they exhibit highly seasonal pulses of primary productivity upon which the fitness of higher trophic levels depends (Cushing 1990). Studies across multiple trophic levels are rare, mainly because phenological data at the appropriate temporal and spatial resolution are lacking. Most studies have investigated single species responses and are unable to explicitly test for mismatch (Leggett & DeBlois 1994). Studies have also compared phenology of a focal consumer with climate data such as sea-surface temperature (SST; e.g. Durant et al. 2003, Frederiksen et al. 2004a, Shultz et al. 2009) that may indicate variation in prey availability, including phenology, or be used as a cue by predators to predict key phenological events in their prey (Frederiksen et al. 2004a, Moe et al. 2009). Several studies have suggested that mismatch may be an important determinant of fitness in seabirds (e.g. Durant et al. 2006, Hipfner 2008, Watanuki et al. 2009).

Here we examine phenological changes across 4 trophic levels of a pelagic food web in the north-western North Sea from 1983 through 2006. This system has a 'wasp-waist' structure (Cury et al. 2000), with high species richness at upper and lower trophic levels but markedly lower richness at the mid-trophic position linking secondary producers (zooplankton) and top predators (mammals, fish and birds). Lesser sandeel *Ammodytes marinus* occupies this key mid-trophic position (Daan et al. 1990). Over the study period there have been significant hydro-biological changes and increased sea temperatures in this area (Edwards et al. 2002). A major ecosystem regime shift occurred in the late 1980s (Beaugrand 2004), and there have been profound changes in plankton communities (Edwards et al. 2002) and fish distributions (Perry et al. 2005). Previous studies in this area have investigated phenological changes in species from primary producers to top predators and found contrasting pat-

terns suggestive of trophic mismatch (Edwards & Richardson 2004, Wanless et al. 2009, Frederiksen et al. 2011). However, none have adopted an integrated approach and compared multiple trophic levels within the same area over the same time period. A major aim of our study was to use a standardised approach to quantify changes in the timing of key events for species or taxonomic groups across all 4 trophic levels (Fig. 1a). Disparity in phenological trends would be indicative of trophic mismatch in the system. We also assessed whether phenology was related to climate variables (SST and winter North Atlantic Oscillation, wNAO) and if climate responses

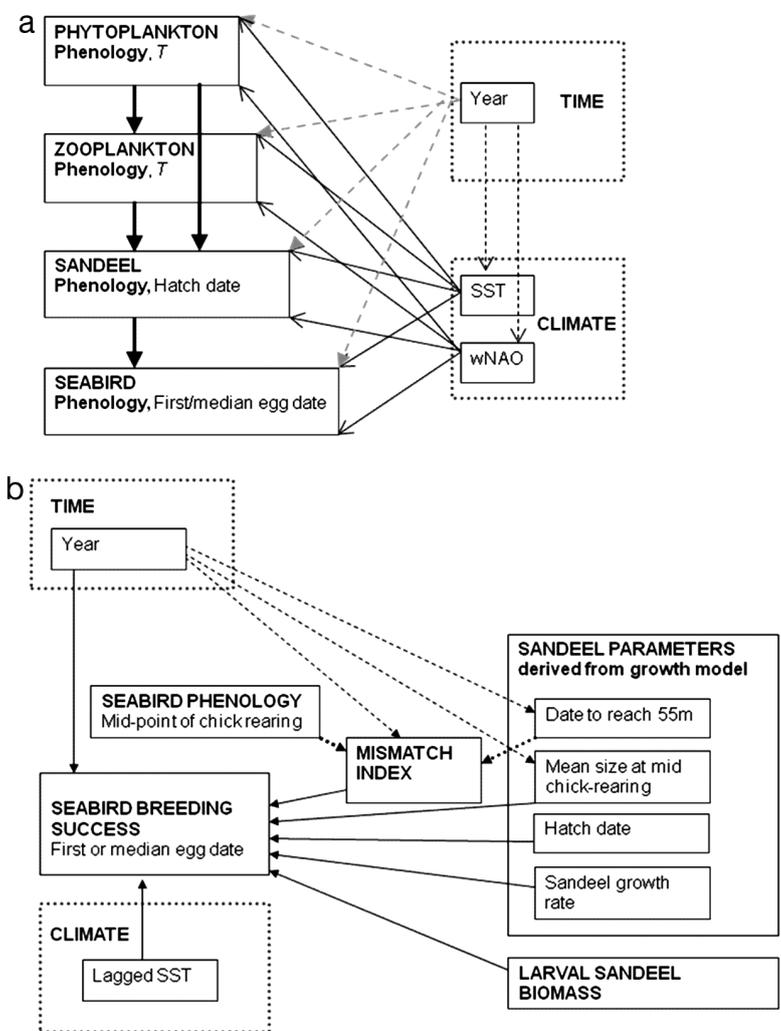


Fig. 1. Schematic illustration of the different stages of analysis undertaken: (a) analyses of the 4 trophic levels to examine trends in phenology; trends between phenology and climate, and relationships between phenologies of adjacent trophic levels; (b) detailed analyses of the seabird and sandeel data to examine phenological trends and the impact of mismatch on breeding success. SST: sea surface temperature; wNAO: winter North Atlantic Oscillation;  $T$ : month (day of year) of central tendency

were similar in terms of their magnitude and direction across the different trophic levels.

To investigate in more detail how the relative timing of trophically linked events have changed over time, we focussed on 5 seabird species and their major sandeel prey (Furness & Tasker 2000, Daunt et al. 2008). Although trophic mismatch theory is most often applied to the timing of peak prey abundance, prey size is a key component and is known to be important for seabirds in our study area (Wanless et al. 2005). We therefore compared modelled annual length-at-date of 0-group sandeels (Frederiksen et al. 2011; sandeel hatched in the current year) with the timing of peak energy demand in each seabird species, which we assumed corresponded to the mid-chick-rearing period (Drent & Daan 1980) (Fig. 1b). Under this modified version of the mismatch hypothesis our prediction was that mid-chick-rearing should coincide with sandeels having attained a threshold size, since individuals are expected to balance increasing prey quality through the season with the fitness advantages of breeding as early as possible (Daunt et al. 2007, Harris et al. 2007). We assessed whether the timing of chick-rearing had become decoupled from seasonal changes in sandeel length, and estimated mean size of fish at mid-chick-rearing to quantify the consequences of mismatch on prey energy value. Finally, we used the mismatch index to explore the fitness consequences of mismatching on seabird breeding success.

## MATERIALS AND METHODS

### Climate

Monthly average SST data were obtained from NOAA Pathfinder Version 5.0 (Kilpatrick et al. 2001) for an area of the North Sea (55 to 58°N, 3°W to 0°E) between 1983 and 2006. Since spring events were our main interest for comparison across the trophic levels we focussed SST analysis on February and March values (hereafter winter/spring SST). June and July (hereafter summer SST) values were also modelled with seabird breeding phenology as this period overlapped with mid-chick-rearing. As large-scale seasonal measures of climate have been found to be useful predictors of ecological processes (Hallett et al. 2004) and as 4 of the 5 seabird species being considered may be distributed outside the western North Sea during winter, we also considered wNAO indices ([www.cgd.ucar.edu/cas/jhurrell/indices.html](http://www.cgd.ucar.edu/cas/jhurrell/indices.html)) for the winter prior to spring phenology events.

### Phenology data

Phenology data were available across all trophic levels between 1983 and 2006, and analyses were thus restricted to this period.

Phytoplankton (primary producers) and zooplankton (primary consumers)

The continuous plankton recorder (CPR) survey is an upper layer plankton monitoring programme (Richardson et al. 2006). We analysed a subset of plankton data that are important in the diet of sandeels *Ammodytes marinus*. Phytoplankton and copepod nauplii are the main prey of larval sandeels (Monteleone & Peterson 1986), while older stages of calanoid copepods (particularly *Temora* spp. and *Calanus* spp.) are important for postlarval stages, <10 cm in length (Macer 1966). Accordingly, we focussed on spring-peaking copepod species (sandeel hatch date occurred mainly in February to March) and analysed data for *C. helgolandicus*, *C. finmarchicus*, *T. longicornis*, *Calanus* spp. Stages I to IV, and copepod nauplii. *Calanus* spp. nauplii feed preferentially on diatoms (Soreide et al. 2008). As there was no evidence that particular diatom species were important for copepods, we analysed the total summed monthly abundances of the 10 most abundant diatoms in spring (individual species data are presented in Table S1 of the supplement at [www.int-res.com/articles/suppl/m454p119\\_supp.pdf](http://www.int-res.com/articles/suppl/m454p119_supp.pdf)) and a colour index of phytoplankton. Data were obtained from an area of the North Sea (55 to 58°N, 3°W to 0°E; Johns 2009) that provided a balance between sampling resolution and proximity to the Isle of May, Scotland (56° 11' N, 2° 33' W), the focal point of seabird observations.

