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Climate change impact on Balearic shearwater through a trophic cascade

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A recent study showed that a critically endangered migratory predator species, the Balearic shearwater *Puffinus mauretanicus*, rapidly expanded northwards in northeast Atlantic waters after the mid-1990s. As a significant positive correlation was found between the long-term changes in the abundance of this seabird and sea temperature around the British Isles, it was hypothesized that the link between the biogeographic shift and temperature occurred through the food web. Here, we test this conjecture and reveal concomitant changes in a regional index of sea temperature, plankton (total calanoid copepod), fish prey (anchovy and sardine) and the Balearic shearwater for the period 1980–2003. All three trophic levels exhibit a significant shift detected between 1994 and 1996. Our findings therefore support the assertion of both a direct and an indirect effect of climate change on the spatial distribution of post-breeding Balearic shearwater through a trophic cascade.

Keywords: Balearic shearwater; climate change; trophic cascade; regime shift

1. INTRODUCTION

Current climate change is altering the biodiversity, structure and functioning of marine ecosystems and many studies report an increase in biogeographic and phenological shifts throughout the ocean [1,2]. In some cases, ocean warming has affected ecosystems in a nonlinear way, species or communities responding by a sequence of sudden and stepwise shifts followed by subsequent periods of more relative stability [3]. Recently, Wynn and colleagues showed that a critically endangered migratory predator species, the Balearic shearwater *Puffinus mauretanicus*, rapidly expanded northwards in northeast Atlantic waters after the mid-1990s [4]. As they found a significant correlation between the long-term changes in the abundance of this seabird and sea temperature around the British Isles during post-breeding dispersal, they conjectured that the link between the biogeographic shift and temperature might occur through the food web.

Votier *et al.* [5] criticized the study of Wynn and colleagues, stating that the evidence to support a causal connection between sea surface temperature (SST) and Balearic shearwater was speculative and not robust.

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Several non-SST-related alternative explanations were proposed such as inappropriate analytical approach, change in observer awareness as a consequence of the taxonomic split from Manx shearwater *Puffinus puffinus* in 1991 [6] and the failure to recognize the importance of fisheries discards. In their response, Wynn *et al.* [7] highlighted the lack of evidence to support this last point. However, their study did not include investigation of the biological intermediate mechanisms by which the climatic signal may affect the abundance and spatial distribution of the Balearic shearwater [7].

In this study, we investigate these intermediate biological processes and evaluate the relationship between climate change and the Balearic shearwater, incorporating data on zooplankton and fish prey. We show that long-term changes in the number of Balearic shearwaters around the UK paralleled concomitant biological changes ranging from zooplankton (calanoid copepods) to their fish prey (*Sardina pilchardus* and *Engraulis encrasicolus*) [4,5]. Our findings therefore support Wynn's hypothesis of a climate-driven range expansion of the Balearic shearwater in the waters of the northeast Atlantic through trophic cascade.

2. MATERIAL AND METHODS

(a) Sea surface temperature

We used an index of change in sea surface temperature (SST) for the northern part of the North Atlantic. This index is the first principal component derived from a principal component analysis performed on average annual SST [3]. The geographical area in which this index was calculated is roughly similar to the one used by Wynn *et al.* [4].

(b) Biological data

Zooplankton data come from the Continuous Plankton Recorder (CPR) survey [8]. We used total calanoid copepod from the CPR survey. As the CPR survey uses a silk with a mesh size of 270 μm , a reduction in the value of this index also indicates a change in zooplankton composition from large-dominated to small-dominated zooplankton species [9]. The annual average of total calanoid copepods was calculated in the geographical area (17°W–4°E and 48–60°N) considered in Wynn *et al.* [4].

We used modelled data on the probability of occurrence of both European anchovy (*Engraulis encrasicolus*), European sardine (*Sardina pilchardus*), sprat (*Sprattus sprattus*) and herring (*Clupea harengus*), because these species are potentially important prey for the Balearic shearwater [4]. Probability of fish occurrence was calculated from the non-parametric probabilistic ecological niche model [10,11]. Our modelling is based on actual occurrence data point from the database 'Ocean Biogeographic Information System'. It uses information on sea surface temperature, bathymetry and sea surface salinity to reconstruct the ecological niche of a species and project onto a geographical space [11]. Spatial distribution of the average mean of these variables is shown in Beaugrand *et al.* [10]. An average annual value was calculated for all four species in the geographical area (17°W–4°E and 48–60°N) considered in Wynn *et al.* [4] and in the Bay of Biscay (7.9°W–0°W and 43.5–47.8°N) for both sardine and anchovy.

