Global Change Biology (2007) **14**, 1–12, doi: 10.1111/j.1365-2486.2007.01471.x

Detecting the impact of oceano-climatic changes on marine ecosystems using a multivariate index: The case of the Bay of Biscay (North Atlantic-European Ocean)

GEORGES HEMERY*, FRANK D'AMICO†, IKER CASTEGE*, BERNARD DUPONT‡, JEAN D'ELBEE§, YANN LALANNE† and CLAUDE MOUCHES†

*Muséum National d'Histoire Naturelle, Department of Ecology and Biodiversity Management, USM 305 Conservation of Species, Plateau de la Petite Atalaye, F-64200 Biarritz, France, †UPPA – Department of Ecology, UFR Sciences and Techniques – F-64600 Anglet, France, ‡Météo-France, Station de Biarritz-Parme, F-64200 Biarritz, France, §LAPHY – 1341 chemin d'Agerrea, F-64210 Ahetze, France

Abstract

Large-scale univariate climate indices (such as NAO) are thought to outperform local weather variables in the explanation of trends in animal numbers but are not always suitable to describe regional scale patterns. We advocate the use of a Multivariate Oceanic and Climatic index (MOCI), derived from 'synthetic' and independent variables from a linear combination of the total initial variables objectively obtained from Principal Component Analysis. We test the efficacy of the index using long-term data from marine animal populations. The study area is the southern half of the Bay of Biscay (43°–47°N; western Europe). Between 1974 and 2000 we monitored cetaceans and seabirds along 131000 standardized line transects from ships. Fish abundance was derived from commercial fishery landings. We used 44 initial variables describing the oceanic and atmospheric conditions and characterizing the four annual seasons in the Bay of Biscay. The first principal component of our MOCI is called the South Biscay Climate (SBC) index. The winter NAO index was correlated to this SBC index. Inter-annual fluctuations for most seabird, cetacean and fish populations were significant. Boreal species (e.g. gadiformes fish species, European storm petrel and Razorbill . . .) with affinities to cold temperate waters declined significantly over time while two (Puffin and Killer Whale) totally disappeared from the area during the study period. Meridional species with affinities to hotter waters increased in population size. Those medium-term demographic trends may reveal a regime shift for this part of the Atlantic Ocean. Most of the specific observed trends were highly correlated to the SBC index and not to the NAO. Between 40% and 60% of temporal variations in species abundance were explained by the multivariate SBC index suggesting that the whole marine ecosystem is strongly affected by a limited number of physical parameters revealed by the multivariate SBC index. Aside the statistical error of the field measurements, the remaining variation unexplained by the physical characteristics of the environment correspond to the impact of anthropogenic activities such overfishing and oil-spills.

Keywords: abundance patterns, cetaceans, climatic index, disturbance ecology, fish stocks, oil-spills, regime shifts, seabirds

Received 4 May 2006; revised version received 27 September 2006 and accepted 10 August 2007

Correspondence: Georges Hemery, e-mail: georges.hemery@univ-pau.fr

Introduction

It is well known that climate affects both the abundance and distribution of species populations and that a blend of weather variables – rather than a single one- is operating (Hughes, 2000; Stenseth *et al*., 2003). Given

© 2007 The Authors
Journal compilation © 2007 Blackwell Publishing Ltd

the increasing evidence that our planet is facing rapid climate change, ecological effects of large-scale climate patterns are increasingly being studied. Today the climate literature describing those variations is vast (Stenseth *et al*., 2003). Not surprisingly, various indices (cf. Stenseth *et al*., 2003) describe climate patterns over the Northern and the Southern hemispheres. Most of them are characteristically derived from simple difference in one weather variable (e.g. difference in sea level pressure anomalies between two distant locations) although complex and pertinent statistical approaches based on multivariate analysis of time-series exist. Following seminal reviews (Kappelle *et al*., 1999; Hughes, 2000), there has been an increasing number of papers using the available simple (one-variable-based) climate indices to assess the biological consequences of large-scale climate patterns and change on continental and marine ecosystems (Forchhammer & Post, 2000; Kozlov, 2000) despite the fact that they reduce complex space and time variability into simple measures (Stenseth *et al*., 2003). Among those large-scale climate indices now easily available on the Internet are the set of NAO- and ENSO-related climate indices reviewed extensively by Stenseth *et al*. (2003). The first hypotheses explaining why NAO and perhaps all large-scale indices seem to perform better than local weather variables are just coming out (Hallet *et al*., 2004; Stenseth & Mysterud, 2005).

Several studies using such simple climate indices have demonstrated that large-scale climate patterns have major implications for the functioning of different continental and marine ecosystems (Post *et al*., 1999; Bradley & Ormerod, 2001; Thompson & Ollason, 2001; Møller, 2002; Rodriguez & Bustamante, 2003; Hallet *et al*., 2004; Hays *et al*., 2005). By contrast, other studies have failed to identify significant trends (Blenckner & Hillebrand, 2002) and this could be explained by the fact that such one-variable-based synthetic climatic indices may be too simple to describe complex patterns in ecosystem function. Some researchers, like Kitayski & Golubova (2000), have thus assessed the impact of the interannual climate and oceanographic change on seabird populations by using a larger set of climatic and physical variables: sea-surface temperature (SST), time of permanent ice disappearance, wind and current vectors. Many studies though also fail to track effects of large-scale climate patterns on community composition or abundance because confounding regional or local human-borne disturbance (such as overfishing and oil spills in marine ecosystems) interact with them (Hémery *et al*., 1986a; Castège *et al*., 2004; Hémery *et al*., 2005).

In complex marine environments where many physical factors other than climatic are at work, large-scale climate indices are considered drivers of ecological variability because they could act through local hydrology and meteorology (e.g. on plankton – see Hays *et al*., 2005). So far, few studies use multivariate indices that have the potential to explain effects of marine environmental change driven by large-scale climate patterns (Lehman, 2000; Feistel *et al*., 2003; Schwing *et al*., 2003) despite a few synthetic multivariate approaches are available such as the multivariate ENSO index (called MEI and combining sea-level pressure, surface wind, sea-surface temperature, surface air temperature and cloudiness – see Wolter & Timlin, 1998).

The main aim of this paper is to relate the long-term change in abundance of marine animals to a new Multivariate Oceano-Climatic index (hereafter MOCI) that fits better to the local marine environment. As a first step, a definition of the MOCI and a rationale for its calculation are given. We also present its statistical properties. Because we apply it to the case of the Bay of Biscay in the North-Atlantic-European region, the MOCI for this region is called the South Biscay Climatic (SBC) index and can be compared with the well-known univariate NAO index. Then, we present for the same region of the Bay of Biscay the long-term variation in the abundance of several marine fish, seabird and cetacean species along with one crustacean species. Finally, we investigate the relationship existing between climate variations and the temporal variation in marine biota abundance at the community level, comparing the relative success of the multivariate MOCI vs. the univariate NAO.

