Rapid shifts in a marine fish assemblage follow fluctuations in winter sea conditions

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ABSTRACT: Patterns of interannual variation are described for an inshore fish assemblage off the Arrábida rocky coast (Portugal). During an 11 yr period, the fish assemblage showed pronounced changes especially within its tropical, warm-temperate and cold-temperate elements. These changes followed a fluctuating pattern connected with the North Atlantic Oscillation (NAO) with a series of years where the modifications were slight, interspersed with years where faunal changes were very rapid, affecting up to 35 % of the total number of species recorded in those years. After a transition year from a cold to a warm period or vice versa, the majority of the newcomers from the preceding phase were eliminated. Winter conditions, but not summer conditions, were good predictors of the observed patterns. Increases in sea surface temperature (SST) were associated with increases in the proportions of tropical and warm-temperate fish and with decreases in the proportion of cold-temperate elements, the reverse being true for decreases in SST. Interannual variation in faunal composition was not simply a consequence of changes in SST. Changes in other factors such as current flow direction and transport mechanisms, capable of bringing fishes from different biogeographical sources, may also play a role in the observed patterns. The influence of the NAO is therefore not only mediated by its effects on SST but also by the changes it induces in wind and current patterns along the Portuguese shore. Long-term trends caused by persistent changes, like those involving global warming, may be masked by the fact that at an intermediate time scale, faunal changes are characterised by a succession of oscillations rather than by a steady modification in a single direction. This outlines the importance of long-term monitoring data, since short-term studies may only capture single phases of a complex oscillation, giving a false picture of the overall pattern of change.

KEY WORDS: Faunal changes · Portugal · North Atlantic Oscillation · NAO · Sea surface temperature · SST · Wind stress · Temperate fish assemblage

INTRODUCTION

Global warming consequences are stimulating an increasing research effort to study the responses of marine fauna and flora to changes in sea surface temperature (SST) (Beaugrand et al. 2002, Schiel et al. 2004). Several pioneering studies encompassing several decades of the last century have unambiguously demonstrated that inshore fish assemblages, as well as those of other taxa, displayed clear shifts associated with long-term patterns of sea temperature changes (Southward et al. 1995). These temperature changes in the sea follow quite complicated processes that are only gradually being understood (Speth & Kohne 1983, Levitus et al. 2000, Jones et al. 2001, Ottersen et al. 2001). Within the course of a century there may be several warming and cooling periods, spanning several decades each. This has been documented, for example, in British waters where a cooling trend was detected up to about 1930, followed by a warming phase that lasted until about the late 1950s, a new cooling phase that persisted until the early 1980s, and a new warming phase that apparently still persists in the north-east Atlantic and is expected to last at least for the first decades of this century (Paeth et al. 1999, Hawkins et al. 2003, Woehrling et al. 2005).

Superimposed on these long-term oscillations, there are other shifts in SST that last for shorter periods of less than a decade and are mostly related to the North Atlantic Oscillation (NAO) (Hurrell 1995, Rodwell et al. 1999, Ottersen et al. 2001, Saunders & Qian 2002, Hurrell et al. 2003). This NAO seems to be particularly active during the winter (Rodwell et al. 1999) and may be quantified by the difference in atmospheric pressure between a high pressure zone located at mid latitudes and a low pressure zone located at higher latitudes (Hurrell et al. 2003). The Azores high pressure zone and the Iceland low pressure zone are typical points of reference to quantify the NAO index (Hurrell 1995), although other pairs of locations are also frequently used (Rogers 1984, Jones et al. 1997).

On a year-to-year basis, there may be rapid changes in SST, for instance when there is a change from a period of consecutive years of positive NAO to a period when the NAO becomes negative, as was the case of the 1996 winter along western European shores (Kushmir 1999, Greene & Pershing 2003). In this region, much of the short-term SST variation seems to be strongly influenced by the NAO (Wanner et al. 2001, Hurrell et al. 2003). In years where the NAO is strongly positive, storms crossing the Atlantic travel through northwest Europe. In the British Isles and adjacent areas, southwest winds become prominent, winters are mild and rainy and SST tends to be relatively higher. In contrast, in southwest Europe and in the Mediterranean, winters are sunny, dry and cold, and northern winds tend to be prominent. SST is relatively lower, as water transported from the south and southwest does not reach the shore and upwelling events may even occur, further cooling nearshore waters. In years of negative NAO, the situation is much the reverse. The storm track is displaced to the south, meaning that southwest Europe and the Mediterranean receive considerable amounts of rain, warmer southwest winds become prominent and SST tends to be higher. In these same years, northwest Europe experiences extremes of cold air and water temperature and fewer storms (for a comprehensive overview of NAO impacts, see Hurrell et al. 2003).

The plurality of time scales of SST changes is one of the main confounding factors in the analysis of global warming consequences in the marine environment, since a perceived persistent trend toward increasing temperatures may sometimes, when viewed at a broader time scale, turn out to be a temporary phase of an oscillation. For marine biologists, however, these oscillations provide excellent 'natural experiments' that can tell us much about the ways marine fauna and flora respond to fluctuations in SST and other oceanographic variables. These oscillations range from phenomena that span several decades (Hawkins et al.

2003) to shorter cycles like those associated with the NAO (Atrill & Power 2002). Even abrupt interannual changes in sea conditions may substantially affect fish assemblages, especially in areas that are at or near biogeographical barriers, where faunas adapted to waters of different temperatures come into contact. For instance, in Baja California, Thomson & Lehner (1976) stated that cold water events in the winter could, in some years, temporarily but drastically affect the tropical and subtropical components of the littoral ichthyofauna.