For plankton, the phenology measure was the month of central tendency,  $T$ , (see Edwards & Richardson 2004) converted to day of year for comparison with other taxa. The average monthly abundances over the 24 yr period for each species were used to determine whether the seasonal pattern was unimodal or bimodal (spring and autumn). For unimodal taxa,  $T$  was calculated using data from the entire year, whereas, for bimodal taxa, it was calculated using data from the first 6 mo of the year (see Edwards & Richardson 2004). Due to missing monthly values for all species of plankton in 1995, this year was omitted from plankton phenology analyses.

### Sandeels (secondary consumers)

Estimates of sandeel phenology (hatch dates) were obtained from a statistical model implemented using Markov Chain Monte Carlo procedures that combined 2 time series of sandeel size at date data, i.e. from larval fish captured during CPR surveys and 0-group fish obtained from foraging puffins (see Frederiksen et al. 2011 for full details).

### Seabird predators

Analysis focussed on 5 species of seabirds for which 0-group sandeels are an important dietary component for adults and/or chicks on the Isle of May (Daunt et al. 2008): common guillemot *Uria aalge* (hereafter guillemot), razorbill *Alca torda*, European shag *Phalacrocorax aristotelis* (hereafter shag), black-legged kittiwake *Rissa tridactyla* (hereafter kittiwake) and Atlantic puffin *Fratercula arctica* (hereafter puffin). Median egg dates were recorded in guillemots and razorbills from daily checks of monitoring plots (mean of ca. 800 and ca. 100 breeding sites, respectively). For shags, annual median ringing dates of chicks were analysed (mean ca. 800 chicks ringed mid-way through the chick-rearing period at a mean age of 20 to 25 d) since median laying dates (estimated from weekly checks of ca. 100 pairs) were only available for a subset of years and were strongly correlated with median egg date ( $r = 0.94$ ,  $df = 20$ ,  $p < 0.001$ ). Kittiwake first egg dates were analysed (from daily checks of the whole colony of >3000 pairs) as median egg dates were only recorded in a subset of years (from 5 d checks of ca. 200 pairs; correlation between first and median:  $r = 0.90$ ,  $df = 8$ ,  $p < 0.001$ ). First egg dates were also analysed for puffins, back-calculated from daily checks of the entire colony for adults bringing fish back to chicks (>10 000 pairs; see Wanless et al. 2009 for details) since median egg dates (based on back-calculation from wing and bill measurements of chicks from a mean of ca. 30 individuals; see Harris & Wanless 2011 for details) were only available for a subset of years (correlation between first and median:  $r = 0.61$ ,  $df = 13$ ,  $p = 0.015$ ). Even though first egg dates are likely to be subject to a higher level of stochastic variation than median egg dates (Wanless et al. 2009), they were assumed to be reliable indicators of the timing of breeding for kittiwakes and puffins because of the correlation with median egg dates in the subset of years where both were recorded.

### Phenological regressions

Standard linear regressions with year were used to investigate temporal trends in SST, wNAO and phenology of trophic levels. In order to avoid false detection of significant correlations due to multiple testing, we applied the Benjamini & Hochberg (1995) correction factor to this set of models. In all cases we report the uncorrected p-values. Phenology data for sandeel hatch date showed evidence of a break-point (Frederiksen et al. 2011), and were therefore analysed using a piecewise regression model employing the segmented package in R (Muggeo 2008). In order to assess whether the phenologies of consumers and their prey covaried over time, we examined whether there were pairwise correlations between phenologies of taxa across successive trophic levels. We investigated whether phenology was correlated with climate by regressing the phenology of each species against SST or wNAO. We analysed trends using simple linear regression, without taking temporal autocorrelation into account, and thus assume that consecutive years are independent. Autocorrelation plots of model residuals were examined and, in general, showed no apparent evidence of autocorrelation, suggesting that the assumption of independence was reasonable. There was only 1 case (linear regression of kittiwake first egg phenology and wNAO) in which the regression coefficient was significant and the model residuals showed evidence of autocorrelation.

### Trophic mismatch in seabirds and sandeels

To evaluate phenological mismatch in greater detail we focussed on interactions between seabirds and 0-group sandeels, since, not only was the temporal resolution of these data markedly better than for lower trophic levels, but information on other aspects of performance such as sandeel growth rates and seabird breeding success was also available. We focussed on the peak period of energy demand for the seabirds, i.e. the mid-point of the chick-rearing period (Drent & Daan 1980). For shags this was estimated directly from median chick ringing date as this occurs midway through the chick-rearing period. For guillemots and razorbills we used the species- and year-specific median laying date plus the average incubation period plus the average chick-rearing period/2, while for kittiwakes and puffins we used first egg date plus average difference between first and median egg dates plus average incubation period plus the average chick-rearing period/2. Val-

ues for incubation and fledging periods were obtained from Cramp & Simmons (1978, 1983). The average difference between first and median egg dates was 11 d for kittiwake (range: 6 to 18 d,  $n = 10$ ) and 12 d for puffin (range: 6 to 17 d,  $n = 15$ ).

The sandeel model (Frederiksen et al. 2011) estimated mean hatch dates and growth rates, from which daily size of juvenile sandeels was then estimated. We compared relationships between the timing of mid-chick-rearing in seabirds and 2 phenological metrics for sandeels: hatch dates and the date each year that 0-group sandeels reached a predicted mean threshold length of 55 mm. This was undertaken because many phenological studies investigate the timing of appearance of prey (hatch dates), but we also wanted to test whether phenology of sandeel size and hence prey quality was more relevant to seabird predators. Other threshold sizes were also analysed (Fig. S1 in the supplement at [www.int-res.com/articles/suppl/m454p119\\_supp.pdf](http://www.int-res.com/articles/suppl/m454p119_supp.pdf)), and model fit was found to increase with sandeel size, with 55 mm being the largest threshold size that sandeels attained in all years of the study. Thus, this was a useful measure to compare with timing of mid-chick-rearing for each seabird species. Linear regression with year was used to assess whether the date sandeels reached 55 mm showed evidence of a temporal trend.

In order to evaluate whether the timing of seabird mid-chick-rearing had become decoupled from the timing of availability of quality sandeel prey over the study period, a 'mismatch index' was calculated as the difference (in days) between the date of the mid-point of chick-rearing for each seabird species and the date that mean sandeel size was predicted to reach the threshold of 55 mm. We emphasise that as the mismatch index is based on a threshold sandeel size, a mismatch index of 0 does not indicate perfect matching of predator and prey timing. Instead positive values of the index indicate that the seabirds' peak energy demand occurred after sandeels reached 55 mm, while negative values indicated that peak demand preceded this threshold being attained. Thus, more positive values potentially indicated better matching with higher quality prey (larger fish) and more negative values indicated peak demand coinciding with poorer quality prey. We assessed temporal changes in this mismatch index for each seabird species using linear regressions with year. Finally, we estimated mean sandeel size at mid-chick-rearing to quantify the effects of mismatch on prey energy value using the equation relating sandeel length to energy value from Hislop et al. (1991). Due to the non-linear

nature of this relationship, declines in size of large fish are more energetically costly than similar declines in smaller fish. Linear regression with year assessed whether there had been any systematic change in sandeel size at this time.

Generalised linear modelling was used to evaluate whether changes in seabird breeding success were associated with sandeel phenology and mismatch parameters, selecting models by Akaike's information criterion corrected for small sample sizes (AICc; Hurvich & Tsai 1989, Burnham & Anderson 2002). Breeding success was defined to be the ratio of the total number of chicks fledged to the total number of chicks that could potentially have fledged (a proportion). The total number of chicks that could potentially have fledged is equal to the maximum brood size multiplied by the total number of nests at which eggs were laid. Maximum brood size is invariably 1 for guillemots, razorbills and puffins, and typically 3 for kittiwake and 4 for shag (Cramp & Simmons 1978, 1983). Details of sample sizes and field methodology for monitoring breeding success are given in Harris et al. (2005). In addition to the sandeel phenology and mismatch parameters (sandeel hatch date, sandeel growth rate, length of sandeels at the mid-point of chick-rearing and mismatch index) we also included in model selection the following extrinsic factors that have previously been shown to correlate with breeding success for these seabird species on the Isle of May (Frederiksen et al. 2004b, 2006): lagged sandeel biomass index (an annual index modelled from the probability of sandeel larvae occurring in CPR samples and summed mass of larvae in a sample; see Frederiksen et al. 2006 for details); lagged SST (previous year) and sandeel fishery presence (kittiwake only; Frederiksen et al. 2008).

As the sandeel variables (apart from sandeel biomass index) arise from the same statistical model (Frederiksen et al. 2011; see Table S3 in the supplement at [www.int-res.com/articles/suppl/m454p119\\_supp.pdf](http://www.int-res.com/articles/suppl/m454p119_supp.pdf)) we included at most one of these variables in each model. We used summed Akaike weights to calculate the relative strength of support for each of the potential predictors. Note that sandeel phenology and mismatch parameters each appeared in 8 of the 40 models within the candidate set (a prior weight of 0.2), whereas the variables relating to extrinsic factors each appeared in 20 of the 40 models (a prior weight of 0.5) — this difference must be taken into account when drawing comparisons between the 2 groups of variables.