Material and methods

Study area

The study area is the southern half of the Bay of Biscay (from 43 to 47°N; western Europe – Fig. 1). It corresponds mainly to the International Council for the Exploration of the Sea (ICES) zone VIII-b1. The bathymetry of this zone is characterized by the canyon of Capbreton, a unique feature in Europe where the shelf break (isobath 200 m) is only 1.3 nautical miles from the coast and a depth of 1000 m lies no more than 15.6 nautical miles offshore. The remaining area consists of the continental shelf (depth <200 m). The mean SST usually vary between 10–11 °C in winter and 19–22 °C in summer (Koutzikopoulos *et al*., 1998) during which an area of hot SST appears (Hémery & Wald, 1986). The Bay of Biscay encompasses the more or less fluctuating limit or transitional region between the cold boreal waters and the warm waters of the temperate biogeographical province for zooplankton and fish species (Quéro *et al*., 1989; Herbland & Quéro, 1998; d'Elbée & Prouzet, 2001; Souissi *et al*., 2001). The climate shows high seasonality and also important inter annual

© 2007 The Authors

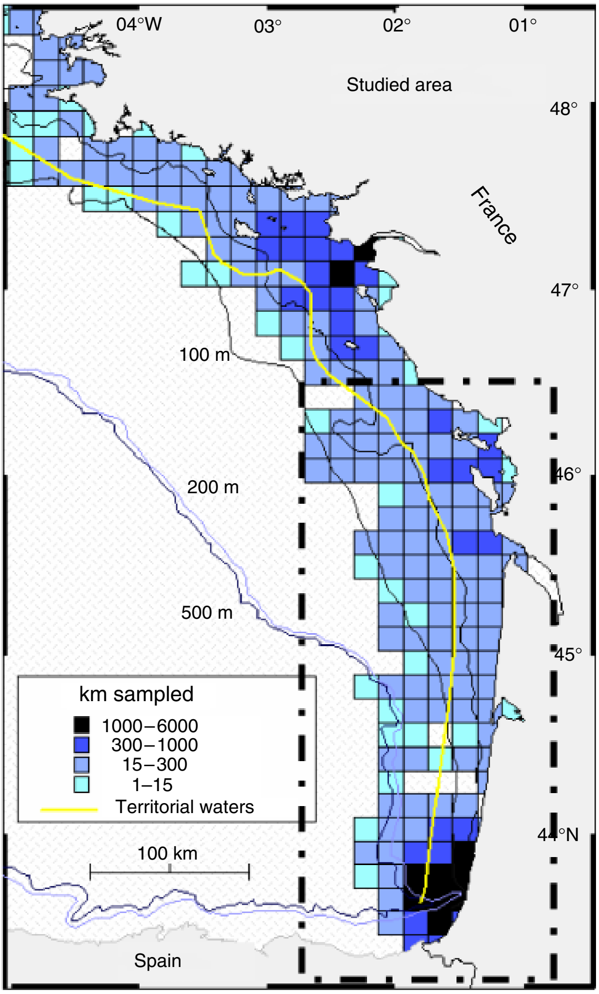

Fig. 1 The study area in the south Bay of Biscay (north-east Atlantic, Europe) is delimited by the dotted line. Square grid indicates kilometres travelled during the whole study (see also Castège *et al*., 2004).

variations; formally described as temperate it is induced by two main phenomena: on one hand, the marine anticyclone of the Azores (in summer essentially) or the continental anticyclone of Siberia (mostly in winter) and on the other hand, the low pressure of Iceland which produces a general westerly flux of perturbations in the direction of Europe.

Assessing oceano-climatic change

On a global scale, atmospheric and oceanic physical features such as temperature, atmospheric pressure, wind, rainfall and sea state are linked together; the nature of these links being more or less deterministic and the strength variable. Each parameter taken independently brings partial information on the existing conditions of the physical environment made up of a large number of simultaneously interacting variables. A multivariate approach can successfully detect and describe the essential structure of the information held in this large set of correlated variables. A principal component analysis (PCA) on the normalized variables correlation matrix objectively builds new 'synthetic' and independent variables made up of a linear combination of the total initial variables. The first principal component is the more informative and corresponds to the MOCI. This general approach leads to the definition of a general index based on a potentially high number of oceano-climatic variables that has then to be restricted to a more specific one describing best the region under study. In this study, we used 11 initial variables (Table 1) characterizing each of the four annual seasons (spring, summer, autumn and winter, providing 44 variables in total) to describe the yearly oceanic and atmospheric conditions during the last 3 decades in the Bay of Biscay. Thus, the data matrix was composed of 27 rows each for 1 year from 1974 to 2000 and 44 columns corresponding to oceano-climatic variables (data not shown).

We then compared the SBC index with the widely used (Stenseth *et al*., 2003) and well-described North Atlantic Oscillation index (NAO index – Hurrell, 1995; Hurrell & van Loon, 1997). Here, the values of the NAO index used are those of the winter season (http://www.cgd.ucar.edu/jhurrell/nao/html).

Modelling animal abundance: cetaceans, seabirds and fishes

As the Bay of Biscay presents the limit between the cold (boreal) and hotter (meridional or Lusitanian) temperate waters, the various species were classified as distributed preferentially either of the two waters or showing no preference/link with sea temperature. For fishes, species were attributed to this classification based on Quéro *et al*. (2003). Similarly, sea birds and cetaceans were categorized according to their breeding range and overall spatial distribution.

Data collection. Cetaceans and seabirds at sea were recorded under standardized conditions (Hémery *et al*., 1986b; see also Hammond *et al*., 2002) of line transects (Skellam, 1958; Seber, 1982; Buckland *et al*., 1993). We realized 131 000 counts, each of 1 min (total observation time 22:00 hours), made from vessels of the Douanes Françaises and the Affaires Maritimes (thereafter referred to as Coast Guard ships), The protocol imposed the following main conditions: a visibility at least of 1 nautical mile, a sea under the state 4 (international sea state code *S* ranging from 1 to 9), an angle of view of 360°, observer placed at 6–8 m a.s.l. and a cruise speed ranging from 15 to 22 knots. The

© 2007 The Authors
Journal compilation © 2007 Blackwell Publishing Ltd, doi: 10.1111/j.1365-2486.2007.01471.x

Table 1 The 11 variables used in the Oceano-Climatic Multivariate Index in the Bay of Biscay (= SBC index)

No.		Climatic variable	Comment
1	Oceanic variables	Sea surface temperature	
2		Sea surface agitation: minimum	Range: 0–2, waves: 0–0.5 m
3		Sea surface agitation: medium	
4		Sea surface agitation: maximum	Range: 5–9, waves: 2.5 to >14 m
5	Atmospheric variables	Atmospheric pressure	
6		Temperature: mean of the minima	
7		Temperature: mean of the maxima	
8		Cumulated rainfall	
9		Sunshine duration	
10		Maximal instantaneous wind	Number of days $<25\,\mathrm{km\,h^{-1}}$
11		Maximal instantaneous wind	Number of days $>60\,\mathrm{km\,h^{-1}}$

They characterize each of the four seasons, a year being thus described by 44 variables.

detection of animals was made by naked eye, binoculars being used only for confirmation of the species and characteristics of the individuals. No *a priori* maximal distance of detection was fixed. Records made in the vicinity (within 2 min of observation) of other ships, in particular fishing vessels, were eliminated in the present analysis to exclude possible bias due to temporal changes of the flotilla. In the present case, only relative density of seabirds and cetaceans, expressed by the number of animals detected under these standardized conditions by unit of time or distance travelled, were considered. Shipboard surveys were conducted from June 1976 to June 2002 and the means of their relative abundances at sea were calculated for each of the 12 months of the year. Line transects were all homogenous and comparable within and between years simply because they were made from vessels of the Coast Guard ships, using no predetermined trip or at least giving the same probability for each sea trip to be made at any place in the region. Of course, because vessels depart to sea and come back from the same harbour, the amount of kilometers travelled and sampled is higher near those harbours (Fig. 1). This methodology was used for all bird species except the European storm petrel *Hydrobates p. pelagicus* for which the population was estimated by the number of breeding pairs at the Basque French colonies (Hémery *et al.*, 1986b). It has been shown that this population abundance is effectively a good indicator of abundance of the first year fish (class 0) and the zooplankton (d'Elbée *et al.*, 1998; Hémery, 2001).