In 1996, an exceptional year marked by an abrupt transition from a series of positive NAO years to a very negative one, the effects of this short-term climatic shift could be detected in a variety of groups of marine animals around western Europe (Stenseth et al. 2002). An 11 yr (1992–2002) study on the interannual fluctuations in the composition of an inshore fish assemblage at Arrábida (western Portugal) is presented here. During this survey, 2 warm periods interspersed with cold periods were detected, which gave us the opportunity to assess the magnitude and patterns of ichthyofaunal changes that followed these rapid shifts in oceanographic conditions.

MATERIALS AND METHODS

Study area. The Arrábida Marine Park between Cape Espichel (38° 25′ N, 9° 13′ W) and Portinho da Arrábida (38° 29′ N, 8° 58′ W) on the west Portuguese shore (Fig. 1) constituted the study area. Most of this area faces south, being protected from the prevailing north and northwest winds by the adjacent mountain chain of Arrábida. The coast is very steep, and the intertidal zone consists mainly of rocky cliffs, small beaches and several areas covered by boulders. The rocky subtidal extends offshore for some tens of metres, and to depths of less than 15 m (except at Cape Espichel, where it reaches more than 30 m). Boulders of many different sizes resulting from the erosion of the nearby calcareous cliffs increase habitat complexity. Following this narrow band of rocks and boulders are sandy bottoms with very gentle slopes.

During the summer, the prevailing north and northwest winds on the Portuguese west shore cause frequent upwelling events, which often keep nearshore waters cooler than offshore waters at the same latitude. Surface currents tend to flow to the south and southwest. During the winter, the prevailing conditions vary considerably depending on the intensity and the sign of the NAO. Typically, poleward surface circulation prevails, which is particularly enhanced in years when the NAO is predominantly negative, promoting south and southwest winds and an increase in
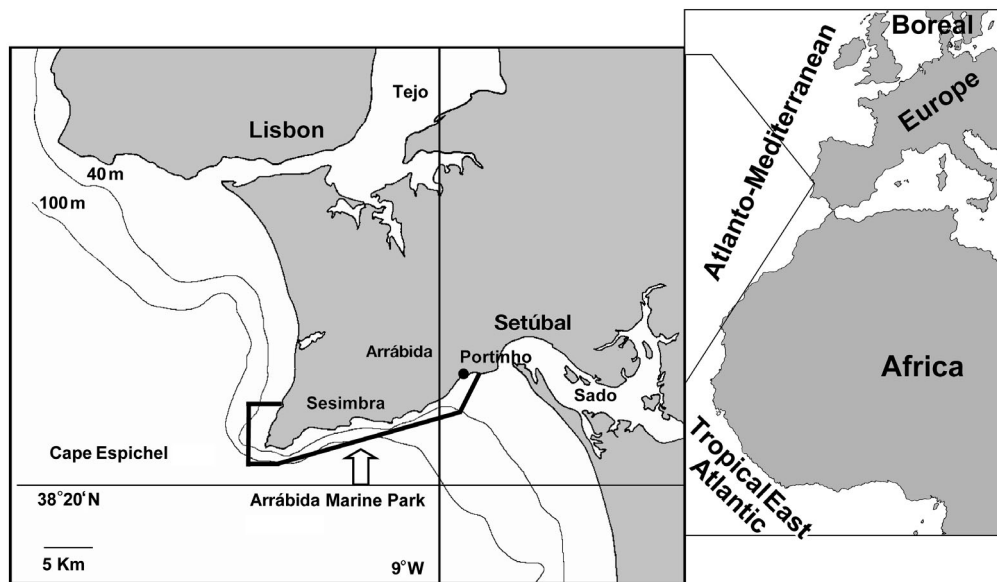
Fig. 1. Study area (Arrábida Marine Park) on the west coast of Portugal. Right panel shows main biogeographic provinces of the north-east Atlantic

SST. However, these conditions are reversed in winters of positive NAO, with the prevailing northern winds being sufficiently strong to disrupt the poleward water movement along the shore. They can even promote winter upwelling events. These 2 factors link winters of positive NAO to lower values of SST. A detailed characterisation of the oceanography of the area can be found in Fiúza et al. (1982), Fiúza (1983), Martins et al. (2002), Bischof et al. (2003) and Peliz et al. (2005).

Data collection. Data were collected from May 1992 to December 2002 by scuba diving. Dives were distributed uniformly among all months in each year, with a few exceptions in the winter when the sea was very rough. More than 320 dives were undertaken. Each dive lasted 1 h and followed a regular path beginning on the sandy bottom, 10 m off the rocky substrate, and ending on the shore. All habitats, including sand, bedrock and boulders were inspected in a similar way during all dives. These visual inspections included searching crevices, holes and spaces beneath stones to detect cryptic fish species, as well as surveying the water column. The annual mean number of dives was 29.6 (min. = 13, max. = 60, SD = 29.6). Since each dive lasted 1 h, the number of dives corresponds to the number of observation hours per year. The aim of the surveys was to compile an inventory of all fish species detected in the study area for each year. Thus, for the purpose of this study, no attempts at estimating abundances were undertaken, and each species was counted only once for each year. For each dive, only the species spotted for the first time in that year were added to the annual list. Whenever possible, the pres-

ence of juveniles presumed to be young-of-the-year was recorded. Since different fish species grow at very different rates in their first year of life, fish were ascribed to this category based on the authors' own experience of following the recruitment phase of these coastal fish species, as well as on the published information for each species.

