

Modelling past and present geographical distribution of the marine gastropod *Patella rustica* as a tool for exploring responses to environmental change

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Abstract

A climate envelope approach was used to model the distributions of the intertidal gastropod *Patella rustica*, to test the robustness of forecast responses to climate change. The model incorporated variables that were likely to determine the abundance and the northern range limit of this species in the NE Atlantic. The model was built using classification and regression tree analysis (CART) trained with historical distribution data from the mid 1950s and a set of corresponding climatic and oceanographic variables. Results indicated air and sea temperature, in particular during the reproductive and settlement periods, as the main determinants of the Atlantic distribution of *P. rustica*. The model was subsequently fed with contemporary climatic data and its output was compared with the current distribution and abundance of *P. rustica*, assessed during a 2002–2003 survey. The model correctly hindcasted the recent collapse of a distributional gap in northern Portugal, as well as an increase in abundance at locations within its range. The predicted northward expansion of the northern range limit did not occur because the absence of the species was confirmed in a survey encompassing the whole Atlantic French coast up to Brest. Stretches of unsuitable habitat too long to be overcome by dispersal are the likely mechanism controlling the northern limit of the distribution of this intertidal species.

Keywords: biogeography, classification and regression trees (CART), climate change, intertidal, marine gastropod, modelling, *Patella rustica*

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Introduction

The application of species distribution models has considerably increased in the last two decades, mainly driven by the need to predict the potential impacts of climate change on the distribution of organisms (Guisan & Thuiller, 2005). From the vast array of methods currently available, single-species bioclimatic envelope models (BEMs) have been widely used (Heikkinen *et al.*, 2006). These models use the current geographic distribution of a species to infer its environmental require-

ments, and then to predict its geographic distribution for the current, or for past or future climates (Hijmans & Graham, 2006). Yet, given their correlative nature, the validity of such approaches has been progressively questioned (see Araújo & Guisan, 2006). The problem is twofold. First, BEMs seldom account for the effects of biotic interactions, adaptive change and dispersal (Pearson & Dawson, 2003). This results in highly biased models that tend to produce inaccurate scenarios (Davies *et al.*, 1998; Hampe, 2004). Second, independent validation of models is often not possible, because the events being predicted have not yet occurred or are poorly known (Araújo & Guisan, 2006). Nonindependent validation (resubstitution, data splitting) usually ends up in unrealistically optimistic estimates of their predictive ability (Araújo *et al.*, 2005).

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Despite being highly deterministic, BEMs have some advantages over the more complex rule-based mechanistic models (see Guisan & Zimmermann, 2000), provided that they are used in the appropriate context (Araújo *et al.*, 2005), that the choice of the model is well grounded (Hijmans & Graham, 2006) and that results are interpreted with caution (Hodkinson, 1999). BEMs can present a fast and useful tool for the identification of key relationships between species and the factors controlling their distribution (Huntley *et al.*, 2004), especially at large scales (e.g. continental and global) where the importance of climatic forcing is thought to be higher (Pearson *et al.*, 2002; Pearson & Dawson, 2003). When range-limiting physiological factors for a given species are poorly known, these methods may represent the best possible approach (Crumpacker *et al.*, 2001).

In the marine environment, BEMs have been sparsely applied to model species distributions (but see De'ath & Fabricius, 2000; Clark *et al.*, 2003; Friedlaender *et al.*, 2006; Kaschner *et al.*, 2006). This is unfortunate because there are many well-documented cases of recent changes (either expansions or retractions) of species' ranges which are thought to be a direct consequence of global warming (for a review see Helmuth *et al.*, 2006b). Rocky intertidal communities, in particular, are well suited for studying climate-driven community changes (Herbert *et al.*, 2003; Simkanin *et al.*, 2005) because their ecologies are well-known (Southward *et al.*, 1995) from decades of experimental studying of recruitment dynamics and biological interactions (see Raffaelli & Hawkins, 1996; Bertness *et al.*, 2001 for reviews). Moreover, their inhabitants are often exposed to temperature and weather extremes, living close to their thermal tolerance (Wolcott, 1973; Tomanek & Helmuth, 2002). Also, intertidal organisms can be easily surveyed because they are generally conspicuous, slow moving or sedentary, and their ranges are roughly one-dimensional, conveniently defined by the coastal end points (Sagarin & Gaines, 2002). Thus, the seashore provides both a trackable testing ground for scientific debate on the utility and applicability of BEMs to model and predict species distributions under climate change and a wealth of insight into the probable complexity of the phenomena being modelled (see Helmuth *et al.*, 2006b).