Fish and the large crustacean *Crangon crangon* abundance was estimated from commercial fishery landings by coastal ships operating in the southern half of the Bay of Biscay (Centre Régional de Traitement Statistique des Pêches de La Rochelle, French Ministry of the Sea). According to the size and age classes of the fish species caught by fisheries (Quéro & Vayne, 1997) a time lag of 2 (*Merluccius merluccius*, *Pollachius pollachius*, *Trisopterus* sp., *Thunnus thynnus*) or 3 years (*C. crangon*, *Trachurus trachurus*, *Scomber* sp., *Mugil* sp.) was applied explaining why years of reference vary slightly in the different analysis.

Patterns and trends in seabirds and cetaceans community. The characteristics of the community of seabirds and cetaceans were examined by Correspondence Analysis (CA) (Jongman *et al*., 1995; Leps & Smilauer, 2003). The data matrix was composed of 12 rows corresponding to the mean monthly abundance of the 12 most abundant species, or group of species, monitored and 23 columns each for 1 year from 1979 to 2001. No chronological order of the years was included in the calculation of the factorial axis.

Trend analysis and correlation for SBC, NAO and population abundance were performed using Kendall τ rank correlation and Pearson linear correlation depending on the statistical properties of the data.

Decline in population size was calculated by approximating the temporal change to a linear decline considering slope as a measure of the decline; we first log-transformed data over the whole study period for each species, then made a linear regression and taking the exponential of the slope value we got the estimate of the decline.

All analysis were made with the Statistical Analysis System (procedures PRINCOMP, CORRESP and CORR), CANOCO software (Ter Braak & Smilauer, 2002) and MAPINFO software for Fig. 1.

Results

Temporal trends in the SBC index

The first principal component PC1 extracted 29% of the whole information contained in the initial data matrix.

© 2007 The Authors
Journal compilation © 2007 Blackwell Publishing Ltd, doi: 10.1111/j.1365-2486.2007.01471.x

The corresponding SBC index varied according to year from −3.0 to +5.8. Negative values characterized years with important rainfall and rough sea surface, conditions occurring mainly during winter and linked to low pressures with the arrival of north-west cold fronts moving south-east. By contrast, positive values of this index indicated years with high pressures, atmospheric temperature above the normal mean value, heavy sunshine and a smoother sea-surface state which corresponded to stable conditions (or with moderate eastward wind). These variations are explained by the relative location of the region Bay of Biscay along the eastern front of the anticyclone. Temporal variations for the period 1974–1994 were described by an increasing and significant trend (Kendall Test of ranks, $\tau = +0.610$; $P < 0.0001$) toward positive values of the SBC corresponding to anticyclonic-type situations with low agitated sea-surface (Fig. 2). Recently (1994–2000), this trend significantly switched back (Kendall Test of ranks, $\tau = -0.556$; $P < 0.025$) marking a come back of cyclonic-type weather characterized by important rainfall, cold conditions and rough sea-surface.

The winter NAO index was significantly correlated to the SBC index ($\rho = +0.489$; $P = 0.011$, Fig. 2). The autocorrelation of first order was high ($\rho = +0.489$) and significant ($P = 0.0005$) for the SBC index but low ($\rho = +0.228$) and not significant ($P = 0.112$) for the NAO index. An overall positive temporal trend (Fig. 2) was significant for the SBC index (Kendall Test of ranks, $\tau = +0.504$, $P = 0.0002$) but there was no significant trend for the NAO index ($\tau = +0.133$, $P = 0.343$).

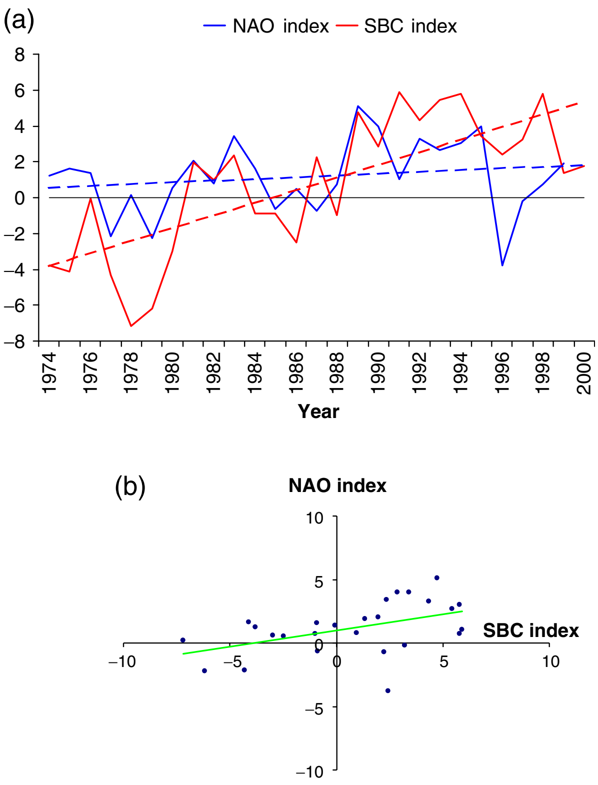

Fig. 2 Compared variation in univariate index (NAO index; blue line) and application of the Multivariate Oceano-Climatic index (MOCI) in the Bay of Biscay (SBC index; red line) over the period 1974–2000. (a) Dotted lines depict long-term trends. There was a significant increasing trend toward positive values of the SBC index (Spearman coefficient correlation $r = +0.7296$, $P < 0.0001$) but not for NAO index ($r = +0.1929$, $P = 0.3451$). (b) Positive correlation between SBC and NAO (Pearson correlation coefficient $r = +0.4727$, $P = 0.0147$).

Temporal changes in animal populations abundances (mammals, seabirds and fishes)

There were important variations in abundance for most of the species studied during the period 1974–2000 (Fig. 3 and Table 2) and despite inter-annual population fluctuations the trends were significant for most of them and indicated medium-term demographic trends (Table 2). Species with affinities to hotter temperate waters (lusitanian or meridional biogeographical zone) increased in population size during the period (Fig. 3a). This was particularly true for the Common Dolphin *Delphinus delphis* and the Chub Mackerel *Scomber japonicus* whom average abundance increased (per year +1.4% and +11.8%, respectively) significantly during the whole period. But it is important to note that their abundance has slightly decreased since 1997 (see Appendix S1 in Supplementary Material). By contrast, the abundance of boreal species with affinities to cold temperate waters decreased significantly during the period (Fig. 3b and Table 2). This was particularly obvious for the European storm petrel and the Razorbill which breed merely on the British Isles, in Scandinavia and Iceland. It is important also to note the total disappearance, in the southern part of the Bay of Biscay, of two species: the Atlantic Puffin (*Fratercula arctica*) and the Killer whale (*Orcinus orca*) over the study period. Boreal Gadiformes fish species also decreased in abundance (European hake *M. merluccius*, Pouting *Trisopterus luscus* principally, Pollack *P. pollachius* . . .). The only crustacean so far studied (*C. crangon*) also markedly decreased in abundance (−2.5% per year).