SST data and information on wind direction and intensity were based on ICOADS (International Comprehensive Ocean-Atmosphere Data Set, available at: www.cdc.noaa.gov/coads/), using cells of 1° latitude and longitude (38° N, 10° W). NAO data were obtained from the Climate Analysis Section, National Center for Climate Research (NCAR), Boulder, Colorado, USA, available at: www.cgd.ucar.edu/cas/jhurrell/. Since our goal was to study the influence of regional sea conditions on the coastal fish assemblages, the choice of SST and wind data from a larger scale data set was considered a better option than using field measurements at the study site since these are influenced by local conditions.

Classification of the ichthyofauna. All fish species were classified according to their distribution in the following groups of biogeographic affinity. Tropical: species that range from tropical west Africa (Tropical East Atlantic, Fig. 1) to the entrance of the Mediterranean or the south of the Iberian Peninsula; warm-temperate: species that occur from the Mediterranean and north-western coasts of Africa to the western entrance of the English Channel; cold-temperate: species that have their southern limit at or near the Atlantic coast of the Iberian Peninsula and extend in range into the North Sea or even farther north; temper-

ate: species that are present in the whole temperate Atlanto-Mediterranean region, i.e. they occur from Mauritania to the North Sea, and also in the Mediterranean but not in tropical Africa.

Very eurythermal species that range from the tropical Atlantic to boreal areas, and oceanic fish that are only accidentally found nearshore, were excluded since they do not provide any information useful to this type of study. In the case of Ammodytidae n. id., the species of the genera *Ammodytes* and *Gymnamodytes* could not be distinguished visually during the dives. As they differ in ecology and distribution, we excluded them from the analyses. The gobiesocids *Lepadogaster lepadogaster* and *L. purpurea* were considered to be the same species until 2002 (Henriques et al. 2002) and were therefore recorded as *L. lepadogaster*. Appendix 1 presents the list of all fish species and their respective group of biogeographic affinity as defined above. The information on species distributions was based on Whitehead et al. (1984, 1986), Quéro et al. (1990) and Froese & Pauly (2006) (FishBase) with updates presented by Henriques et al. (1999, 2002).

Data analysis. To reduce redundancy and dimensionality, the oceanographic variables were subjected to a principal components analysis (PCA), followed by a varimax rotation. The faunistic data, comprising the number of species of each biogeographic category, were also independently subjected to a PCA. After identification of the relevant components of oceanographic and faunistic data sets, the relationships among them were analysed using non-parametric Kendall's tau correlations. To control for the possibility that interannual variation in observation time could affect the results, the number of species of each category was also expressed as a percentage of the total number of species in that year, and the relationships between faunistic and oceanographic variables were again analysed using non-parametric Kendall's tau correlations. To objectively test if years were grouped in cold and warm periods regardless of oceanographic information and without biogeographical criteria, multidimensional scaling (MDS) was performed on the similarity matrix of all 11 yr. Similarities were computed using Sorenson's index. To identify whether differences between warm and cold years were significant, an analysis of similarities (ANOSIM) test was used (462 permutations). ANOSIM analysis was performed with the PRIMER 5 programme. All other statistical analyses were performed with STATISTICA 6 (StatSoft).

RESULTS

During the 11 yr of this work, a total of 115 coastal fish species were recorded in the study area. Of these, 106 were included in the analysis. Thirty-two species were present in all years, with an additional 7 species present in all but one year. However, in spite of this permanent group, there was a considerable amount of variation in the fish assemblage between consecutive years. These interannual fluctuations were noticeable both in the total number of species recorded in each year, and in the contributions of each biogeographic group (Fig. 2). The mean number of fish species recorded per year was 63.4 (min. = 52, max. = 75, SD = 7.4), while the corresponding figures for the percent contributions of the different biogeographic groups were: tropical (mean = 11.4, min. = 7.3, max. = 18.1, SD = 3.3); warm-temperate (mean = 44.7, min. = 40.9, max. = 49.2, SD = 3.0); cold-temperate (mean = 11.7, min. = 5.6, max. = 16.4, SD = 3.6); and temperate (mean = 32.2, min. = 28.8, max. = 36.5, SD = 2.4).

Even with 18 new species added to the faunal list in the 1996–1998 warming period, the cumulative number of species detected in the study area was already 79% after 4 yr of sampling (49% in the first year), and no correlation between the number of recorded species in each year and observation time for that year was found (Kendall's tau correlation = 0.09, p = 0.69, n = 11). These facts give us confidence that the year-to-year variations detected represent real changes in assemblage structure and are not an artifact caused by variations in the number of observation hours between years.

The oceanographic and climatic parameters used in our study are presented in Fig. 3. A PCA performed on these parameters showed that the first 2 principal com-
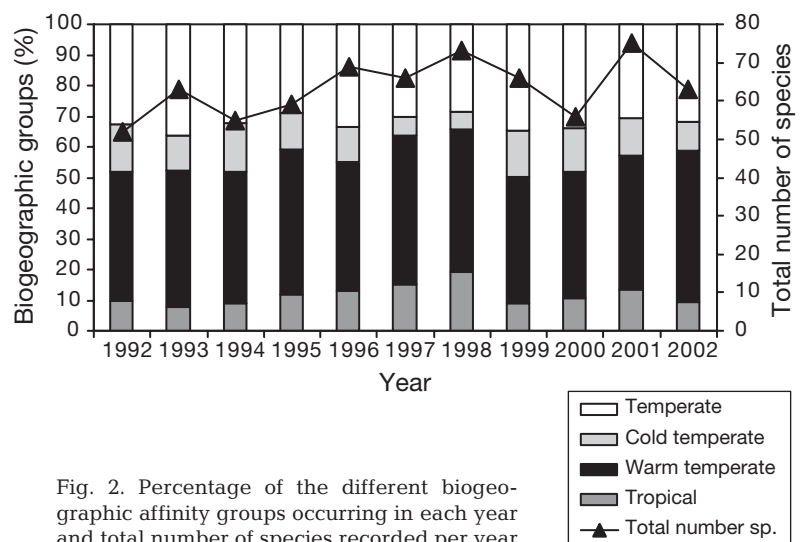