In this work, a single-species bioclimatic envelope approach was used to gain further insights into the factors driving the distribution of a marine gastropod, *Patella rustica* Linnaeus 1758, in the northeast Atlantic. In a recent paper, Lima *et al.* (2006) described the collapse of an historical distributional gap, in northern Portugal, which occurred in the late 1990s and coincided with a combination of unusual climatic and hydrographic events that were particularly pronounced between 1997 and 1999. In this period, a significant

warming of sea-surface temperature (SST) during autumn/early winter was observed in addition to the general increase in average SST off the Portuguese coast (Lemos & Pires, 2004; Peliz *et al.*, 2005; Lemos & Sansó, 2006). This, combined with strong river runoff and weak upwelling (Dong *et al.*, 2000; Santos *et al.*, 2004), may have facilitated the bridging of the gap.

The present work focused only on the northern part of *P. rustica* distribution in the Atlantic, mainly because empirical evidence showed that recent changes have already occurred in this area, and a northwards expansion was expected. *P. rustica* ranges from the Mediterranean to the Atlantic coast of the Iberian Peninsula and Northern Africa, including the Macaronesian Islands, except the Azores (Ridgway *et al.*, 1998). In the Atlantic, its southern limit is speculated to occur further south than Mauritania (Christiaens, 1973). However, apart from this reference, no reliable data exist that could have been used for modelling purposes. Thanks to the exhaustive work of Fischer-Piétte and colleagues (Crisp & Fischer-Piétte, 1959; Fischer-Piétte & Gaillard, 1959) the distribution of *P. rustica* along the Atlantic European coast is well-known for the late 1950s. These data were used together with several climatic and oceanographic variables to build a BEM. The model was subsequently evaluated by feeding it with climatic and oceanographic data from the 1990s, when the distributional gap was bridged, hindcasting the present day distribution of the species. The output was then compared with the extant distribution of *P. rustica* surveyed in 2002–2003. Thus, the model was implemented to 'understand' the likely mechanisms governing the distribution of this limpet rather than to 'predict' its future distribution and model evaluation was used to assess the 'robustness' of inferred mechanisms rather than to estimate its predictive accuracy (Araújo & Guisan, 2006). More importantly, evaluation was done with an independent data set (apart from spatial and temporal autocorrelation), which is highly recommended but rarely used in BEMs (Araújo *et al.*, 2005).

Materials and methods

Biological data

Data on the distribution and abundance of *P. rustica* along the European coastline (from the English Channel to Morocco) were gathered for the 1950s from the comprehensive works of Fischer-Piétte (1953, 1955, 1958, 1963), Crisp & Southward (1958), Crisp & Fischer-Piétte (1959) and Fischer-Piétte & Gaillard (1959). Because in each work, density of limpets was expressed by different abundance scales, the number of abundance categories was reduced to three: absent, rare and

abundant. This caused some information loss (in some cases true densities were available), but avoided wrong categorization and provided comparable data for the Atlantic range of *P. rustica*. Contemporary abundances were recorded by thoroughly resurveying historical localities between 2002 and 2003 and from Biarritz towards the north in 2006 (see Fig. 1). Density of limpets was estimated using several randomly placed $50 \times 50 \text{ cm}^2$ quadrats, and then converted to the three-class abundance scale.

Environmental data

Two climatic data sets were assembled and used in the model. Because climatic and oceanographic factors such as temperature and salinity are highly variable over the years (Levitus *et al.*, 2000), a time window large enough to encompass a significant amount of variability but simultaneously representative of the sampling years and correlated with changes in distribution of *P. rustica* was selected (Lima *et al.*, 2006). The first set included data from the 1950s (January 1950–December 1959) and the second one incorporated data from the decade of 1990 (January 1991–December 2000). The environmental conditions were described using six main climatic and oceanographic variables: near surface air temperature (NSAT), cloud cover (CC), precipitation (PP), SST, sea surface salinity (SSS) and wave action (WA).