The trends for the remaining species, those without any thermal affinities varied widely during the same period. Pilot whale *Globicephala melas* and Anchovy (*Engraulis encrasicolus*) did not show any trend while there was an increase in population size of Guillemot (*Uria aalge*). By contrast Mullets (*Mugilidae* family) and Pilchard (*Sardina pilchardus*) sharply decreased in abundance (ca. −10% mean annual decrease).

© 2007 The Authors
Journal compilation © 2007 Blackwell Publishing Ltd, *Global Change Biology*, doi: 10.1111/j.1365-2486.2007.01471.x

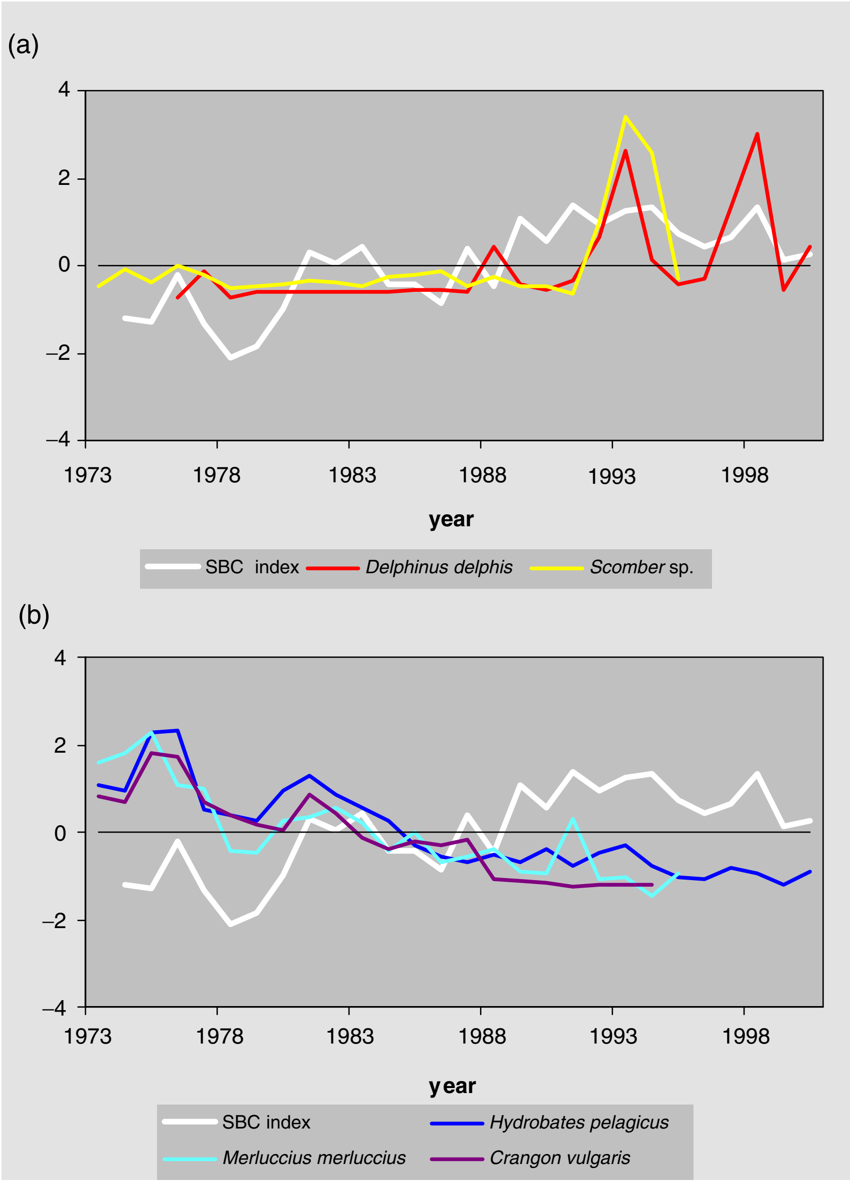

Fig. 3 Variation in abundance (the original field data were normalized to mean = 0 and SD = 1) for different species in the Bay of Biscay (1974–2000) according to their preferendum. (a) Meridional species with affinities to hot temperate waters and (b) Boreal species with affinities to cold temperate waters. White line indicates variation in SBC index.

The ordinations made by the three first axis of the CA described patterns in community structure for marine birds and cetaceans. The first and second axis extracted 28.9% and 17.6%, respectively, of the variance of the data. Positive score values on axis 1 were related to an increasing abundance of the majority of marine birds (Fig. 4), whereas negative values depicted the three cetacean species and the Northern Gannet *Morus bassanus*. The third axis extracted 15.9% of the information. It was due essentially to the year 1999 during which an unusual abundance of Pilot whales occurred with a very high standard error. CA further identified (it is particularly obvious on the ordination axis 1–axis 3, Fig. 4b) three main sets of community types that broadly follow a chronological sequence, although they include a few years 'out of phase'. The first set A, concerns the years 1979–1986, excluding year 1985. The second set B, goes from 1987 to 1996, excluding year 1993. The third set C, runs from 1997 to 2001. Each of those sets is broadly attributable to the three community types identified above on the basis of their thermal preferendum; sets A and C correspond to the communities of cold (boreal) and hot (meridional or Lusitanian) temperate waters while

© 2007 The Authors
Journal compilation © 2007 Blackwell Publishing Ltd,

Table 2 Comparison between the multivariate SBC index and the NAO index for the correlations with the variation in abundance of the different species monitored in the Bay of Biscay (1974–2000) according to their *preferendum* (see text)

	Trends (Kendall test; *P*)	Mean annual variation	Correlation with SBC Index (Pearson; *P*)	Correlation with NAO Index (Pearson; *P*)
Cold water				
Orcinus orca	*−0.32 (P = 0.062)*	*	*−0.30 (P = 0.170)*	*−0.29 (P = 0.172)*
Hydrobates pelagicus	**−0.74 (*P* = 0.001)**	−7.1%	**−0.54 (*P* = 0.005)**	*+ 0.01 (P = 0.968)*
Fratercula arctica	**−0.51 (*P* = 0.01)**	*	*−0.35 (P = 0.148)*	*−0.17 (P = 0.508)*
Alca torda	**−0.59 (*P* = 0.001)**	−1.6%	*−0.22 (P = 0.405)*	*−0.1 (P = 0.960)*
Merluccius merluccius	**−0.68 (*P* = 0.0001)**	−3.3%	**−0.49 (*P* = 0.021)**	*−0.33 (P = 0.132)*
Trisopterus sp.	**−0.49 (*P* = 0.001)**	−3.4%	*−0.40 (P = 0.068)*	*−0.18 (P = 0.431)*
Pollachius pollachius	**−0.76 (*P* = 0.0001)**	−4.1%	**−0.63 (*P* = 0.002)**	*−0.39 (P = 0.069)*
*Crangon crango*n	**−0.66 (*P* = 0.0001)**	−2.5%	**−0.49 (*P* = 0.019)**	*−0.23 (P = 0.310)*
No preferendum				
Globicephala melas	*0.16 (P = 0.347)*	–	–	–
Uria aalge	**0.41 (*P* = 0.012)**	+ 3.1%	**+ 0.67 (*P* = 0.001)**	**+ 0.49 (*P* = 0.028)**
Mugil sp.	**−0.29 (*P* = 0.054)**	−9.7%	**−0.42 (*P* = 0.049)**	*−0.16 (P = 0.464)*
Sardina pilchardus	**−0.35 (*P* = 0.020)**	−10.2%	*−0.26 (P = 0.244)*	*−0.32 (P = 0.149)*
Engraulis encrasicolus	*−0.10 (P = 0.509)*	–	–	–
Hot waters				
Delphinus delphis	**0.35 (*P* = 0.025)**	+ 1.4%	**+ 0.43 (*P* = 0.043)**	*+ 0.26 (P = 0.236)*
Thunnus thynnus	*−0.07 (P = 0.653)*	–	–	–
Trachurus sp.	*−0.20 (P = 0.185)*	–	–	–
Scomber sp.	**0.13 (*P* = 0.0383)**	+ 11.8%	**+ 0.44 (*P* = 0.040)**	*+ 0.27 (P = 0.228)*