Regression models were applied to logit-transformed data on breeding success for guillemot, razorbill and puffin, and to log-transformed data for

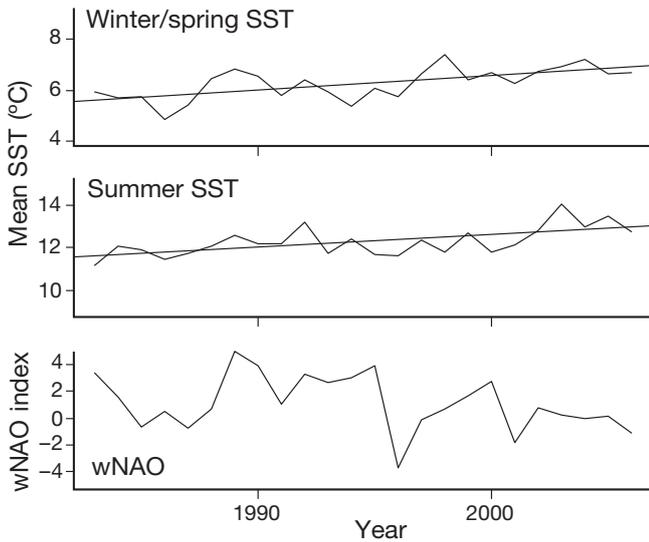


Fig. 2. Mean winter/spring and summer sea-surface temperature (SST) values, and the winter North Atlantic Oscillation (wNAO) index score over the study period. Fitted lines show significant regressions

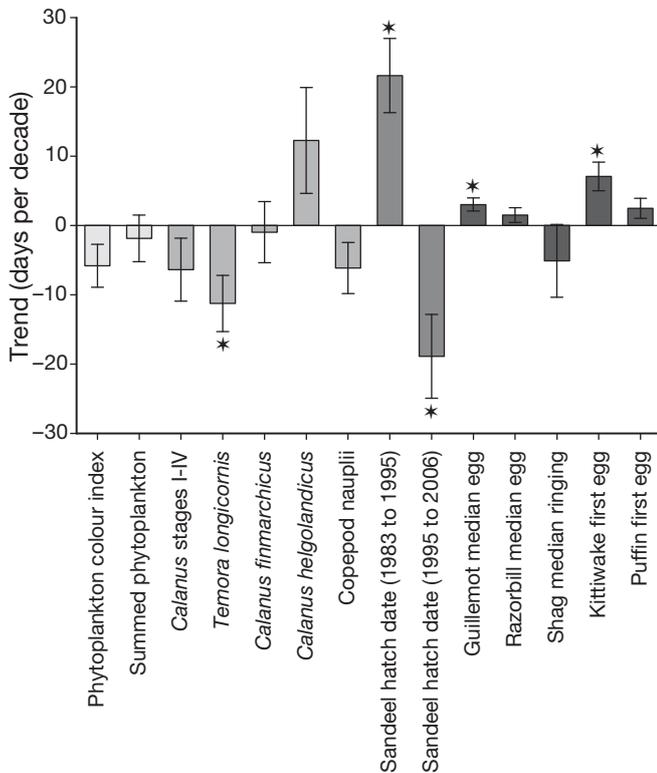


Fig. 3. Phenology trends (negative values below the line indicate timing becoming earlier, and positive values above the line indicate timing becoming later;  $n = 23$  for plankton species and  $n = 24$  for sandeel and seabirds) for species/groups from the 4 trophic levels with standard errors (trophic levels are shaded differently: palest grey: primary producers; darkest grey: top predators) in a North Sea pelagic food web between 1983 and 2006. \*Significant trends after correction ( $p < 0.05$ )

kittiwake and shag, as well as being applied to untransformed data for all species. The same models (i.e. the same sets of explanatory variables) were selected by AICc for both transformed and untransformed data; we present the results for the untransformed data solely in order to allow direct comparison with the results of Frederiksen et al. (2006). We considered the inclusion of quadratic, as well as linear, relationships and sandeel parameters lagged by 1 yr, but found no support for inclusion of these terms. Spurious relationships between an explanatory variable and the response variable can arise if both are correlated with a third variable, particularly time (Grosbois et al. 2008). We therefore included year as an explanatory variable in order to assess whether the same best model was selected once year was included, and whether the addition of year improved model fit.

## RESULTS

### Climate

Winter/spring SST increased by an average ( $\pm$ SE) of  $0.056 \pm 0.014^\circ\text{C yr}^{-1}$ ;  $p < 0.001$ , an increase of  $1.34^\circ\text{C}$  over the study period. Summer SST also increased significantly (overall increase:  $1.42^\circ\text{C}$ ;  $0.059 \pm 0.016^\circ\text{C yr}^{-1}$ ;  $p = 0.002$ ). In contrast, there was no significant trend in the wNAO (estimate:  $-0.097 \pm 0.060$ ;  $p = 0.118$ ; Fig. 2).

### Phenological trends

For primary producers, neither the timing of the seasonal peak of overall summed phytoplankton abundance, nor that of the colour index showed a statistically significant trend (Fig. 3). Similarly, phenology of primary consumers appeared to be largely unchanged and only 1 species, *Temora longicornis*, showed a significant advancement in timing. Sandeel *Ammodytes marinus* hatch date showed, within the piecewise regression model, a highly significant break-point in 1995 (95% CI from 1991 to 1998,  $p = 0.001$ ; model  $R^2 = 0.452$ ), with hatching initially becoming later and then becoming earlier (Fig. 3). With the exception of shags, whose timing varied greatly from year to year, seabird breeding tended to become later, with significant trends for guillemot and kittiwake (Fig. 3). All significant trends remained significant after the Benjamini and Hochberg correction factor was applied to this set of models.

Table 1. Linear regressions of phenology against mean winter/spring sea-surface temperature (SST) and winter North Atlantic Oscillation (wNAO), together with uncorrected p-values. Significant regressions (at the 5% level, after applying the Benjamini and Hochberg correction factor) are highlighted in bold. *T*: central tendency for monthly plankton data

Phenology measure	n	Day of year		Spring SST				wNAO			
		Mean	SD	Slope estimate	SE	p	R <sup>2</sup> (%)	Slope estimate	SE	p	R <sup>2</sup> (%)
Phytoplankton colour <i>T</i>	23	103.00	11.09	-1.89	3.82	0.63	1.16	2.54	1.04	0.02	22.20
Summed phytoplankton <i>T</i>	23	98.35	11.24	-1.32	3.88	0.74	0.55	-0.86	1.18	0.47	2.50
<i>Calanus</i> spp. Stages I to IV <i>T</i>	23	115.65	15.73	-10.40	4.95	0.05	17.35	1.18	1.65	0.48	2.39
<i>Temora longicornis</i> <i>T</i>	23	120.35	15.72	-12.64	4.70	0.01	25.66	0.29	1.67	0.86	0.14
<i>C. finmarchicus</i> <i>T</i>	23	96.09	14.65	-3.66	5.01	0.47	2.48	-0.37	1.55	0.82	0.26
<i>C. helgolandicus</i> <i>T</i>	23	66.70	26.82	12.64	8.88	0.17	8.81	3.97	2.71	0.16	9.26
Copepod nauplii <i>T</i>	23	123.87	13.00	0.80	4.50	0.86	0.15	-0.28	1.38	0.84	0.20
Sandeel hatch date	24	71.44	9.03	0.52	3.12	0.87	0.13	0.93	0.90	0.31	4.65
Date sandeels reach 55 mm	24	162.17	16.45	7.62	5.45	0.18	8.18	-1.88	1.62	0.26	5.79
Guillemot median egg	24	128.13	3.79	0.71	1.30	0.59	1.33	-0.93	0.33	0.01	26.28
Razorbill median egg	24	130.17	3.69	-0.76	1.26	0.55	1.63	-0.76	0.34	0.03	18.93
Shag median ringing	22	132.55	19.82	-7.14	5.96	0.24	6.13	0.71	1.80	0.70	0.70
Kittiwake first egg	24	131.50	8.46	1.37	2.91	0.64	0.99	<b>-2.35</b>	<b>0.70</b>	<b>0.00</b>	<b>34.14</b>
Puffin first egg	24	99.88	5.10	1.59	1.73	0.37	3.68	-0.70	0.50	0.17	8.41

### Phenological regressions with climate

Overall there was little evidence that trends in phenology were associated with either of the climate variables. Significant relationships between phenology and winter/spring SST (see Table 1) for *Temora longicornis* and *Calanus* spp. Stages I to IV were apparent, but did not remain significant after applying the Benjamini and Hochberg correction to this set of models. None of the regressions were significant

between seabird egg-laying phenology and winter/spring SST (Table 1) or summer SST (guillemot:  $t = 0.50$ ,  $p = 0.62$ ; razorbill:  $t = -1.22$ ,  $p = 0.24$ ; shag:  $t = -0.69$ ,  $p = 0.50$ ; kittiwake:  $t = 0.911$ ,  $p = 0.37$ ; puffin:  $t = 0.40$ ,  $p = 0.70$ ). Phytoplankton colour index, but not summed abundance, was positively related to wNAO, while timing of guillemots, razorbills and kittiwakes showed a negative relationship. Only the regression with kittiwake phenology remained significant once the correction factor had been applied to this set of models. However, this model also showed some evidence of autocorrelation when model residuals were examined and hence should be interpreted with caution.