Fig. 2. Percentage of the different biogeographic affinity groups occurring in each year and total number of species recorded per year
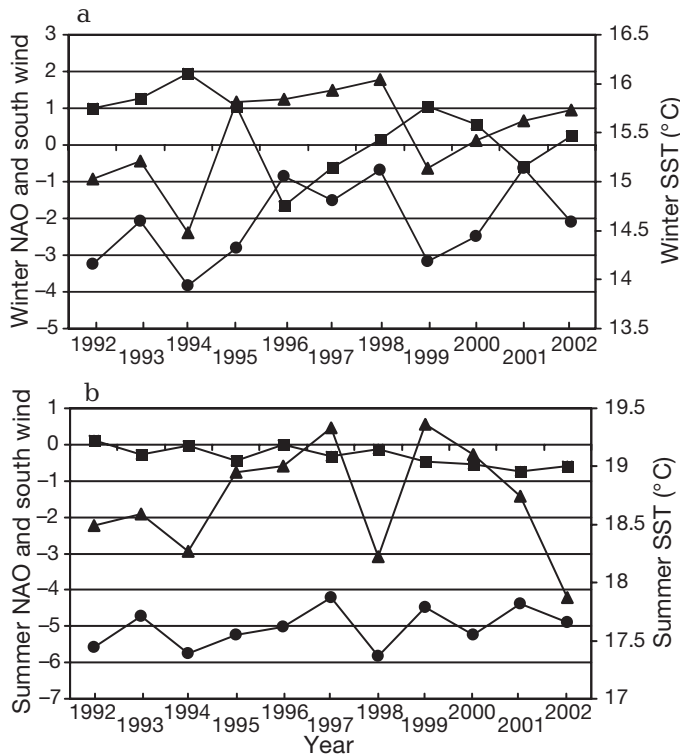
Fig. 3. Oceanographic and climatic parameters used in this study. (a) Winter conditions, from December of the previous year to April. (b) Summer conditions, from June to September. NAO (■): North Atlantic Oscillation index; SST (▲): sea surface temperature (mean °C value for the grid 38–39° N: 9–10° W); and south wind (●): southward wind for the same grid (minus sign indicates that the net wind is northwards)

matic PCA (Fig. 4b), are also apparent in the factor scores of the faunistic data (Fig. 5b). The only discrepancy involves the 1996 to 1998 warm period, which, according to faunistic criteria, was initiated in 1995.

To evaluate to what extent an objective analysis based on the faunal similarities between years, regardless of any biogeographic classification, recovered the same separation between cold and warm years, MDS was performed (Fig. 6a). Similarities among years were computed based on Sorenson's index, which only considers presence-absence data regardless of any previous classification of the species. Although considerable scattering is apparent, the cold years are clearly grouped on one side of the x-axis and the warm years on the other. One-way ANOSIM revealed that differ-

ponents explained 76% of the variance and can be interpreted as representing winter and summer conditions, respectively (Fig. 4a). Winter SST, amount of winter south wind and, at the opposite end of the axis, winter NAO were associated with the first principal component, PC1, while summer conditions were clearly associated with PC2. This observation indicates that summer and winter conditions are poorly correlated and that instead of speaking of warm and cold years, different seasons (winter and summer) must be analysed separately.

A PCA applied to the faunistic data is presented in Fig. 5a. When inspecting the factor loadings of the 2 components retained in the analysis, it becomes apparent that PC1 contains a group of close relationships involving the tropical and warm-temperate biogeographic affinity groups on one end and the cold-temperate group, with an opposite sign, on the other end. Interestingly, the temperate group is almost entirely associated with the second axis, indicating that its pattern of interannual variation is poorly correlated with the other groups. Moreover, the warm and cold periods derived from the factor scores of the oceanographic and cli-
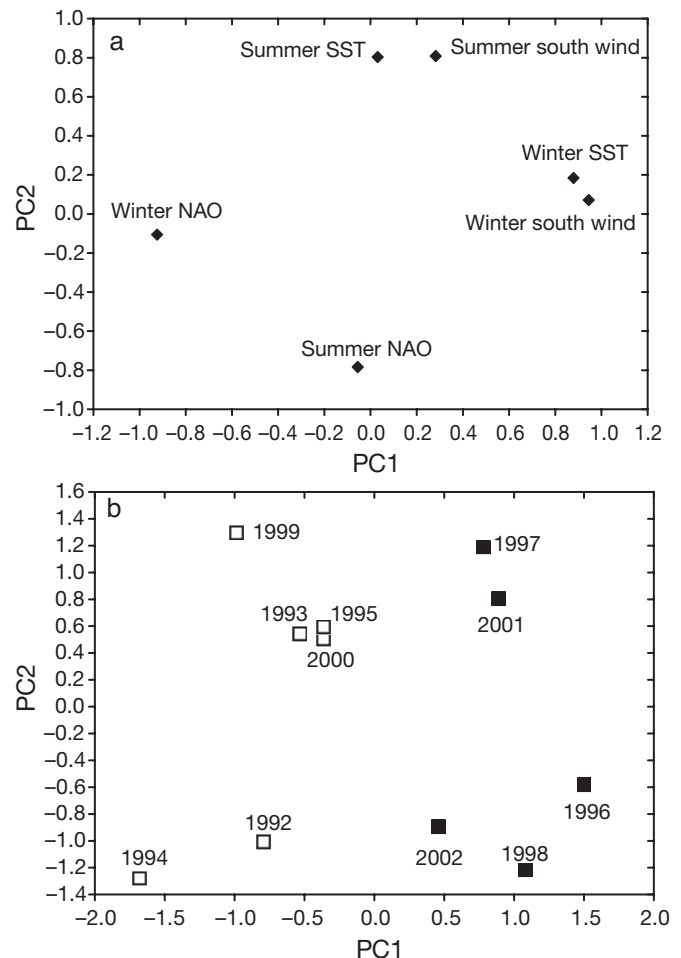