Mean annual variation is based on the linear regression of the log of abundance against time.
Bold characters indicate statistically significant results and italic characters indicate nonstatistically significant results.
*Disappearance of the species in the studied area.

set B is related to the community showing no link with sea temperature (Fig. 4 and Table 2). It is noticeable that within each of these three homogeneous sets, two particular years (1985 and 1993) are out of the sequence in respect to the characteristics of communities. Plotting axis 1 scores against years confirmed this clustering (Fig. 5) and outlines the peculiar 'behaviour' of communities in years 1985 and 1993.

Relationships between climate indices and variation in abundance

Except[1] for Guillemot, none of the observed trends was correlated to the NAO index. However, most of the observed trends (detailed above; Table 2) were highly correlated to the SBC index although being not significant for a few species (*O. orca*, *F. arctica*, *A. torda*, *Trisopterus* sp. and *S. pilchardus*). For all species pooled, between 40% and 60% of temporal variations in population abundance were explained by the multivariate SBC index.

[1]Note that a type I error is not totally excluded given the fact that we used a set of 12 statistical tests.

Discussion

Spatio-temporal pattern and univariate vs. multivariate climatic indices

Temporal variability in atmospheric and oceanic conditions is very high between seasons and may be random or auto-correlated between years. Beyond these short-range variations, there are medium- or long-term temporal variations occurring at decennial or centennial scale that are of interest when studying ecological patterns or processes. Nevertheless, ecologists use synthetic climate indices like those for the North Atlantic Oscillation (NAO – Hurrell, 1995; Hurrell & van Loon, 1997) and the Southern Oscillation index (SOI) despite the fact that they reduce complex space and time variability into simple measures (see Stenseth *et al.*, 2003 for an overview of NAO and ENSO indices). Most of those indices (SOI and NAO) rely on the measure of the atmospheric pressure (SLP) difference between two distant meteorological stations at different latitude or SST only. Their advantage lies in the geographic extent taken into account and the relative simplicity of their meteorological and climatic meaning. Evidence that they can explain some climate-related variation in life-history traits and animal numbers is just arising and

© 2007 The Authors
Journal compilation © 2007 Blackwell Publishing Ltd,

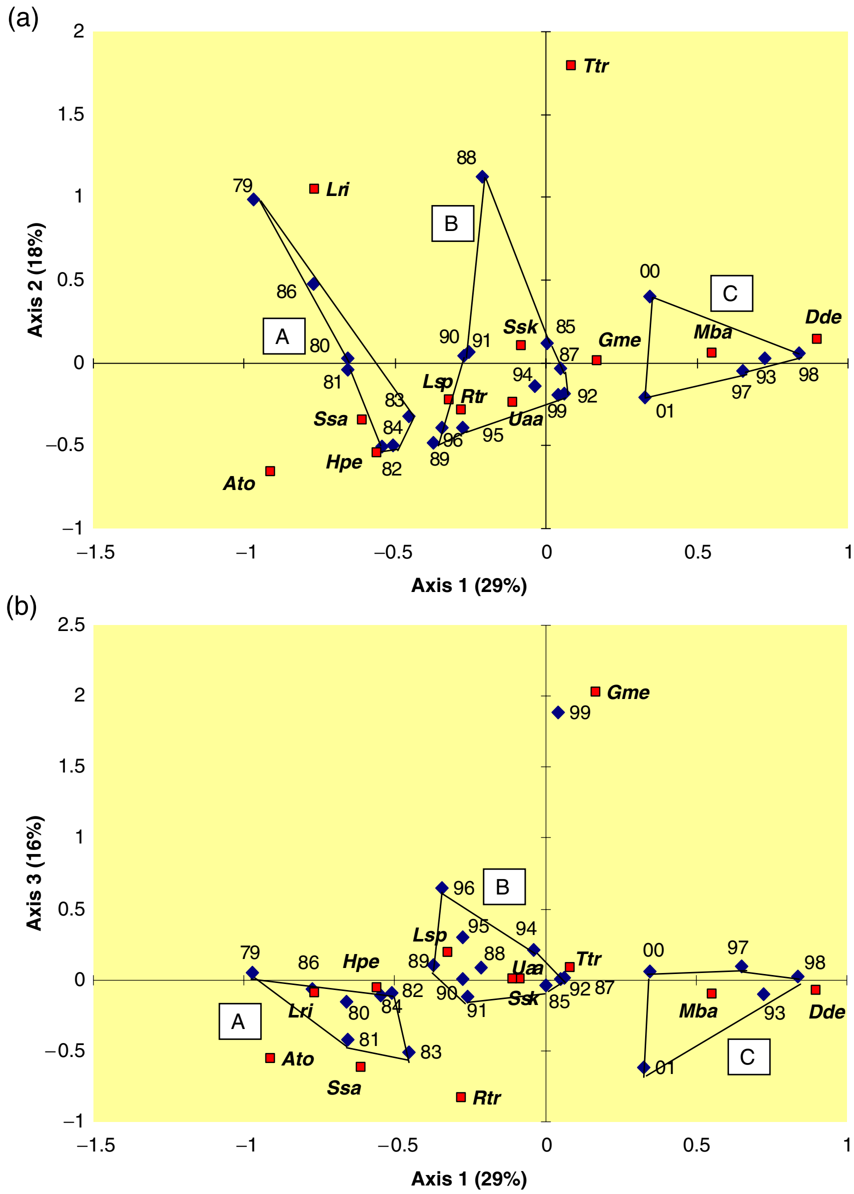

Fig. 4 Community structure of marine birds and cetaceans revealed by Correspondence Analysis (matrix 23 years × 12 species). (a) Axis 1 and axis 2 plan. (b) Axis 1 and axis 3 plan. Numbers indicate the last two digits of the year. Polygons joining consecutive years show three chronological periods A, B and C corresponding each to a particular assemblage of species. Abbreviations of species used: *Lsp*, *Larus* sp.; *Lri*, *Larus ridibundus*; *Ssa*, *Sterna sandvicensis*; *Hpe*, *Hydrobates pelagicus*; *Rtr*, *Rissa tridactyla*; *Ssk*, *Stercorarius skua*; *Mba*, *Morus bassanus*; *Dde*, *Delphinus delphis*; *Ttr*, *Tursiops truncatus*; *Gme*, *Globicephala melas*; *Uaa*, *Uria aalge*; *Ato*, *Alca torda*.