Table 2. Linear regressions of phenology of upper trophic level species/group against that of the relevant lower trophic level, together with uncorrected p-values. Results for summed total phytoplankton abundance were similar to the colour index (see Table S2 in the supplement at [www.int-res.com/articles/suppl/m454p119\\_supp.pdf](http://www.int-res.com/articles/suppl/m454p119_supp.pdf)). *T* is the central tendency for monthly plankton data

Response	Explanatory	Slope estimate	SE	<i>t</i>	p
<i>Calanus finmarchicus</i> <i>T</i>	Phytoplankton colour <i>T</i>	-0.476	0.269	-1.768	0.092
<i>C. helgolandicus</i> <i>T</i>	Phytoplankton colour <i>T</i>	-0.119	0.527	-0.227	0.823
<i>Calanus</i> stages <i>T</i>	Phytoplankton colour <i>T</i>	0.277	0.304	0.914	0.371
<i>Temora longicornis</i> <i>T</i>	Phytoplankton colour <i>T</i>	0.282	0.303	0.929	0.363
Copepod nauplii <i>T</i>	Phytoplankton colour <i>T</i>	0.258	0.250	1.032	0.314
Sandeel hatch	<i>C. finmarchicus</i> <i>T</i>	0.038	0.111	0.344	0.734
Sandeel hatch	<i>C. helgolandicus</i> <i>T</i>	0.128	0.054	2.377	0.027
Sandeel hatch	<i>Calanus</i> stages <i>T</i>	0.096	0.101	0.949	0.354
Sandeel hatch	<i>T. longicornis</i> <i>T</i>	-0.011	0.103	-0.110	0.913
Sandeel hatch	Copepod nauplii <i>T</i>	-0.175	0.119	-1.469	0.157
Sandeel hatch	Phytoplankton colour <i>T</i>	-0.056	0.146	-0.380	0.708
Guillemot median egg	Sandeel hatch	0.034	0.089	0.376	0.711
Razorbill median egg	Sandeel hatch	0.075	0.086	0.874	0.392
Shag median ring	Sandeel hatch	-0.332	0.414	-0.802	0.431
Kittiwake first egg	Sandeel hatch	0.088	0.199	0.440	0.664
Puffin first egg	Sandeel hatch	0.106	0.118	0.893	0.382

### Comparisons of phenological change among trophic levels

There was no evidence that predator and prey phenologies were related, with no significant pairwise regressions between any of the trophic comparisons (the significant relationship between sandeel hatch and timing of peak abundance of *Calanus helgolandicus* was no longer significant after correction (Table 2 and Table S2 in the supplement at [www.int-res.com/articles/suppl/m454p119\\_supp.pdf](http://www.int-res.com/articles/suppl/m454p119_supp.pdf)).

**Trophic mismatch in seabirds and sandeels**

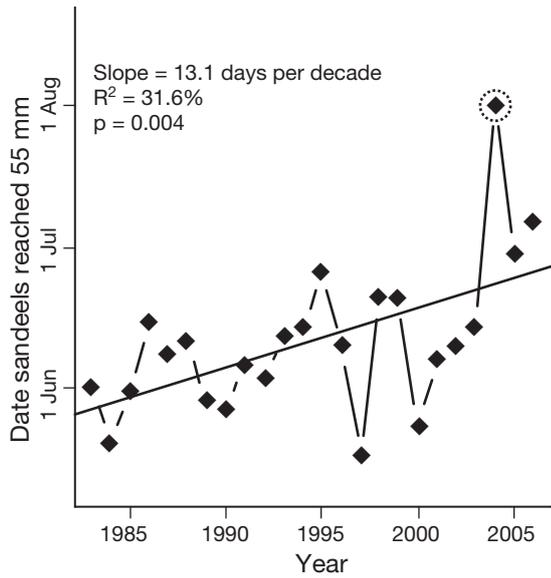


Fig. 4. Regression between the date that mean sizes of sandeel *Ammodytes marinus* are predicted to attain a threshold of 55 mm and year. The line shows the significant fitted regression. Relationship remained significant even when the latest date sandeels reached 55 mm (in 2004, dotted circle) was removed from the analysis

The date at which 0-group sandeels reached a predicted mean threshold length of 55 mm became significantly later, at an average rate of 13.1 d decade<sup>-1</sup> over the study period (Fig. 4). The date of mid-chick-rearing was significantly related to the estimated date this threshold length was reached for 4 of the seabird species (guillemot, razorbill, puffin and kittiwake; Fig. 5), and relationships for guillemot, razorbill and kittiwake remained significant even when year was also included in the model. However, the regression coefficient (slope) of mid-chick-rearing against the date sandeel threshold length was reached was substantially less than unity for these species (Fig. 5). This indicated that although mid-chick-rearing had become later in these 4 species, the shift in timing of sandeel size had been even faster. Razorbills showed the slowest rate of change in timing of breeding, and kittiwakes, the fastest. In contrast, shags showed no temporal trend in breeding phenology or relationship with sandeel size phenology (Fig. 5).

In addition to differing rates of phenological change, there was also interspecific variation in the

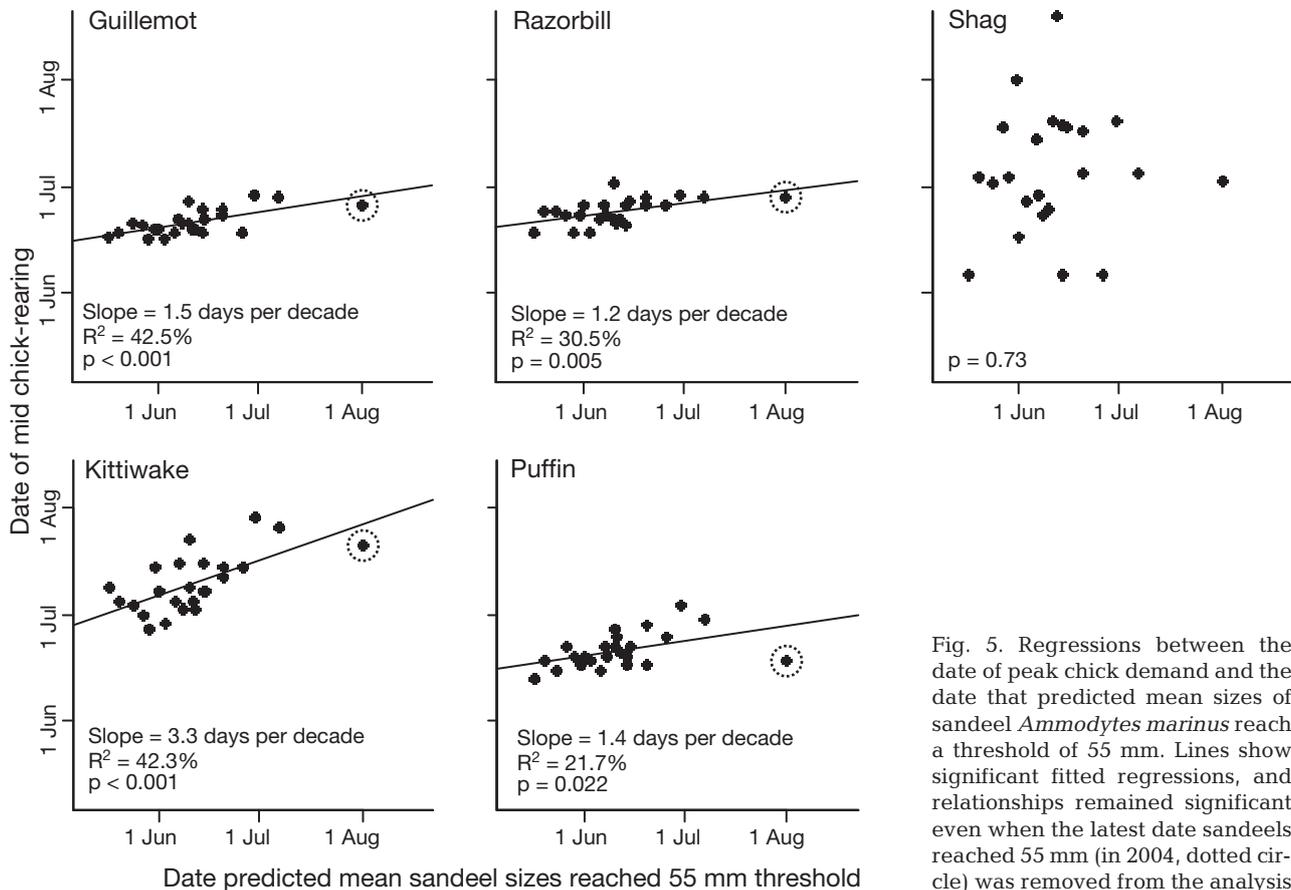


Fig. 5. Regressions between the date of peak chick demand and the date that predicted mean sizes of sandeel *Ammodytes marinus* reach a threshold of 55 mm. Lines show significant fitted regressions, and relationships remained significant even when the latest date sandeels reached 55 mm (in 2004, dotted circle) was removed from the analysis