Fig. 4. Principal axis factor analysis of the 6 oceanographic and climatic parameters displayed in Fig. 3. (a) Principal components; (b) factor scores: cold years (□), warm years (■). The first principal component (PC1) expresses winter conditions while the second principal component (PC2) expresses summer conditions. Factor loadings are varimax normalised. Determinant of correlation matrix: –2.1258. Eigenvalues: 2.987 (PC1) and 1.585 (PC2); % total variance: 49.78 (PC1) and 26.42 (PC2)
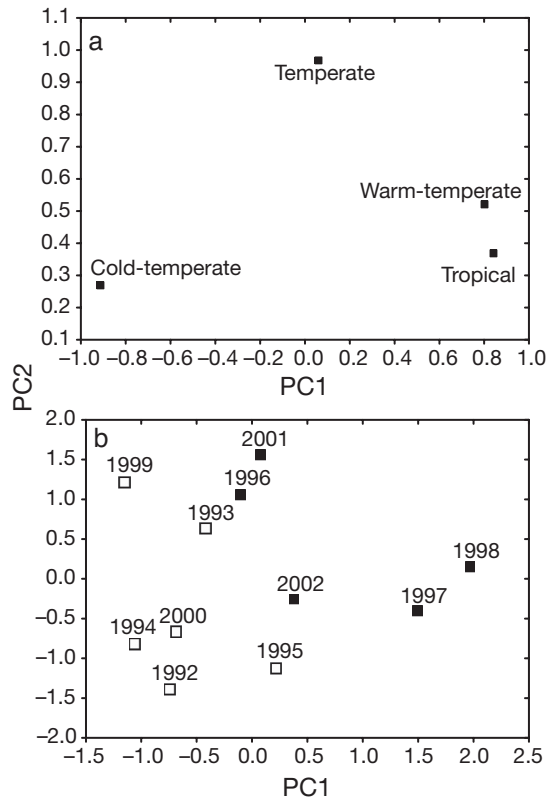
Fig. 5. Principal axis factor analysis of the 4 biogeographic affinity groups shown in Fig. 2. (a) Principal components; (b) factor scores: cold years (□), warm years (■). Factor loadings are varimax normalised. Determinant of correlation matrix: −0.9851. Eigenvalues: 2.463 (PC1) and 1.131 (PC2); % total variance: 61.57 (PC1) and 28.28 (PC2)

ences between these 2 groups were significant (Global $R = 0.46$, $p = 0.004$).

Looking at Sorenson's similarity values between consecutive years, 2 main changes in assemblage composition (shown by a reduction in similarity) are evident: one between 1995 and 1996 and a second one between 2000–2001 and 2001–2002 (Fig. 6b).

Kendall's tau correlations between the 2 principal components derived from the PCA on oceanographic conditions and the 2 components derived from faunistic data showed the following patterns. There was a significant correlation between winter conditions and the component that involves tropical, warm-temperate and cold-temperate groups ($r = 0.60$, $p = 0.01$). This correlation was still significant after Bonferroni correction for multiple testing. The temperate group, on the other hand, was not correlated with winter conditions ($r = 0.35$, $p = 0.14$). Summer conditions were not correlated with either faunistic variables ($r = 0.02$, $p = 0.94$ for the tropical, warm-temperate and cold-temperate groups; and $r = 0.13$, $p = 0.59$ for the temperate group). These data show that the tropical, warm-temperate

and cold-temperate faunal groups co-vary with winter conditions, with warm-temperate and tropical species following a similar trend, while the cold-temperate fish follow an inverse relationship.

It could be argued that summer conditions would have an effect on the assemblage only in the autumn and winter, i.e. only on a fraction of the time sampled per year. On the other hand, the effects of winter conditions would be more easily captured because these are felt throughout the year and therefore many more dives would be needed to detect their possible effects on the fish fauna. However, correlations of the PC1 of faunistic data (tropical, warm-temperate and cold-temperate groups) with summer conditions of the previous year also yielded non-significant results and low correlation coefficients (data not shown).