underlying mechanisms are just being identified (Hallet *et al.*, 2004; Stenseth & Mysterud, 2005). However, despite this, Stenseth & Mysterud (2005) admit that other 'weather packages' could outperform the NAO and other large-scale indices. Most of the large spatial scale indices are defined by only one variable, thus they neither reveal the full range of physical conditions characterizing oceanic habitats nor the complexity of their consequences on marine and terrestrial ecosystems. NAO and univariate ENSO indices reveal large-scale events such as those observed at the whole oceanic basin or even at the global scale. But large scale indices depict different patterns according to the area; for example, along a line in middle Europe there is no effect of NAO on any specific variable (http://www.cpc.ncep.noaa.gov/data/teledoc/nao_tmap.shtml). Because they are made up of a single variable, large-scale indices are easily reconstructed from chronological

© 2007 The Authors
Journal compilation © 2007 Blackwell Publishing Ltd, doi: 10.1111/j.1365-2486.2007.01471.x

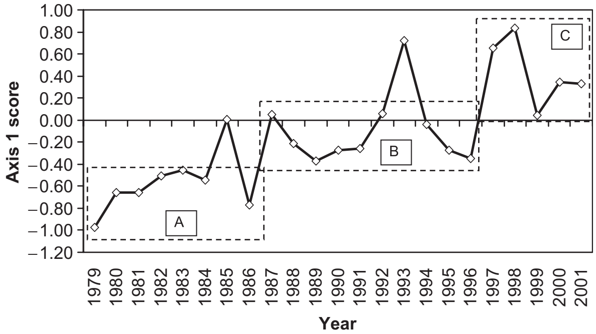

Fig. 5 Temporal variations of the community of marine birds and mammals (1979–2001) measured by the axis 1 score of the CA (cf. Fig. 4).

series gathered over more than one century. However, revealing patterns at regional scale (that one of the south Bay of Biscay in our case) requires more sophisticated multivariate indexes able to depict ecological processes depending on oceano-climate temporal variability. The SBC index proposed here fits better to this regional context at the scale of a whole bay (regional scale) because it relies on a large number of environmental variables and especially ones that describe oceanographic conditions. The winter NAO index is correlated to the SBC index. Overall, a higher autocorrelation of factors within the SBC index than for NAO is more prone to describe natural processes with lag effects between subsequent years. It also highlights the possibility to better detect statistically significant trends and consequently may serve as a predictor tool.

One other factor of interest of any multivariate index such as the MOCI SBC is that its use can be further refined by using the second and third principal components. It also gives the opportunity to extract other finer temporal details such as those describing seasonal or monthly variations and also finer spatial details within a same oceanic bay.

Stenseth *et al*. (2003) pointed out that ecologists have two alternatives when studying the effects of climate on any given ecosystem either use local weather measures either choose large-scale climate indice the latter ones being said to out perform the former (see Stenseth & Mysterud, 2005). They listed the many advantages use of large-scale climate indices. In particular, they wrote that 'using a large-scale index is similar to the use of principal components regression, where a PC analysis is first used to reduce the number of predictor variables.' We disagree partially with this view as the large-scale indices can be either univariate (calculated from SLP or SST) or multivariate. The reverse is true also as local weather can be described by a single variable (temperature for example) or a large number (and be synthetized into a new one using PCA – as we do). What we showed in our study is that (at least in this part of the Atlantic Ocean) a multivariate indice synthetically derived from local weather variables (here the SBC index) better explained changes in animal abundance than the univariate NAO indice (see below and Table 2).

Physical determinism of the southern Bay of Biscay characteristics and biological patterns

Climate change has been related to change in composition and structure of oceanic communities for different taxa such as plankton (Hays *et al*., 2005), fishes (Genner *et al*., 2004), seabirds (Schreiber, 2001) and cetaceans (MacLeod *et al*., 2005). It is also known that marine systems may undergo rapid and key reorganization in plankton and fish communities, a phenomenon known under the term 'regime shift' (Scheffer & Carpenter, 2003; Steele, 2004) which serves also to describe marked climate-linked changes in biological systems (Hays *et al*., 2005). Such regime shifts have already been identified in the North Sea (Beaugrand, 2004), the North Atlantic (Reid *et al*., 1998a, b), in the North Pacific Ocean (Hare & Mantua, 2000) and in north-west Scotland (MacLeod *et al*., 2005). Because the dominance in cetaceans and seabirds communities in the Bay of Biscay is also switching from cold-water (community set A) to warm-water species (community set C), our study may be the first to depict such a regime shift in this area. If true, we make the hypothesis that changes may be not as abrupt as theory predicts and that 'transition' communities (set B in Fig. 4) could occur over a significant period (Fig. 5) as our study clearly shows. It is interesting to note that changes depicted in Fig. 5 follow those described by SBC index (Fig. 2) as confirmed by Pearson correlation coefficient ($r^2 = 0.46$, $P = 0.0005$), thus emphasizing the interest of multivariate index.

The search for mechanistic links between climate and switches in biological communities continues. Simple physical features might be one of the major harbingers of rapid changes in marine systems. We develop the hypothesis that the principal mechanism linking physical conditions of the habitat to the abundance of the different species of marine vertebrates lies in the conditions prevailing at thermocline formation. The intensity and the depth of this vertical stratification following sea agitation and sun exposure determine the seasonal development of the phytoplankton first and then the zooplankton (Hays *et al*., 2005), at the base of the trophic webs. It is also the case that water temperature affects directly fish egg survival (Richardson & Schoeman, 2004) and indirectly – through the abundance of feeding plankton – the development of larvae and young individual fish during their early life (Horwood *et al*.,

© 2007 The Authors
Journal compilation © 2007 Blackwell Publishing Ltd, doi: 10.1111/j.1365-2486.2007.01471.x

2000). Thus, atmospheric and oceanic conditions would determine the abundance of young individual fish that compose, after a time lag of 2–4 years, the major part of the mammal and seabird prey. Of course, those same fish populations make up a target for coastal fisheries. Such a clear physical determinism of the southern Bay of Biscay characteristics and biological richness has two major consequences. First, it means that the marine ecosystem as a whole is heavily affected or determined by a limited number of physical parameters as revealed by the multivariate SBC index. The data suggest that not only biological diversity as a whole but also total biomass, trophic web structure and energetic transfers have been impacted during the last decades. Secondly, in the 40–60% of the variation that remain unexplained by the physical conditions (cf. above and ignoring in a first step measurement errors), anthropogenic activities could also play a role.

Global change vs. human-borne local sources of variation

In many parts in the world, overfishing or indirect effects of fisheries has been considered as the main event responsible for direct decline of fish stocks (Hall, 1999; Pinnegar *et al*., 2002; Ormerod, 2003; Blyth *et al*., 2004) and indirect decline in predators population or effect on benthic production processes (Jennings *et al*., 2001). Indeed, it should now be regarded as only one of the underlying causes as shown by Frederiksen *et al*. (2004) who demonstrate that climate and fisheries together have caused the decline in North Sea Kittiwakes with an equal weighting given to these two factors. In the Bay of Biscay, this is also true for the successive oil-spills such as the Erika (Castège *et al*., 2004) and more recently the Prestige, pollution events for which the real ecological impact assessment should be estimated in the more complex frame of natural population variations especially for large size mammals and seabirds characterized by a high generation time (Hémery *et al*., 2002). The consequence is that disentangling short term anthropogenic (such as oil spills) sources of variation from climate change may not be always easy (cf. 'disturbance ecology'; Hémery *et al*., 2005).