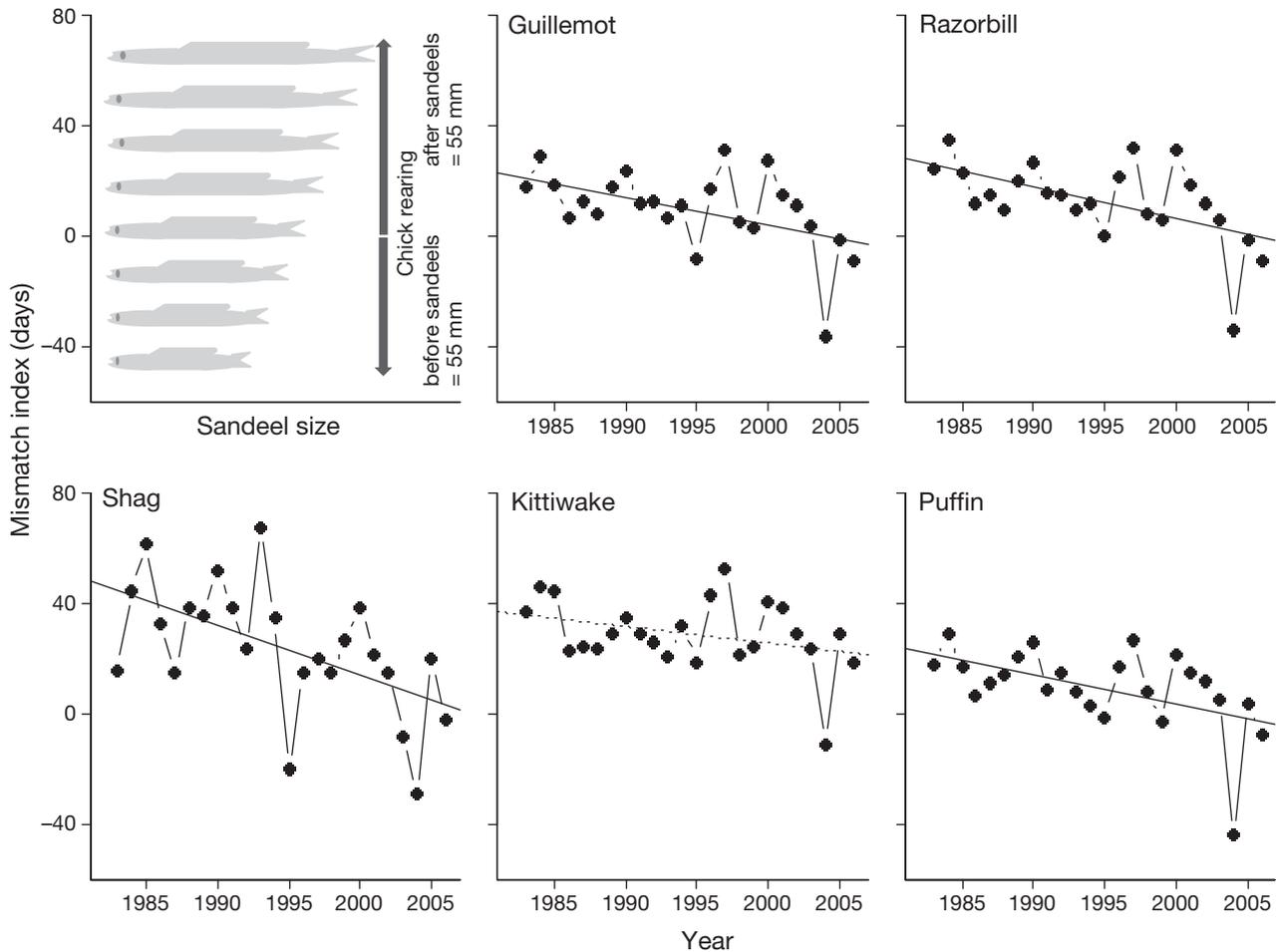


Fig. 6. Temporal changes in mismatch index (difference in days between timing of seabird mid-chick-rearing and the mean date that sandeels *Ammodytes marinus* were predicted to reach a threshold of 55 mm). As shown in upper left panel, a negative index means that mid-chick-rearing occurred before sandeels attained a threshold length of 55 mm; hence, sandeels would have been 55 mm and smaller during chick-rearing. Positive index values indicate that mid-chick-rearing occurred after this threshold; hence, sandeels would have been 55 mm or larger during chick-rearing. Solid lines: significant fitted regressions; dashed line (kittiwakes): non-significant. We emphasise that because the mismatch index is based on a threshold size of sandeel, a value of 0 for the mismatch index does not indicate perfect matching between seabirds and sandeels; rather the higher the mismatch index the larger the sandeels available

absolute timing of breeding. Ranking of the timing of breeding for 4 of the 5 seabird species was generally constant across the study period, with puffins and guillemots breeding earliest, followed by razorbills, and with kittiwakes breeding last. In contrast, shag mid-chick-rearing was highly variable, being the earliest studied bird in 3 of the years and the latest in 9 of the years.

These disparities in absolute timing and rates of change in seabird breeding schedules and sandeel sizes were integrated in the mismatch index (Fig. 6). Thus, in the 1980s, mid-chick-rearing for all the species considered occurred well after 0-group sandeels reached 55 mm (positive values of the mismatch index), whereas, in recent years, mid-chick-

rearing coincided with (mismatch index around 0) or occurred before (negative values) the date at which sandeels had attained this size in 4 of the 5 seabird species. Kittiwakes were the exception; they bred latest and hence had generally higher mismatch index values than the other species (Fig. 6). As a result, the mean length of 0-group sandeels at mid-chick-rearing has significantly decreased over the study period in all seabird species (Fig. 7). The total estimated decrease over 24 yr and rates of decline ( $\pm$ SE) were as follows: for guillemots: 10.2 mm,  $-0.44 (\pm 0.16)$  mm yr $^{-1}$ ; for razorbills: 12.4 mm,  $-0.54 (\pm 0.16)$  mm yr $^{-1}$ ; for shags: 21.7 mm,  $-0.94 (\pm 0.28)$  mm yr $^{-1}$ ; for kittiwakes: 10.2 mm,  $-0.44 (\pm 0.19)$  mm yr $^{-1}$ ; and for puffins: 10.7 mm,  $-0.47 (\pm 0.15)$  mm

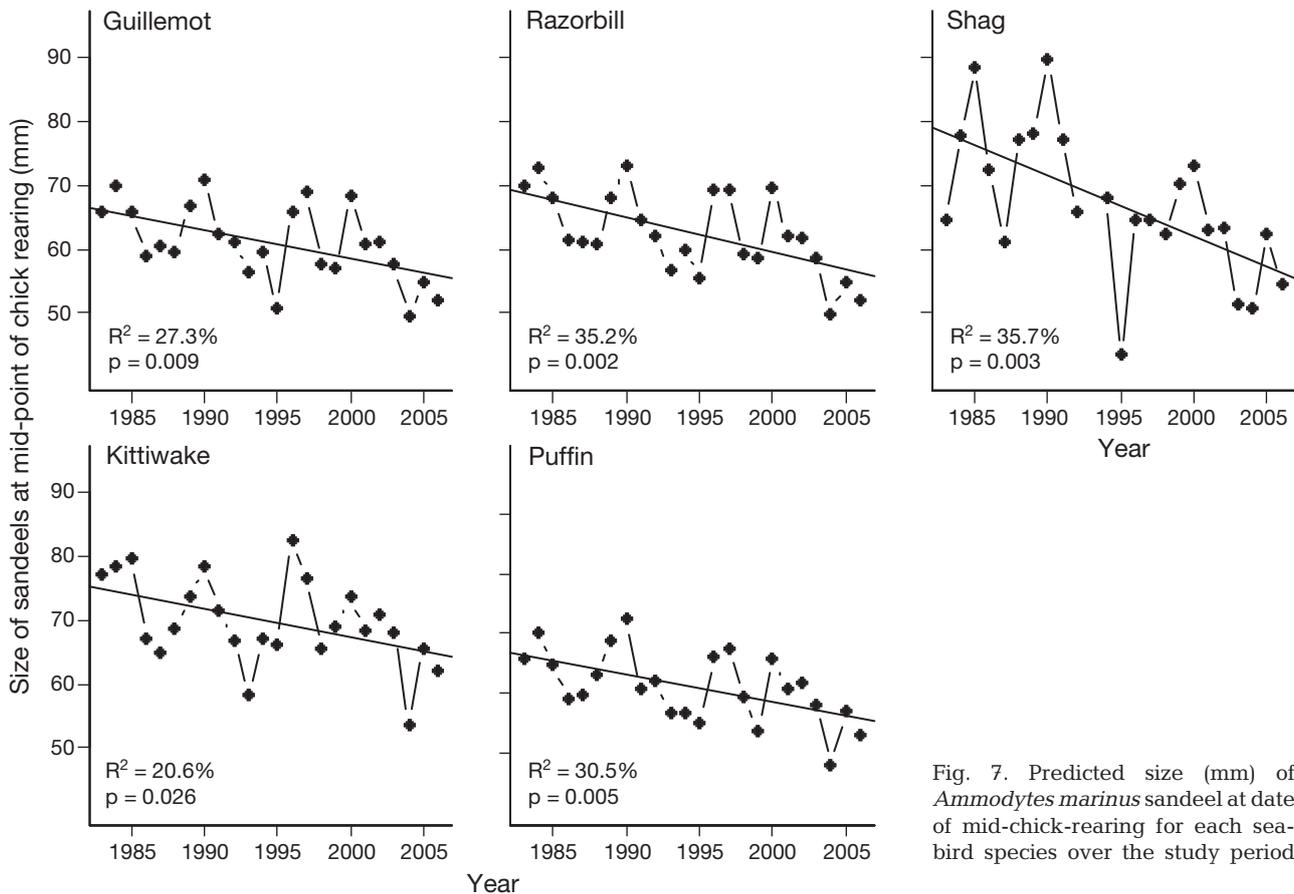


Fig. 7. Predicted size (mm) of *Ammodytes marinus* sandeel at date of mid-chick-rearing for each seabird species over the study period