NSAT, CC and PP monthly averaged data covering European land surface at a 10 min resolution were obtained from the CRU TS 1.2 dataset, available from the Tyndall Centre for Climate Change Research and Climate Research Unit (<http://www.cru.uea.ac.uk/>, Mitchell *et al.*, 2002, 2004). These were imported into GRASS Geographical Information System (GRASS Development Team, 2006) as raster maps. SST along the north-eastern Atlantic coast, was derived from *in situ* raw data obtained from the International Comprehensive Ocean – Atmosphere Data Set (ICOADS, <http://icoads.noaa.gov/>, Woodruff *et al.*, 1988). To avoid bias due to different daytime measurements, only data from 12:00 GMT were used. Point data were imported into GRASS GIS and transformed into monthly raster maps with a spatial resolution of 4 km using a surface interpolation method. Each cell was derived from the 12 nearest data points using the distance squared weighting algorithm (Jarvis & Stuart, 2001). The variables NSAT, CC, PP and SST are thought to be a surrogate not only for the air and sea temperature to which limpets are exposed, but also for other climatic factors that potentially affect the heat budget of intertidal organisms during low tide, like the amount of solar irradiance and the evaporation rate (see Denny & Harley, 2006). Sea salinity is another environmental

factor potentially important for the physiology and fitness of limpets (Fischer-Pi ette, 1948). Monthly averaged SSS data, with an average resolution of 0.5° latitude \times 0.5° longitude cells, were extracted from SODA-POP v1.2 model data set, available at the National Virtual Ocean Data System live server webpage (<http://ferret.pmel.noaa.gov/NVODS/servlets/dataset>) and imported into GRASS GIS as raster maps. Because data were only available from January 1958 onwards, the computed average for the decade of 1950s was based solely on 2 years.

The resulting set of 240 (20 years \times 12 months) SST, NSAT, CC, PP and 164 SSS maps was stored in GRASS GIS as monthly layers and sampled along the studied coastline in the locations visited by D. J. Crisp, E. Fisher-Pi ette and J. Gaillard during the 1950s (Fischer-Pi ette, 1955, 1958, 1963; Crisp & Southward, 1958; Crisp & Fischer-Pi ette, 1959; Fischer-Pi ette & Gaillard, 1959). Sampled data for each parameter were combined to build a table with each row denoting a geographical location and each column a month/year combination. For SST and NSAT, the general 10-year mean and the average value of winter, summer and reproductive seasons were computed, as well as the mean value of the coldest and hottest month during those seasons. Reproductive season was assumed to be from September to November (according to Ibanez *et al.*, 1986, P. A. Ribeiro, unpublished data). For CC and PP, the 10-year average and the values of the percentiles 25, 50 and 75 were calculated. For SSS, only the long-term average value during each studied period was considered. An overview of the climatic variables can be found in Table 1.

On the Atlantic coasts of Europe and North Africa the presence of *P. rustica* is generally associated with steep surfaces found in the upper eulittoral of exposed rocky shores (Fischer-Pi ette & Gaillard, 1959; Lima *et al.*, 2006). Thus, a quantitative measure of sea exposure was included in the model. Average wave power was used as surrogate for the exposure of sampled locations to the effects of wave action (WA). The EXposure estimates for fragmented Archipelagos (EXA) procedure as described by Ekebom *et al.* (2003) was generally followed, apart from the need to obtain wave climatology parameters from prevailing winds because they were directly incorporated in the exposure model. Hence, that computational step was skipped. Wave climate data were downloaded from the European Environmental Agency database (<http://www.eea.europa.eu>). Data were only available for regularly spaced offshore locations 50–100 km away from the coastline (Fig. 1). Therefore, in every coastal location the wave parameters of the nearest offshore point were used. The fetch length was measured for each direction