Conclusion

From a methodological point of view, the multivariate oceano-climatic MOCI applied in a regional context (the SBC index, in the Bay of Biscay) shows interesting statistical properties; in particular an important temporal autocorrelation between the conditions of 1 year and those of the following one. This corresponds well to the physical inertia of oceanographic phenomena and their interactions with the atmosphere. Simultaneously, this index was capable of detecting a significant trend in physical and climatic conditions during the last decade. From this point of view, given its multivariate nature, it can be said a robust and pertinent physical index.

In comparison, the univariate NAO index for winter is not or only poorly auto-correlated in time and presents no capacity to detect significant temporal trends for the period 1980–2000. This is due to three facts. The first is this index is defined by only one variable (atmospheric pressure). The second reason is that this variable characterizes the atmosphere which is significantly variable in time and so unstable that only very sharp variations and very strong trend can be detected statistically. The third reason is that it relates to a wide area, perhaps too wide to be of significance and utility for biological investigations. This leads in consequence to erratic information on the physical conditions of the marine ecosystems at a more regional scale. Eventually, by contrast to recent studies (Stenseth & Mysterud, 2005), we conclude that in the Bay of Biscay at least the well-known large scale univariate NAO climate index is better replaced by a regional scale multivariate index such as the MOCI. The debate is open and we would like to advocate scientists to build their own regional multivariate index (MOCI) and test whether it is more useful or not than other well-known and largely used indices in their study area. Then, a meta-analysis across different regions and for different communities will tell whether regional multivariate index outperform large-scale ones.

From a biological point of view, in the context of the Bay of Biscay, we successfully used the multivariate SBC index to explain a major part of annual changes and trends in the abundance of marine vertebrate populations. More important perhaps, also highlighted a possible primary mechanism determining the fluctuations and the evolution of the entire marine community in the context of a global change. The NAO index alone failed to attain these objectives. This is a second reason to further develop the approach with the MOCI at the medium scale and regional level. This approach could also have applications to planktonic and benthic invertebrate animals and algal communities. Globally, as illustrated by the case of the Bay of Biscay, the variations of marine fishes, seabirds and cetaceans communities reflect an important and significant shift northward of the biogeographical limit between communities of cold and hot temperate waters. Ultimately, the more direct impact of human activities, especially those involving pollution by hydrocarbons and over fishing, cannot be cited as the unique cause of the medium and long-term variation of the vertebrate marine communities. Anthropogenic effects cannot be assessed properly without taking into account the

© 2007 The Authors

underlying temporal variability and trends of the physical natural environment. Thus, adaptive management to climate change appears as a challenging problem (Hulme, 2005).

Acknowledgements

As usual, a 30-year long study cannot acknowledge all the participants without involuntary omissions. Special thanks are due to different cruise leaders, crew members of the Brigade des Douanes Françaises DF43, Direction Interdépartementale des Affaires Maritimes, the 'Institut des Milieux Aquatiques', the 'Musée de la Mer' and the 'Centre de la Mer Côte Basque' (Biarritz), to our students at UPPA and to biologists working on ships (LPO, SEPNB) and especially Bernard Recorbet since 1976. This work was funded in part by the French Ministry of the Environment and the Conseil Général des Landes. A first draft of this manuscript has profited from thoughtful comments by P. Giller, G. Kerby and M. Frederiksen. Many thanks go to two anonymous referees and Mikhaïl Kozlov for providing helpful suggestions and substantially improving the manuscript. This work is dedicated to the memory of Elie d'Elbée who was a main manager of shipboard surveys since the early beginning of the study in 1976.

References

Beaugrand G (2004) The North Sea regime shifts: evidence, causes, mechanisms and consequences. *Progress in Oceanography*, **60**, 245–262.

Blenckner T, Hillebrand H (2002) North Atlantic Oscillation signatures in aquatic and terrestrial ecosystems: a meta-analysis. *Global Change Biology*, **8**, 203–212.

Blyth RE, Kaiser MJ, Edwards-Jones G, Hart PJB (2004) Implications of a zoned fishery management system for marine benthic communities. *Journal of Applied Ecology*, **41**, 951–961.

Buckland ST, Anderson DR, Burnham KP, Laake JL (1993) *Distance Sampling: Estimating Abundance of Biological Populations*. Chapman & Hall, London.

Bradley DC, Ormerod SJ (2001) Community persistence among stream invertebrates tracks the North Atlantic Oscillation. *Journal of Animal Ecology*, **70**, 987–996.

Castège I, Hémery G, Roux N, d'Elbée J, Lalanne Y, D'Amico F, Mouchès C (2004) Changes in abundance and at-sea distribution of seabirds in the Bay of Biscay prior to, and following the '*Erika*' oil spill. *Aquatic Living Resources*, **17**, 361–367.

D'Elbée J, Hémery G, Cadioux B (1998) Dietary and foraging behaviour of the British storm-petrel *Hydrobates pelagicus* in the Bay of Biscay during summer. *Ardea*, **86**, 1–10.

D'Elbée J, Prouzet P (2001) Océanographie du golfe de Gascogne. VIIe colloq. Int., Biarritz, 4–6 avril 2000. *Ed. Ifremer*, **31**, 369 pp.

Feistel R, Hagen E, Grant K (2003) Climatic changes in the subtropical Southeast Atlantic: the St. Helena Island Climate Index (1893–1999). *Progress in Oceanography*, **59**, 321–337.

Forchhammer MC, Post E (2000) Climatic signatures in ecology. *Trends in Ecology & Evolution*, **15**, 286.

Frederiksen M, Wanless S, Harris MP, Rothery P, Wilson LJ (2004) The role of industrial fisheries and oceanographic change in the decline of North Sea black-legged kittiwakes. *Journal of Applied Ecology*, **41**, 1129–1239.

Genner MJ, Sims DW, Wearmouth VJ, Southall PS, Southward AJ, Henderson PA, Hawkins SJ (2004) Regional climatic warming drives long-term community changes of British marine fish. *Proceedings of the Royal Society, Series B*, **271**, 655–661.

Hall SJ (1999) *The Effects of Fishing on Marine Ecosystems and Communities, Fish Biology and Aquatic Resources Series*, vol. 1. Blackwell Science, London.

Hammond PS, Berggren P, Benke H *et al*. (2002) Abundance of harbour porpoise and other cetaceans in the North Sea and adjacent waters. *Journal of Applied Ecology*, **39**, 361–376.

Hare SR, Mantua NJ (2000) Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography*, **47**, 103–145.

Hays G, Richardson AJ, Robinson C (2005) Climate change and marine plankton. *Trends in Ecology & Evolution*, **20**, 337–344.

Hallet 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. *Nature*, **430**, 71–75.

Hémery G (2001) Biodiversity and adaptations of extant marine birds: an overview. In: *Secondary Adaptations of Tetrapods to Life in Water* (ed. de Buffrénil M), pp. 119–139. Verlag, München.

Hémery G, Castège I, Dupont B, d'Elbée J, André R (2002) *Ecosystème et climat dans le Golfe de Gascogne*. *Meteorologie Maritime*, **194**, 3–5.

Hémery G, Castège I, Lalanne Y *et al*. (2005) La pollution du milieu marin: vers une ≪ écologie de la perturbation ≫. *Le Courrier de la Nature*, **220**, 39–45.

Hémery G, d'Elbée E, Terrasse JF (1986a) Regulation of a Storm Petrel *Hydrobates pelagicus* population by intermittent breeding. *Comptes Rendus de l'Académie des Sciences de Paris*, **303**, 353–356.