yr<sup>-1</sup>. Shags, with the steepest rate of predicted decline, showed the highest net reduction in energetic value of fish over the 24 yr study period (4.80 kJ, a 70.4% decline from 1983). Despite kittiwakes having the lowest rate of decline in sandeel size, this species showed the next highest overall reduction in net energetic value of 2.46 kJ (42.2% decline from 1983). As the latest breeding seabird, mid-chick-rearing of kittiwakes occurred when sandeels were predicted to be larger and, due to the non-linear nature of the relationship between sandeel length and energetic content, declines in the length of large fish are more energetically costly than equivalent declines in smaller fish. Net declines in the energetic value of fish were 1.70 kJ (46.7%) for guillemot, 2.21 kJ (52.4%) for razorbill and 1.79 kJ (48.2%) for puffin.

#### Consequences of mismatch for seabird breeding success

Despite the energetic implications associated with the pronounced decline in 0-group sandeel length

at mid-chick-rearing, there was no evidence that this or sandeel hatch date had a significant effect on the breeding success of any of the 5 species of seabirds considered once other significant variables were included in the models. The breeding success of guillemot, razorbill and shag was, however, positively related to sandeel growth rates (slope estimates  $\pm$  SE:  $0.849 \pm 0.204$ ,  $0.341 \pm 0.193$ , and  $0.729 \pm 0.333$ , respectively) such that in years with poorer sandeel growth these species had poorer breeding success.

Breeding success for shags, kittiwakes and puffins was poorer in years following a year with warmer winter/spring SST (slope estimates  $\pm$  SE:  $-0.101 \pm 0.042$ ,  $-0.126 \pm 0.030$ ,  $-0.108 \pm 0.028$ , respectively) and higher following years with a high sandeel biomass index (slope estimates  $\pm$  SE:  $0.047 \pm 0.020$ ,  $0.035 \pm 0.018$ , and  $0.032 \pm 0.013$ , respectively). All species except kittiwake showed evidence of a linear trend (negative for all species except shag) in success over time that was not accounted for by the other model variables (Table 3). The inclusion of quadratic or lagged sandeel terms did not lead to models with lower AICc values.

## DISCUSSION

### Phenological changes across trophic levels

To our knowledge, this is the first direct comparison of phenologies across multiple trophic levels of the North Sea pelagic food web. We found contrasting trends across the 4 trophic levels that were suggestive of trophic mismatch, supporting the assertion from other studies that this phenomenon is widespread (Visser & Both 2005). However, in contrast to mismatch theory for marine systems (Cushing 1990) and empirical results from terrestrial studies (Visser & Both 2005, Both et al. 2009), we found no evidence of strong pairwise relationships between predator and prey phenologies, except for timing of mid-chick-rearing in some seabird species and threshold size of 0-group sandeels *Ammodytes marinus*, and hence no evidence of matching in this system. This suggests that phenologies of North Sea species may have been mismatched since at least 1983, which is possible as most of our study followed the abrupt increase in SST and regime shift in the late 1980s (Beaugrand 2004).

Contrasting phenological responses can arise for several reasons. For example, if organisms at different trophic levels vary in their ability to respond to climate warming or in the extent to which their phenology is influenced by alternative drivers. The absence of significant relationships between any of the phenology metrics considered and SST, apart from suggestive relationships with *Calanus* spp. stages and *Temora longicornis*, suggests that differential re-

sponses to climate warming may be unimportant, at least in this part of the western North Sea. Alternatively winter/spring or summer SST may not be at the appropriate temporal or spatial scale for elucidating such responses. Indeed, there was evidence that timing of breeding for 3 of the 4 seabirds that disperse outside the North Sea in winter (kittiwakes, guillemot and razorbills, but not puffins) was related to broader scale climate cues (wNAO), particularly in the case of the kittiwake which exhibits the widest dispersal (Wernham et al. 2002, Bogdanova et al. 2011). High abundance and/or broad peaks of seasonal prey can potentially mask phenological relationships (Durant et al. 2005), with phenological matching likely to be particularly apparent when prey abundance is reduced or only available for a short duration of time. In the North Sea, dramatic changes in abundance and spatial distributions of phytoplankton and copepods (Beaugrand et al. 2009) have been observed. However, patterns of change are not consistent within trophic levels, with increases apparent for some species (for example *C. helgolandicus*), while others are decreasing (e.g. *C. finmarchicus*) (Planque & Fromentin 1996). Thus it is unclear to what extent changing abundance may be masking phenological matching in our system. Finally, there may potentially be lagged responses of predators to prey phenology such that comparison of phenologies in the same year does not elucidate relationships. For example, phenology of juvenile zooplankton abundance is related to the reproductive timing of parent generations (Ellertsen et al. 1987).

Table 3. Importance of variables associated with seabird breeding success, based upon summed Akaike weights (range from 0 to 1; high values indicate strong support), were calculated using the full candidate set of  $n = 40$  models (see Table S4 in the supplement at [www.int-res.com/articles/suppl/m454p119\\_supp.pdf](http://www.int-res.com/articles/suppl/m454p119_supp.pdf)). Note that parameters derived from the sandeel model (hatch date, growth rate, size and mismatch index) were present in 8 of the 40 models within the candidate set, whereas the remaining predictors were present in 20 models — the prior weights for these variables are therefore 0.2 and 0.5, respectively, and this difference needs to be taken into account when drawing comparisons between the 2 groups of variables. Predictors included in the model with the lowest value of the corrected Akaike's information criterion (AICc) for each species are shown in **bold**, and we report the overall  $R^2$  values for these models. SST: sea-surface temperature

Predictor	No. of models	Guillemot	Razorbill	Shag	Kittiwake	Puffin
Sandeel size	<b>8 / 40</b>	0.001	0.125	0.083	0.135	0.125
Sandeel hatch date	<b>8 / 40</b>	0.025	0.090	0.099	0.071	0.171
Sandeel growth rate	<b>8 / 40</b>	<b>0.966</b>	<b>0.364</b>	<b>0.319</b>	0.176	0.097
Mismatch index	<b>8 / 40</b>	<b>0.004</b>	<b>0.135</b>	<b>0.110</b>	0.019	0.121
Sandeel biomass index lagged	20 / 40	0.169	0.237	<b>0.560</b>	<b>0.872</b>	<b>0.679</b>
SST lagged	20 / 40	0.177	0.116	<b>0.477</b>	<b>0.985</b>	<b>0.979</b>
Year (linear time trend)	20 / 40	<b>0.956</b>	<b>0.924</b>	<b>0.507</b>		<b>0.585</b>
Sandeel fishery presence	20 / 40				<b>0.847</b>	
$R^2$ for model with lowest AICc (%)		71.80	50.85	49.9	65.38	71.30
n (yr)		24	24	21	22	24

It is also possible that sampling differences between the trophic levels could potentially result in phenology measures that are too crude to identify correlations. The plankton data were at a lower temporal resolution and broader spatial scale than the sandeel and seabird data, and central tendency estimates of plankton phenology are known to have low sensitivity if timing shifts are small (Ji et al. 2010). Moreover, copepods may respond to timing of critical abundance thresholds of diatoms, rather than to seasonal peaks (Runge et al. 2005). In addition, we considered mean phenological values at a broad spatial scale, whereas changes in prey distributions can lead to localised spatial mismatch (Schweiger et al. 2008). Ideally future analyses of phenological trends and mismatch in this system should account for annual variation in prey abundance by investigating overlap between distributions of prey availability and predator peak energetic demands rather than treating them as point estimates.

### **Trophic mismatch between seabirds and sandeels**

A key finding of the present study was that, for most of the Isle of May seabird populations considered, the timing of seabird mid-chick-rearing tracked the timing of 0-group sandeels attaining a threshold size, rather than sandeel hatch dates per se. The rate at which mid-chick-rearing was delayed varied among the species, but in all cases was insufficient to keep pace with the delayed date at which sandeels attained a threshold size. The net result was that for all 5 seabird species the size of 0-group sandeels around the mid-point of chick-rearing, when energetic requirements are likely to be greatest, has significantly declined.