Balearic shearwater data were extracted from figure 2a of Wynn *et al.* [4].

(c) Sequential algorithm for testing regime shift

To test for regime shift, we applied Rodionov's sequential algorithm in which a first-order autoregressive model was inserted to consider temporal autocorrelation (method of inverse proportionality with four corrections, subsample size of 5 years) [12]. We used a probability threshold of 0.01 and cut-off length of 10. These two parameters control the magnitude and the scale of the shift. The Huber's weight parameter was fixed to 1 to account for outliers above 1 standard deviation. This analysis was conducted on the period 1960–2005 for the SST index, zooplankton and fish prey and on the period 1980–2003 for the Balearic shearwater. Results are only presented graphically for the period 1980–2003.

(d) Correlation analysis

Relationships between long-term changes in annual SST, plankton and fish were investigated by linear correlation analysis. Probabilities

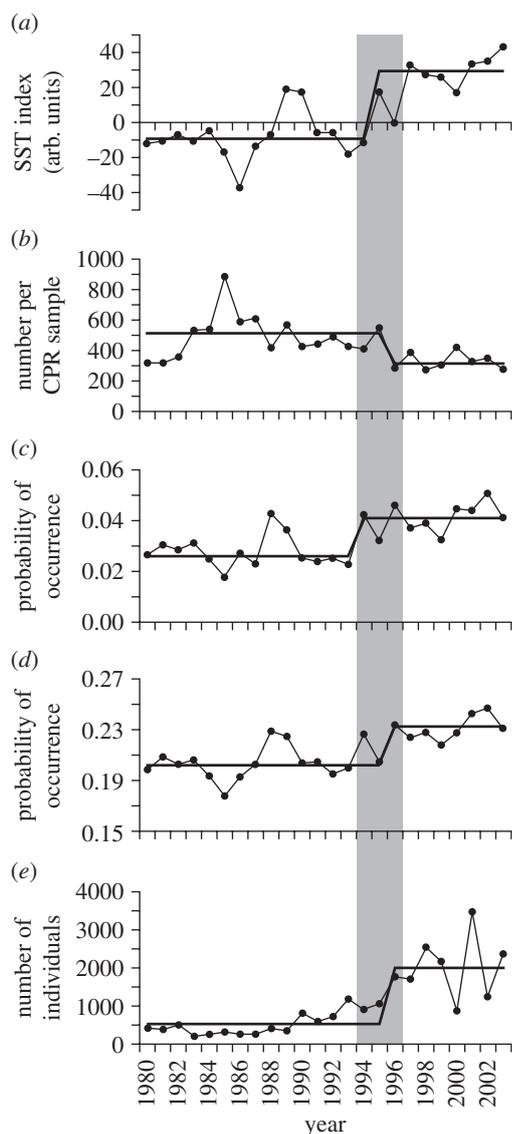


Figure 1. Long-term changes in (a) SST index, (b) total calanoids, (c) sardine, (d) anchovy and (e) Balearic shearwater. The timing of the shift, identified by Rodionov's test, is superimposed. The grey bar indicates the period 1994–1996.

were calculated without and with consideration for temporal autocorrelation [2].