The limited number of data points restricts the interpretation of correlations between the proportion of species of each biogeographic group and the physical parameters ascribed to winter conditions on the PCA of the oceanographic and climatic parameters. Nevertheless, after Bonferroni correction for multiple testing, a number of correlations remained significant (Table 1).
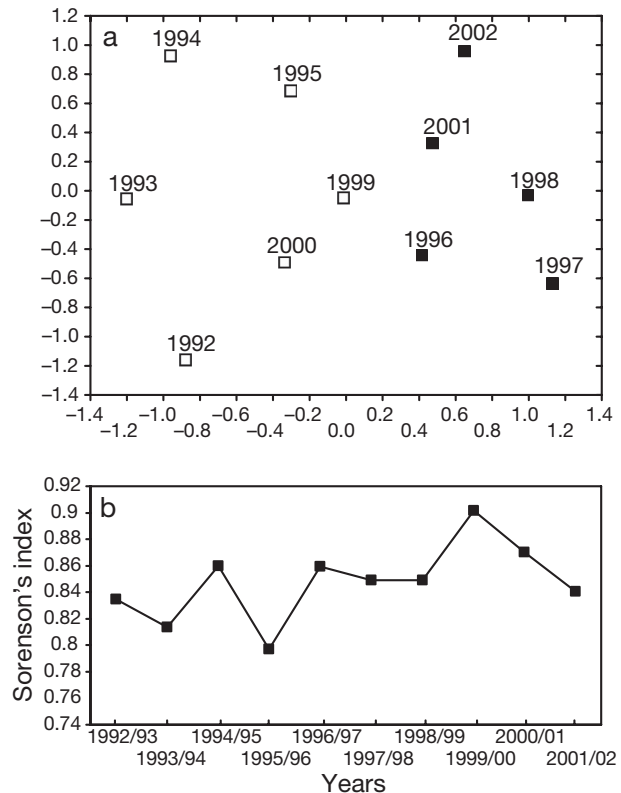

Fig. 6. Multidimensional scaling (MDS) on the similarity matrix (based on Sorenson's index) of all 11 yr. (a) MDS plot: cold years (□), warm years (■); (b) Sorenson's index between consecutive years. A reduction in similarity reveals changes in the assemblage composition

Table 1. Values of non-parametric Kendall's tau significant correlations (at p < 0.05 after Bonferroni correction) between the total number of species and the proportion of species of each biogeographic group and the physical parameters associated with winter conditions (PC1 in Fig. 4a). NAO: North Atlantic Oscillation Index; SST: sea surface temperature; ns: p > 0.05

	Winter NAO	Winter south wind	Winter SST
Total number of species	ns	0.86	0.63
Tropical and warm-temperate	ns	ns	0.83
Cold-temperate	ns	−0.73	−0.82
Temperate	ns	ns	ns

The total number of species was highly correlated with the amount of south wind during the winter as well as with winter SST, while tropical and warm-temperate fish taken together were highly correlated with winter SST. Negative significant correlations were found between the cold-temperate group and winter conditions (SST and south wind). As expected, the temperate group presented no significant correlations with any of the considered variables.

A number of interesting patterns arose when analysing the temporal patterns of occurrence for the set of species that changed markedly at the onset of the first warm period (1996 to 1998), either because they appeared for the first time in the survey (or were only sporadically detected before this period) or ceased to be recorded during this period (Table 2). These patterns were as follows: (1) only 1 species belonged to the temperate group, the others being classified as tropical (5 species), warm-temperate (6 species) or cold-temperate (5 species); (2) during the period 1996 to 1998, the tropical and warm-temperate species increased gradually, each warm winter bringing new additions that remained present in the area until the end of 1998; (3) some of the newcomers were observed breeding in the area, and many cases of very small juveniles, likely locally produced, were recorded; (4) the end of the 1996 to 1998 warm period led to an almost complete disappearance of the warm water newcomers with a single species remaining in the area by the end of 1999 (2 other species had been observed very sporadically at the beginning of that year); (5) the cold-temperate group of species disappeared entirely in this period but recovered almost completely after a single cold winter; (6) during the second transition from cold to warm winters, this process was repeated, although on a smaller scale, with all warm water species reappearing in this second warm period being a subset of those found in the 1996 to 1998 warm period.

DISCUSSION

In the present study, several periods with little change were interspersed with years when faunal changes were remarkably high. Indeed, in years that marked transitions from cold to warm periods and vice versa, faunal changes could reach considerably high

Table 2. Temporal patterns of occurrence of the set of species that changed markedly at the onset of the first warm period (1996–1998) with indication of their biogeographic affinity group. WT: warm temperate; TR: tropical; CT: cold temperate; T: temperate; A: common occurrence of adults; J: common occurrence of juveniles; –: single or extremely sporadic occurrence. The 1996–1998 and 2001–2002 warm periods are in **bold**

Biogeographic group	Species	1992	1993	1994	1995	**1996**	**1997**	**1998**	1999	2000	**2001**	**2002**
WT	*Phycis phycis*					A	A	A			A	A
	Serranus atricauda						JA	A–			AJ	A
	Serranus hepatus				J–	J	J	J			J	J
	Diplodus bellottii							J				J
	Spicara maena						J					
	Pomatoschistus marmoratus						JA	JA	JA	JA	JA	JA
TR	*Diplodus puntazzo*				A–	JA	JA	JA			JA	A
	Oblada melanura	A–				A	JA	JA	A–		JA	A
	Bothus podas podas							J				
	Synaptura lusitanica							A				
	Sphoeroides marmoratus							A				
CT	*Ciliata mustela*	JA			JA				JA	JA		
	Pollachius pollachius	JA	JA	JA	JA				JA	JA	A–	
	Entelurus aequoraeus	A	A						A	A	A–	
	Taurulus bubalis			A	A							
	Zeugopterus punctactus		A	A	A				A		A–	
T	*Syngnathus typhle*		JA	JA					JA			

values. In 1999, a cold year that followed a 3 yr warm period (1996 to 1998), the number of species that ceased to be recorded, added to the number of species that reappeared, totalled 23. This represents 35% of the total number of species recorded in that year. ANOSIM confirmed these patterns, revealing significant differences in assemblage composition between cold and warm years. Moreover, the comparison of Sorenson's similarity index between consecutive years showed 2 main changes in assemblage composition that are consistent with the 2 transitions from cold to warm periods detected during this study.