The seabird species we considered differed to some extent as to the importance of 0-group sandeels in adult and chick diets, with the likely ranking in decreasing order of reliance being kittiwake, puffin, razorbill, guillemot and shag (Daunt et al. 2008). This ranking reflects the species-specific differences apparent in mismatching, with kittiwakes, which show the greatest reliance on the 0-group, tracking changes in size most closely, while shags, for which the 0-group is a minor part of the diet, showed no trend in their breeding phenology. However, the predicted net energetic reduction in 0-group sandeel prey was higher for kittiwakes than for the other seabird species that were also tracking changes in sandeel size, despite kittiwakes showing the greatest phenological shifts in response to changing sandeel timing. This is because variation in net energetic

costs of reductions in sandeel size also depends on the absolute timing of breeding. As the consistently latest breeding seabird on the Isle of May, kittiwake mid-chick-rearing occurred when sandeels were predicted to be larger and, due to the non-linear nature of the relationship between sandeel length and energetic content, declines in the length of large fish are more energetically costly than equivalent declines in smaller fish.

Although the results presented here pertain to seabirds from the Isle of May, the order and annual timing of breeding for the species considered were consistent and varied in parallel with another North Sea colony 90 km distant (Wanless et al. 2009). This suggests consistency, at least at the local scale, with seabirds from these 2 colonies potentially foraging on the same sandeel stock. However, qualitative data from other UK seabird colonies suggests that breeding phenology may vary considerably between locations (Wanless et al. 2009). Moreover, sandeel populations also exhibit significant regional variation in growth rates, length-at-age and abundance (Boulcott et al. 2006), and further work is needed to identify whether interactions between seabirds and sandeel phenology vary regionally.

Very few other studies have considered the role of prey quality in trophic mismatch. However, Beaupre et al. (2003) found a mismatch between the size of larval cod *Gadus morhua* relative to the size of their calanoid copepod prey, resulting in poorer cod survival. Similarly, in a terrestrial system, caribou *Rangifer tarandus* births had become mismatched from the onset of newly emergent nutrient-rich plant growth, resulting in reduced offspring survival (Post & Forchhammer 2008). There are several potential reasons why Isle of May seabirds are failing to track changes in the timing of 0-group sandeel size. Firstly, the cues used by the birds to time their breeding may not accurately predict 0-group sandeel phenology. Secondly, there may be trade-offs between the benefits of delaying breeding to maintain 0-group sandeel size and the fitness benefits of early breeding (Daunt et al. 2007, Harris et al. 2007). Thirdly, the birds may be constrained in their ability to alter their phenology due to having a photoperiodically controlled physiological window of breeding timing (Dawson 2008). Finally, adult birds may compensate for the lower energy value of 0-group sandeels by increasing foraging effort and/or switching to alternative prey. It is probable that some, possibly all, of these factors are operating in our study system.

Despite the apparently serious implications in terms of the reduced energy value of prey associated

with changes in 0-group sandeel length at the time of chick-rearing, particularly for kittiwakes, there was no evidence that this was related to poorer breeding success. This contrasts with studies from a Norwegian seabird colony where breeding success of puffins was positively related to the size of herring prey (Durant et al. 2003) and from a Japanese colony where rhinoceros auklet *Cerorhinca monocerata* breeding success was poorer in years when birds were mismatched from the availability of their prey, Japanese anchovy *Engraulis japonicus* (Watanuki et al. 2009). The reason for this disparity is currently unclear, but may well be linked to differences in the life-history traits of the species involved, hydro-biological characteristics of the study systems — with both the mismatch examples given above being from a conveyor-type system where prey availability is affected by the timing of currents — and whether other factors such as predation or severe weather exert a major effect on breeding success.

It is also plausible that breeding success of some Isle of May seabirds is more closely linked to the scheduling and/or abundance of one or more alternative prey species. The main alternative prey species for Isle of May seabirds are 1+-group sandeels, clupeids (predominantly sprats *Sprattus sprattus*) and butterfish *Pholis gunellus* (Daunt et al. 2008). Time series data on abundance or phenology for these species are lacking; thus, it is impossible to repeat the approach used to look for matching between seabird breeding and 0-group sandeels. Previous findings suggest that the timing of 1+-group sandeel abundance is potentially important for kittiwakes, guillemots and shags (Frederiksen et al. 2004b). Our analyses of breeding success included a range of potentially important variables, and results indicated that these differed among the species. Sandeel abundance as indicated by a sandeel biomass index and the sandeel growth rate, which may be linked with behavioural changes and hence availability of sandeel to seabirds, emerged as being consistently important. However, we emphasise that investigating breeding phenology in relation to prey phenology assumes that this is the single critical activity under selection (Visser & Both 2005). In reality, the entire life-cycle is under selection and responding to multiple environmental drivers, such that breeding phenology may be the outcome of trade-offs between several selection pressures. Ideally, in future work, multiple life-history traits should be investigated at the individual level to understand whether predators are adequately responding to changes in prey phenology and the fitness costs of mismatch.

## CONCLUSIONS

Quantifying the shift in the phenology of a prey species has been suggested as an appropriate yardstick for interpreting whether a predator is shifting its phenology adequately to match the change in its environment often as a result of climate change (Visser & Both 2005). Our study followed this approach to assess phenological changes across multiple trophic levels of the pelagic food web in the western North Sea. At a broad spatial scale we found contrasting phenological trends between trophic levels that may indicate that the system is currently experiencing trophic mismatching. By developing a novel approach we also explored finer scale data on the timing of peak energy for avian predators in relation to temporal changes in the energy value of an important piscivorous prey. This analysis highlighted significant changes over 24 yr in temporal matching of the chick-rearing periods of 5 species of seabirds and in the size of 0-group sandeels such that prey length, and hence energy value of individual items, have declined significantly. To date, there is no evidence that these changes are impacting on the breeding success of any of the seabird species considered, but further changes, particularly if alternative prey are also affected adversely, could well have population level consequences for the North Sea seabird community.

*Acknowledgements.* The present study was funded by the Centre for Ecology & Hydrology Environmental Change Integrating Fund project SPACE (Shifting Phenology: Attributing Change across Ecosystems). SST data were provided courtesy of the NOAA National Oceanographic Data Center and the University of Miami. We thank Mike Harris and many others who collected seabird data, and all past/present members and supporters of the Sir Alister Hardy Foundation for Ocean Science for establishment and maintenance of the CPR dataset and the owners and crews of ships towing the CPRs. We are grateful to the Natural Environmental Research Council and the Joint Nature Conservation Committee for supporting the long-term seabird studies and to the Scottish Natural Heritage for allowing work on the Isle of May. Five anonymous referees provided constructive criticism which significantly improved the original manuscript.

## LITERATURE CITED

- Beaugrand G (2004) The North Sea regime shift: evidence, causes, mechanisms and consequences. *Prog Oceanogr* 60:245–262
- Beaugrand G, Brander KM, Souissie S, Reid PC (2003) Plankton effect on cod recruitment in the North Sea. *Nature* 426:661–664