Hémery G, Pasquet E, Yésou P (1986b) Data banks and population monitoring in France. In: *Mediterranean Marine Avifauna, Population Studies and Conservation. NATO ASI Series G 12* (ed. Monbaillu M), pp. 163–177. Springer Verlag, Berlin.

Hémery G, Wald L (1986) *Etude par thermographie IR des fronts de marée et des déplacements de masses d'eaux sur les côtes atlantiques françaises et en Manche occidentale*. MNHN/SRETIE, Paris.

Herbland A, Quéro JC (1998) Oceanography of the bay of Biscay. *Oceanologica Acta*, **21**, 388 pp.

Horwood J, Cushing D, Wyatts J (2000) Planktonic determination of variability and sustainability of fisheries. *Journal of Plankton Research*, **22**, 1419–1422.

Hughes H (2000) Biological consequences of global warming: is the signal already apparent? *Trends in Ecology & Evolution*, **15**, 56–61.

Hulme PE (2005) Adapting to climate change: is there scope for ecological management in the face of a global threat? *Journal of Applied Ecology*, **42**, 784–794.

Hurrell JW (1995) Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. *Science*, **269**, 676–679.

Hurrell JW, van Loon J (1997) Decadal variations in climate associated with the North Atlantic Oscillation. *Climate Change*, **36**, 301–326.

© 2007 The Authors

Jennings S, Dinmore TA, Duplisea DE, Warr KJ, Lancaster JE (2001) Trawling disturbance can modify benthic production processes. *Journal of Animal Ecology*, **70**, 459–475.

Jongman RHG, Ter Braak CJF, Van Tongeren OFR (1995) *Data Analysis in Community and Landscape Ecology*. Cambridge University press, Cambridge.

Kappelle M, Van Vuuren MMI, Baas P (1999) Effects of climate change on biodiversity: a review and identification of key research issues. *Biodiversity & Conservation*, **8**, 1383–1397.

Kitayski A, Golubova EG (2000) Climate change causes contrasting trends in reproductive performance of planktivorous and piscivorous alcids. *Journal of Animal Ecology*, **69**, 248–262.

Koutzikopoulos C, Beillois P, Leroy C, Taillefer F (1998) Temporal trend and spatial structures of the sea surface temperatures in the bay of Biscay. *Oceanologica Acta*, **21**, 335–344.

Kozlov MV (2000) Climatic signatures in ecology. *Trends in Ecology & Evolution*, **15**, 286–287.

Lehman PW (2000) The influence of climate on phytoplankton community biomass in San Francisco Bay Estuary. *Progress in Oceanography*, **53**, 115–139.

Leps J, Smilauer P (2003) *Multivariate Analysis of Ecological Data using Canoco*. Cambridge University Press, Cambridge.

MacLeod CD, Bannon SM, Pierce GH, Schweder C, Learmonth JA, Herman JS, Reid RJ (2005) Climate change and the cetacean community of north-west Scotland. *Biological Conservation*, **124**, 477–483.

Møller AP (2002) North Atlantic Oscillation (NAO) effects of climate on the relative importance of first and second clutches in a migratory passerine bird. *Journal of Animal Ecology*, **71**, 201–210.

Ormerod SJ (2003) Current issues with fish and fisheries: editor's overview and introduction. *Journal of Applied Ecology*, **40**, 204–213.

Pinnegar JK, Jennings S, O'Brien CM, Polunin NVC (2002) Long-term changes in the trophic level of the Celtic Sea fish community and fish market price distribution. *Journal of Applied Ecology*, **39**, 377–390.

Post E, Peterson RO, Stenseth NC, McLaren BE (1999) Ecosystem consequences of wolf behavioural response to climate. *Nature*, **401**, 905–907.

Quéro JC, Dardignac J, Vayne JJ (1989) *Les Poissons du Golfe de Gascogne*. IFREMER & MNHN, Brest, 229 pp.

Quéro JC, Porché P, Vayne JJ (2003) *Guide des Poissons de l'Atlantique Européen*. Delachaux & Niestlé, Paris.

Quéro JC, Vayne JJ (1997) *Les Poissons de Mer des Pêches Françaises*. Delachaux & Niestlé, Paris.

Reid PC, Edwards M, Hunt HG, Warner AJ (1998a) Phytoplankton change in the North Atlantic. *Nature*, **391**, 546.

Reid PC, Planque B, Edwards M (1998b) Is observed variability in the long-term results of the Continuous Plankton Recorder survey a response to climate change? *Fisheries Oceanography*, **7**, 282–288.

Richardson AJ, Schoeman DS (2004) Climate impact of plankton ecosystems in the Northeast Atlantic. *Science*, **305**, 1609–1612.

Rodriguez C, Bustamante J (2003) The effect of weather on lesser kestrel breeding success: can climate change explain historical population declines. *Journal of Animal Ecology*, **72**, 793–810.

Scheffer M, Carpenter SR (2003) Catastrophic regime shifts in ecosystems: linking theory to observations. *Trends in Ecology & Evolution*, **18**, 648–656.

Schreiber EA (2001) Climate and weather effects on seabirds. In: *Biology of Marine Birds* (eds Schreiber EA, Burger J), pp. 179–207. CRC Press, Boca Raton, FL.

Schwing FB, Murphree T, Green PM (2003) The Northern Oscillation Index (NOI): a new climate index for the northeast Pacific. *Progress in Oceanography*, **53**, 115–139.

Seber GAF (1982) *The Estimation of Animal Abundance and Related Parameters*, 2nd edn. Griffin, London.

Skellam JG (1958) The mathematical foundations underlying the use of line transect in animal ecology. *Biometrics*, **14**, 385–400.

Souissi S, Ibanez F, Ben Hamadou R, Boucher J, Cathelineau AC, Blanchard F, Poulard JC (2001) A new multivariate mapping method for studying species assemblages and their habitats: example using bottom trawl surveys in the Bay of Biscay (France). *Sarsia*, **86**, 527–542.

Steele JH (2004) Regime shifts in the ocean: reconciling observations and theory. *Progress in Oceanography*, **50**, 245–262.

Stenseth NC, Ottersen G, Hurrell JW *et al*. (2003) Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proceedings of the Royal Society of London Séries B*, **270**, 2087–2096.

Stenseth NC, Mysterud A (2005) Weather packages: finding the right scale and composition of climate in ecology. *Journal of Animal Ecology*, **74**, 1195–1198.

Ter Braak CJF, Smilauer P (2002) *CANOCO Reference Manual and Canodraw for Window's user guide: software for Canonical Community Ordination (version 4.5.)*. Microcomputer Power, Ithaca, NY.

Thompson PM, Ollason JC (2001) Lagged effects of ocean climate change on fulmar population dynamics. *Nature*, **413**, 417–420.

Wolter K, Timlin MS (1998) Measuring the strength of ENSO – how does 1997/1988 rank? *Weather*, **53**, 315–324.

Supplementary material

The following material is available for this article online:

Appendix S1. The abundance matrix used in the study for community analysis using CA. Abundance is expressed as the mean number of individuals detected under standardized conditions per nautical mile. Only data from 1979 were used to investigate patterns and trends in seabirds and cetaceans community given that this kind of multivariate analysis admits no missing values.

This material is available as part of the online article from http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2486.2007.01471.x

Please note: Blackwell Publishing are not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

© 2007 The Authors
Journal compilation © 2007 Blackwell Publishing Ltd,