3. RESULTS

We found similar long-term changes in all time series ranging from the SST index to zooplankton, fish and Balearic shearwater (figure 1). The increase in Balearic shearwater paralleled an increase in annual SST, a reduction in total calanoid copepod reflecting a decrease in the size of calanoids and an augmentation of the modelled probability of occurrence of both anchovy and sardine. When correction for autocorrelation was not applied, all correlations between the Balearic shearwater and other time series were significant (figure 2). However, when the correction for autocorrelation was used, the significance level falls to $p_{ACF} = 0.15$ for sardine and $p_{ACF} = 0.11$ for anchovy, indicating that part of the relationship between the Balearic shearwater and its fish prey was

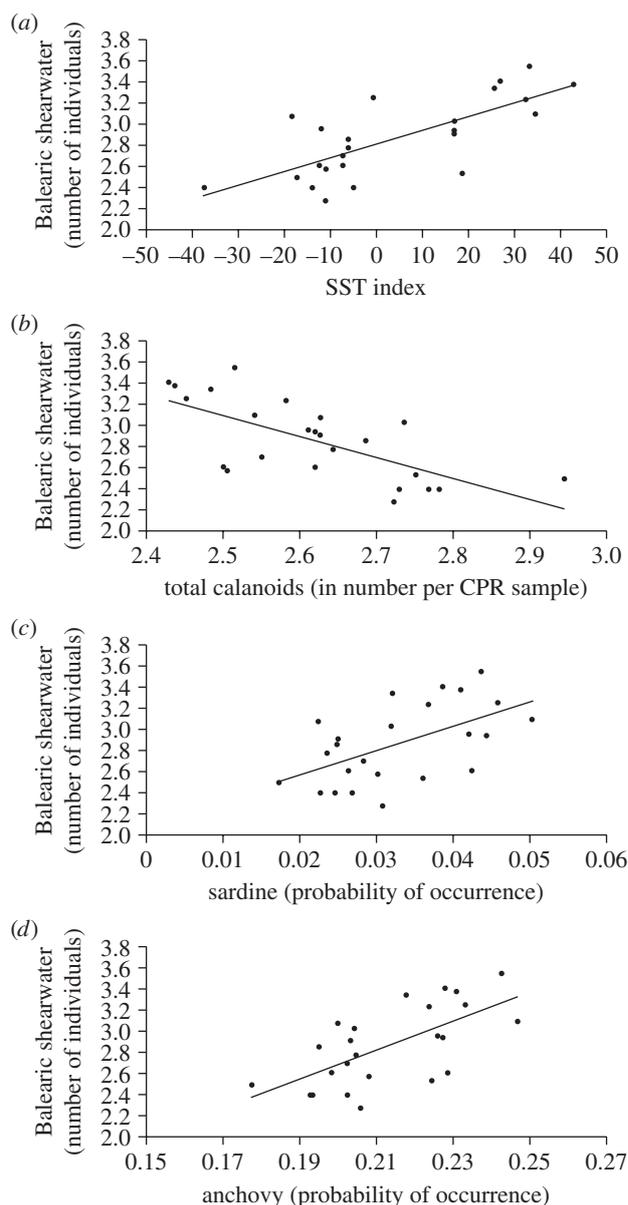


Figure 2. Scatterplot of the number of individuals of Balearic shearwater versus (a) SST index ($r = 0.74$; $p_{ACF} = 0.09$; $p < 0.001$), (b) the plankton index ($r = -0.69$; $p_{ACF} = 0.05$; $p < 0.001$), (c) sardine ($r = 0.56$; $p_{ACF} = 0.05$; $p < 0.005$) and (d) anchovy ($r = 0.65$; $p_{ACF} = 0.09$; $p < 0.001$). The correlation coefficient, the probabilities without (p) and after accounting for autocorrelation (p_{ACF}) are superimposed.

related to the long-term trend (i.e. low-frequency variability) of the series.

Rodionov's sequential algorithm detected a significant shift at the probability level of 0.01 in 1994 for sardine, 1995 for annual SST and 1996 for plankton, anchovy and Balearic shearwater (figure 1). Another shift observed in 1993 was only significant at the probability level of 0.03 (not shown), a year close to the time (1991) when the Balearic shearwater was separated from the Manx shearwater [5].

Recent anecdotal reports indicate that Balearic shearwaters can also feed on herring and sprat in UK waters (R. B. Wynn 2011, personal communication). However, no trend was observed for sprat and a step-wise reduction was observed for herring after 1994 (see the electronic supplementary material, figure S1).

In the Bay of Biscay, both sardine and anchovy also exhibited a stepwise increase after 1993 (see the electronic supplementary material, figure S2). Although long-term changes in the probability of occurrence of fish were only based on average SST, this does not mean that the probability is correlated to long-term changes in SST as the relationship between the two variables is nonlinear in the Euclidean space of the niche [10,11].