If the patterns detected in our work represent a general trend for some coastal fish assemblages (namely those located in important marine biogeographic transition zones), studies with time windows that are too short will very easily fail to capture these 'turning points', providing a falsely stable picture of the fish fauna.

These short-term temporal windows of major faunal changes have already been documented in previous studies. In particular, Thomson & Lehner (1976), in a different ocean and a distinct climatic context, found that years with severe cold winters eliminated much of the tropical littoral fish fauna of Baja California.

The surface waters along the Portuguese shore are dominated by the Canary current, which brings a regular supply of cold water from the north (Bischof et al. 2003), and likely also brings eggs and young fish. In some years, namely if the NAO is positive, this current will prevail in all seasons. When the winter NAO is negative and strong, south and southwest winds become predominant, and this current may be temporarily reverted, being replaced by a poleward flow (Frouin et al. 1990). These oceanographic conditions seem to explain the temporal patterns of faunistic variation observed in this study. In particular, the probable role of the winter south wind, which emerged as an important factor correlated with the total number of species, regardless of their biogeographic affinities, seems to be explained by these conditions.

The reason why the amount of winter south wind affects the total number of species recorded in a given year is as yet unclear. Santos et al. (2001) showed that when strong northwest winds are intense during peak abundances of sardine eggs and larvae, offshore transport of young stages leads to poor recruitment in the following months. In our study area, several coastal fish species breed during the autumn and spring (authors' unpubl. data). Thus, the same process that couples recruitment intensity with wind direction for sardines could also operate on a much broader spectrum of coastal fish, with northwest winds favouring offshore transport and south winds promoting nearshore retention of eggs and larvae.

It is likely that in some winters, the interruption of the nearshore flow to the south, forced by strong south winds, will provide the only opportunity for the northward transport of fish eggs, larvae and even juveniles (for instance, those associated with rafting materials). In the remaining winters, as well as in the other seasons, the predominant north winds and southward flowing currents will most likely bring fish from higher latitudes, a situation that would explain why, for the cold-temperate fish group, water temperature is a better predictor of change than wind direction. This is corroborated by a recent review of the winter upper ocean circulation in the western Iberian Basin by Peliz et al. (2005), who identified a particularly intense poleward flow along western Iberia in the years 1996 to 1998 and again in 2001 to 2002, whereas 1999 and 2000 did not show significant signatures of a poleward current. In contrast with this effect of winter south wind on species richness, high winter SST correlates with an increase in the proportion of fish of warm water affinity, and a decrease of the cold-temperate elements of the fish fauna.

How such an effect could be determined is as yet unknown. Studies of the relationships between the abundance of fish with different thermal preferences and oceanographic conditions have drawn attention to the diversity of causal mechanisms of change. While unusual drops in SST may kill warm water fish (Thomson & Lehner 1976), Attrill & Power (2002) illustrated a situation in which climatic oscillations exerted their effects on fish assemblages by affecting the suitability of estuarine nursery grounds for marine fish. These authors have shown for the first time that increases in the proportion of warm water fish in a given year were not necessarily caused by global warming. They found an increase in diversity during high NAO winters, which is partly explained by the increase in the number of rare species. Most of the additional species were those with a southern distribution. Based on these findings, they pointed out that: '…The appearance of unusual species or the extension of species' ranges have been used as indicators of climate change, but the appearance of warm-water southern species may simply reflect long-term climatic cycles…' (Attrill & Power 2002, p. 277) Also, while some mobile species may engage in long range movements tracking water masses of adequate temperature, for many coastal benthic and benthopelagic fish species, recruitment and spawning opportunities will be affected by changes in SST and other oceanographic conditions. More work is necessary both to characterise patterns of faunal change and their linkages with oceanographic oscillations at different time scales, and also to understand the causal mechanisms through which fish assemblages are being affected by changing sea conditions.

If our interpretation is correct, some changes that at first sight could be attributable to SST variation, may instead be caused by changes in other parameters, such as net changes in wind-driven flow direction, which are also correlated with changes in SST. The NAO is probably best viewed as a means of describing processes that operate at a higher level of control of oceanographic and atmospheric phenomena rather than as an agent that acts directly on the fish assemblages (for a critical review of the use of NAO and other climatic indices, see Stenseth et al. 2003). If this is the case, monitoring of fish assemblages needs to be accompanied by much more detailed surveys of oceanographic and meteorological variables, if we want to disentangle the relative contributions of the different candidate factors.

This view of temporal variations in fish assemblages as a series of oscillations will have important implications for the delimitation of what constitutes natural populations of fish. A given area may alternate between being a source and a sink of eggs, larvae and juveniles (Pulliam 1988), depending on the conditions in specific years and the mean duration of the surviving populations that are initiated by colonists arriving in a given episode of faunal change. While warm water fish may breed successfully in a given area during a long warm period, cold years may prevent those species from breeding or recruiting successfully in that same area.