- Beaugrand G, Luczak C, Edwards M (2009) Rapid biogeographical plankton shifts in the North Atlantic Ocean. *Glob Change Biol* 15:1790–1803
- Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J R Stat Soc B* 57:289–300
- Bogdanova MI, Daunt F, Newell M, Phillips RA, Harris MP, Wanless S (2011) Seasonal interactions in the black-legged kittiwake, *Rissa tridactyla*: links between breeding performance and winter distribution. *Proc Biol Sci* 278:2412–2418
- Both C, van Asch M, Bijlsma RG, van den Burg AB, Visser ME (2009) Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *J Anim Ecol* 78:73–83
- Boulcott P, Wright PJ, Gibb FM, Jensen H, Gibb IM (2006) Regional variation in maturation of sandeels in the North Sea. *ICES J Mar Sci* 64:369–376
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretical approach. Springer-Verlag, New York, NY
- Cramp S, Simmons K (1978) Handbook of the birds of Europe, the Middle East and North Africa: the birds of the western Palearctic, Vol 1. Oxford University Press, Oxford
- Cramp S, Simmons K (1983) Handbook of the birds of Europe, the Middle East and North Africa: the birds of the western Palearctic, Vol 3. Oxford University Press, Oxford
- Cury P, Bakun A, Crawford RJM, Jarre A, Quinones RA, Shannon LJ, Verheve HM (2000) Small pelagics in upwelling systems: patterns of interaction and structural changes in “waspy-waist” ecosystems. *ICES J Mar Sci* 57: 603–618
- Cushing DH (1990) Plankton production and year-class strength in fish populations—an update of the match mismatch hypothesis. *Adv Mar Biol* 26:249–293
- Daan N, Bromley PJ, Hislop JRG, Nielsen NA (1990) Ecology of North Sea fish. *Neth J Sea Res* 26:343–386
- Daunt F, Wanless S, Harris M, Money L, Monaghan P (2007) Older and wiser: improvements in breeding success are linked to better foraging performance in European shags. *Funct Ecol* 21:561–567
- Daunt F, Wanless S, Greenstreet SPR, Jensen H, Hamer KC, Harris MPH (2008) The impact of the sandeel fishery closure on seabird food consumption, distribution, and productivity in the northwestern North Sea. *Can J Fish Aquat Sci* 65:362–381
- Dawson A (2008) Control of the annual cycle in birds: endocrine constraints and plasticity in response to ecological variability. *Philos Trans R Soc Lond B Biol Sci* 363: 1621–1633
- Drent RH, Daan S (1980) The prudent parent: energetic adjustments in avian breeding. *Ardea* 68:225–252
- Durant JM, Anker-Nilssen T, Stenseth NC (2003) Trophic interactions under climate fluctuations: the Atlantic puffin as an example. *Proc Biol Sci* 270:1461–1466
- Durant JM, Hjermmann DO, Anker-Nilssen T, Beaugrand G, Mysterud A, Pettorelli N, Stenseth NC (2005) Timing and abundance as key mechanisms affecting trophic interactions in variable environments. *Ecol Lett* 8: 952–958
- Durant JM, Anker-Nilssen T, Stenseth NC (2006) Ocean climate prior to breeding affects the duration of the nestling period in the Atlantic puffin. *Biol Lett* 2:628–631
- Edwards M, Richardson AJ (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* 430:881–884
- Edwards M, Beaugrand G, Reid PC, Rowden AA, Jones MB (2002) Ocean climate anomalies and the ecology of the North Sea. *Mar Ecol Prog Ser* 239:1–10
- Ellertsen B, Fossum P, Solemdal P, Sundby S, Tilseth S (1987) The effect of biological and physical factors on the survival of the Arctic-Norwegian cod and the influence on recruitment variability. In: Loenge H (ed) The effect of oceanographic conditions on distribution and population dynamics of commercial fish stocks in the Barents Sea. Institute of Marine Research, Bergen, p 101–126
- Forrest J, Miller-Rushing AJ (2010) Toward a synthetic understanding of the role of phenology in ecology and evolution. *Philos Trans R Soc Lond B Biol Sci* 365: 3101–3112
- Frederiksen M, Harris MP, Daunt F, Rothery P, Wanless S (2004a) Scale-dependent climate signals drive breeding phenology of three seabird species. *Glob Change Biol* 10:1214–1221
- Frederiksen M, Wanless S, Harris MP, Rothery P, Wilson LJ (2004b) The role of industrial fisheries and oceanographic change in the decline of North Sea black-legged kittiwakes. *J Appl Ecol* 41:1129–1139
- Frederiksen M, Edwards M, Richardson AJ, Halliday NC, Wanless S (2006) From plankton to top predators: bottom-up control of a marine food web across four trophic levels. *J Anim Ecol* 75:1259–1268
- Frederiksen M, Jensen H, Daunt F, Mavor RA, Wanless S (2008) Differential effects of a local industrial sand lance fishery on seabird breeding performance. *Ecol Appl* 18: 701–710
- Frederiksen M, Elston DA, Edwards M, Mann AD, Wanless S (2011) Mechanisms of long-term decline in size of lesser sandeels in the North Sea explored using a growth and phenology model. *Mar Ecol Prog Ser* 432:137–147
- Furness RW, Tasker ML (2000) Seabird–fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. *Mar Ecol Prog Ser* 202:253–264
- Grosbois V, Gimenez O, Gaillard JM, Pradel R and others (2008) Assessing the impact of climate variation on survival in vertebrate populations. *Biol Rev Camb Philos Soc* 83:357–399
- Hallett TB, Coulson T, Pilkington JG, Clutton-Brock TH, Pemberton JM, Grenfell BT (2004) Why large-scale climate indices seem to predict ecological processes better than local weather variables. *Nature* 430:71–75
- Harris MP, Wanless S (2011) The puffin. T & AD Poyser, London
- Harris MP, Wanless S, Murray S, Mackley E (2005) Isle of May seabird studies in 2004. JNCC Report 375, Joint Nature Conservancy Committee, Peterborough
- Harris MP, Frederiksen M, Wanless S (2007) Within- and between-year variation in the juvenile survival of common guillemots *Uria aalge*. *Ibis* 149:472–481
- Hipfner JM (2008) Matches and mismatches: ocean climate, prey phenology and breeding success in a zooplanktivorous seabird. *Mar Ecol Prog Ser* 368:295–304
- Hislop JRG, Harris MP, Smith JGM (1991) Variation in the calorific value and total energy content of the lesser sandeel (*Ammodytes marinus*) and other fish preyed on by seabirds. *J Zool* 224:501–517

- Hurvich CM, Tsai CL (1989) Regression and time series model selection in small samples. *Biometrika* 76:297–307
- Ji R, Edwards M, Mackas DL, Runge JA, Thomas AC (2010) Marine plankton phenology and life history in a changing climate: current research and future directions. *J Plankton Res* 32:1355–1368
- Johns D (2009) Monthly averaged data for phyto- and zooplankton (55–58°N, 3–0°W) 1983–2007 recorded by the Continuous Plankton Recorder [to 13/11/2009]. Sir Alister Hardy Foundation for Ocean Science, Plymouth
- Kilpatrick KA, Podesta GP, Evans R (2001) Overview of the NOAA/NASA Advanced Very High Resolution Radiometer Pathfinder algorithm for sea surface temperature and associated matchup database. *J Geophys Res C* 106: 9179–9197
- Leggett WC, DeBlois E (1994) Recruitment in marine fishes — Is it regulated by starvation and predation in the egg and larval stages? *Neth J Sea Res* 32:119–134
- Macer CT (1966) Sandeels (*Ammodytidae*) in the southwestern North Sea; their biology and fishery. *Fish Investig Ser II Mar Fish GB Minist Agric Fish Food* 24(6):1–55
- Moe B, Stempniewicz L, Jakubas D, Angelier F and others (2009) Climate change and phenological responses of two seabird species breeding in the high-Arctic. *Mar Ecol Prog Ser* 393:235–246
- Monteleone DM, Peterson WT (1986) Feeding ecology of American sand lance *Ammodytes americanus* larvae from Long Island Sound. *Mar Ecol Prog Ser* 30:133–143
- Muggeo VMR (2008) Segmented: an R Package to fit regression models with broken-line relationships. *R News*, 8/1, 20–25. Available at: <http://cran.r-project.org/doc/Rnews/> (accessed Feb 2011)
- Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. *Science* 308:1912–1915
- Planque B, Fromentin JM (1996) *Calanus* and environment in the eastern North Atlantic. I. Spatial and temporal patterns of *C. finmarchicus* and *C. helgolandicus*. *Mar Ecol Prog Ser* 134:101–109
- Post E, Forchhammer MC (2008) Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Philos Trans R Soc Lond B Biol Sci* 363: 2369–2375
- Richardson AJ, Walne AW, John AWG, Jonas TD and others (2006) Using continuous plankton recorder data. *Prog Oceanogr* 68:27–64
- Runge JA, Franks PJS, Gentleman WC, Megrey BA and others (2005) Diagnosis and prediction of variability in secondary production and fish recruitment processes: developments in physical-biological modeling. In: Robinson AR, Brink K (eds) *The global coastal ocean; multi-scale interdisciplinary processes*, Vol 13. Harvard University Press, Cambridge, MA, p 413–473
- Schweiger O, Settele J, Kudrna O, Klotz S, Kuhn I (2008) Climate change can cause spatial mismatch of trophically interacting species. *Ecology* 89:3472–3479
- Shultz MT, Piatt JF, Harding AMA, Kettle AB, Van Pelt TI (2009) Timing of breeding and reproductive performance in murre and kittiwakes reflect mismatched seasonal prey dynamics. *Mar Ecol Prog Ser* 393:247–258
- Soreide JE, Falk-Petersen S, Hegseth EN, Hop H, Carroll ML, Hobson KA, Blachowiak-Samolyk K (2008) Seasonal feeding strategies of *Calanus* in the high-Arctic Svalbard region. *Deep-Sea Res II* 55:2225–2244
- Thackeray SJ, Sparks TH, Frederiksen M, Burthe S and others (2010) Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Glob Change Biol* 16:3304–3313
- Visser ME, Both C (2005) Shifts in phenology due to global climate change: the need for a yardstick. *Proc Biol Sci* 272:2561–2569
- Wanless S, Harris MP, Redman P, Speakman JR (2005) Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. *Mar Ecol Prog Ser* 294:1–8
- Wanless S, Frederiksen M, Walton J, Harris MP (2009) Long-term changes in breeding phenology at two seabird colonies in the western North Sea. *Ibis* 151:274–285
- Watanuki Y, Ito M, Deguchi T, Minobe S (2009) Climate-forced seasonal mismatch between the hatching of rhinoceros auklets and the availability of anchovy. *Mar Ecol Prog Ser* 393:259–271
- Wernham CV, Toms MP, Marchant JH, Clark J, Siriwardena G, Baillie S (eds) (2002) *The migration atlas: movements of the birds of Britain and Ireland*. T & AD Poyser, London

Submitted: March 30, 2011; Accepted: November 21, 2011

Proofs received from author(s): February 29, 2012