4. DISCUSSION

Wynn *et al.* [4] provided evidence for a rapid northward range expansion of Balearic shearwater in sea regions around the British Isles. Although they estimated an annual number of 500 individuals per year between 1980 and 1990 over the UK and Ireland, this number increased up to 3500 birds in 2001. As they found a significant correlation between mean annual SST and the abundance of the bird, they posited that the relationship was possibly indirect through the food web but the hypothesis was not tested. By using data on zooplankton and fish, here we showed that long-term changes in the abundance of Balearic shearwater paralleled not only changes in a regional SST index (positive correlation), but also changes in total calanoid copepod (negative correlation) and the probability of occurrence of both anchovies and sardine (positive correlation). Our results therefore support the hypothesis of Wynn and colleagues.

We also modelled the probability of occurrence of both sardine and anchovy in the Bay of Biscay. However, modelled data indicate a stepwise increase of both fish species after 1993; this contradicts the observed decrease in anchovy and the recent fishery moratorium [13], and highlights the complicating influence of commercial fishing on these prey species.

Our findings also provide more information on the type of changes exhibited by the Balearic shearwater. Using Rodionov's sequential algorithm, our study detected a pronounced shift centred around the mid-1990s for three trophic levels. Votier *et al.* [5] suggested a potential bias caused by a modification in the taxonomic status of the species at the beginning of the 1990s. However, our study reveals that the shift observed in 1996 is much stronger than the shift in 1993. It is therefore unlikely that the separation of Balearic shearwater from Manx shearwater is at the origin of the increase in abundance after 1996 as pointed out by Votier *et al.* [5]. Since then, the species has continued to be detected at an elevated level in UK waters [13].

The stepwise reduction in total calanoid copepods observed in 1996 reflects a substantial reorganization in the biodiversity of this key trophic group observed around the British Isles between the middle and the end of the 1990s [2]. The average mesh size of the CPR machine being constant, it is very likely that this reduction influenced the number of calanoid caught by the CPR survey, explaining the diminution of the index particularly pronounced in 1996. The reduction also reflects the increase in the number of smaller subtropical calanoids found in the Bay of Biscay and preyed by anchovy and sardine (www.fishbase.org).

Large-scale biogeographic shifts in the Bay of Biscay and over the southern part of the Celtic Sea and the English Channel were detected during the 1990s [2]. An increase in subtropical species (e.g. *Candacia ethiopica*, *Centropages violaceus*) paralleled a reduction in warm-temperate species. These species are also among species caught by anchovy and sardine (www.fishbase.org). This rearrangement in the biodiversity reduced the mean size of calanoid copepods [9].

Simultaneous changes in the number of subtropical fish have also been identified [14] and some findings described latitudinal movements of fish species distribution that coincided to changes in sea surface temperature [15,16]. Here, we show that the modelled probability of both anchovy and sardine increased in the area of concern. The augmentation of the modelled probability corresponds with observations reported of an increase in the abundance of both species in the same area. In the northern part of the North Sea although both anchovy and sardine were seldom observed during the period 1925–1994, they became more prevalent after 1995 [17]. Our study reveals probably a new abrupt ecosystem shift in the region which follows the well-documented shift that occurred in the North Sea in the 1980s [18]. Some observations tend to indicate that the shift might have influenced more species. For example, there is increasing evidence that other seabirds have shown rapid changes in status off southern England since the mid-1990s, e.g. wintering red-throated divers *Gavia stellata* and foraging movements of (probably non-breeding) Manx shearwaters [19].

Our study therefore explains the rapid northward range expansion of the Balearic shearwater in sea regions around the British Isles by the indirect effect of temperature on the bird through trophic cascade. An alternative hypothesis could be that climate influences all these trophic levels independently. This result is particularly plausible for CPR-derived zooplankton indicators. Although our study remains correlative and is subject to the confounding influence of fishing, the coincidence between changes observed in three trophic levels at a macroecological scale support the hypothesis proposed by Wynn *et al.* that the increase in sea temperature may have triggered an increase northwards of the seabird by having influenced plankton composition and their fish prey.

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