LITERATURE CITED

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Appendix 1. Species observed during the survey and their biogeographic affinity group. See 'Materials and methods' for definitions of biogeographic groups

Family	Species	Biogeographic group
Rajidae	*Raja undulata*	Warm-temperate
Myliobatidae	*Myliobatis aquila*	Tropical
Muraenidae	*Muraena helena*	Warm-temperate
Congridae	*Conger conger*	Temperate
Clupeidae	*Sardina pilchardus*	Temperate
Phycidae	*Ciliata mustela*	Cold-temperate
	Gaidropsarus mediterraneus	Temperate
	Gaidropsarus vulgaris	Cold-temperate
	Phycis phycis	Warm-temperate
Gadidae	*Pollachius pollachius*	Cold-temperate
	Trisopterus luscus	Temperate
Batrachoididae	*Halobatrachus didactylus*	Tropical
Mugilidae	*Chelon labrosus*	Temperate
	Liza aurata	Temperate
	Liza ramada	Temperate
	Mugil cephalus	Tropical
Atherinidae	*Atherina presbyter*	Temperate
Belonidae	*Belone belone gracilis*	Temperate
Zeidae	*Zeus faber*	Eurythermic
Syngnathidae	*Entelurus aequoraeus*	Cold-temperate
	Hippocampus hippocampus	Warm-temperate
	Hippocampus ramulosus	Warm-temperate
	Nerophis lumbriciformes	Cold-temperate
	Syngnathus acus	Temperate
	Syngnathus typhle	Temperate
Macroramphosidae	*Macroramphosus scolopax*	Oceanic
Scorpaenidae	*Scorpaena notata*	Warm-temperate
	Scorpaena porcus	Warm-temperate

Appendix 1 (continued)

Family	Species	Biogeographic group
Triglidae	*Trigloporus lastoviza*	Eurythermic
	Aspitrigla obscura	Warm-temperate
Cottidae	*Taurulus bubalis*	Cold-temperate
Moronidae	*Dicentrarchus labrax*	Temperate
Serranidae	*Serranus atricauda*	Warm-temperate
	Serranus cabrilla	Tropical
	Serranus hepatus	Warm-temperate
Carangidae	*Trachurus mediterraneus*	Warm-temperate
	Trachurus picturatus	Warm-temperate
	Trachurus trachurus	Temperate
	Seriola sp.	Oceanic
Sparidae	*Boops boops*	Eurythermic
	Diplodus annularis	Warm-temperate
	Diplodus bellottii	Warm-temperate
	Diplodus cervinus	Warm-temperate
	Diplodus puntazzo	Tropical
	Diplodus sargus	Tropical
	Diplodus vulgaris	Warm-temperate
	Oblada melanura	Tropical
	Pagellus acarne	Temperate
	Pagrus auriga	Tropical
	Pagrus pagrus	Warm-temperate
	Sarpa salpa	Tropical
	Sparus aurata	Warm-temperate
	Spondyliosoma cantharus	Temperate
Centracanthidae	*Spicara maena*	Warm-temperate
Mullidae	*Mullus surmuletus*	Temperate
Pomacentridae	*Chromis chromis*	Tropical
Labridae	*Centrolabrus exoletus*	Cold-temperate
	Coris julis	Temperate
	Ctenolabrus rupestris	Temperate
	Labrus bergylta	Cold-temperate
	Labrus bimaculatus	Temperate
	Symphodus bailloni	Temperate
	Symphodus cinereus	Warm-temperate
	Symphodus mediterraneus	Warm-temperate
	Symphodus melops	Cold-temperate
	Symphodus ocellatus	Warm-temperate
	Symphodus roissali	Warm-temperate
	Symphodus rostratus	Warm-temperate
Ammodytidae	Ammodytidae n. id.	Oceanic
	Hyperoplus lanceolatus	Cold-temperate
Trachinidae	*Echiichthys vipera*	Temperate
	Trachinus draco	Temperate
Tripterygiidae	*Tripterygion delaisi*	Warm-temperate
Blenniidae	*Coryphoblennius galerita*	Warm-temperate
	Lipophrys canevai	Warm-temperate
	Lipophrys pholis	Temperate
	Lipophrys trigloides	Warm-temperate
	Parablennius gattorugine	Warm-temperate
	Parablennius incognitus	Warm-temperate
	Parablennius pilicornis	Tropical
	Parablennius rouxi	Warm-temperate
	Parablennius sanguinolentus	Warm-temperate
Clinidae	*Clinitrachus argentatus*	Warm-temperate
Gobiesocidae	*Apletodon dentatus*	Warm-temperate
	Diplecogaster bimaculata bimaculata	Temperate
	Lepadogaster candollii	Warm-temperate
	Lepadogaster lepadogaster	Warm-temperate

Appendix 1 (continued)

Family	Species	Biogeographic group
Callionymidae	*Callionymus lyra*	Temperate
	Callionymus reticulatus	Temperate
Gobiidae	*Gobius xanthocephalus*	Warm-temperate
	Gobius cobitis	Warm-temperate
	Gobius cruentatus	Warm-temperate
	Gobius niger	Temperate
	Gobius paganellus	Warm-temperate
	Gobius gasteveni	Warm-temperate
	Gobiusculus flavescens	Cold-temperate
	Pomatoschistus marmoratus	Warm-temperate
	Pomatoschistus pictus	Temperate
	Thorogobius ephippiatus	Temperate
Scombridae	*Scomber japonicus*	Tropical
	Sarda sarda	Eurythermic
Bothidae	*Arnoglossus thori*	Warm-temperate
	Arnoglossus imperialis	Tropical
	Bothus podas podas	Tropical
Scophthalmidae	*Phrynorhombus regius*	Warm-temperate
	Scophthalmus rhombus	Warm-temperate
	Zeugopterus puntactus	Cold-temperate
Soleidae	*Buglossidium luteum*	Warm-temperate
	Monochirus hispidus	Tropical
	Solea vulgaris	Temperate
	Solea senegalensis	Warm-temperate
	Synaptura lusitanica	Tropical
Balistidae	*Balistes carolinensis*	Eurythermic
Tetraodontidae	*Sphoeroides marmoratus*	Tropical
Molidae	*Mola mola*	Oceanic