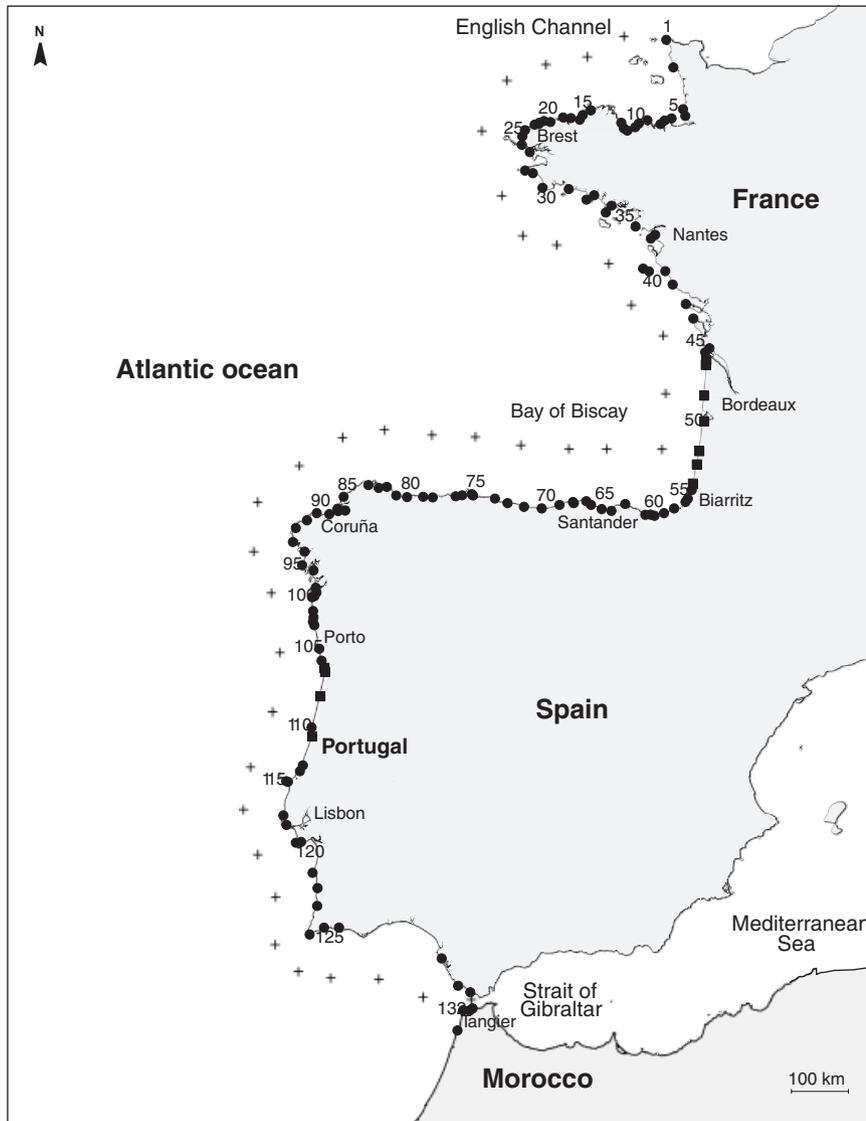


Fig. 1 Study area. Circles represent rocky shore locations and squares represent seawall constructions. Offshore points represent the sites for which wave climatology data were available. 1 – Cap de la Hague, 2 – Cap de Carteret, 3 – Granville, 4 – Carolles, 5 – Pte. Grouin, 6 – Rotheneuf, 7 – Dinard, 8 – Cap Fréhel, 9 – Cap d’Erquy, 10 – Pte. Pléneuf, 11 – Pte. Roselier, 12 – Pte. Pordic, 13 – St. Quay – Portri, 14 – Trestrignel, 15 – Pte. Bihit, 16 – Pte. Locquirec, 17 – Pte. Primel, 18 – Pte. Bloscon, 19 – Greve Poulfoén, 20 – Pontusval, 21 – Guissény, 22 – Greve Vougot, 23 – Greve Lilia, 24 – Trémazan, 25 – Melon, 26 – Le Conquet, 27 – Camaret, 28 – Pte. Raz, 29 – Pte. Lervily, 30 – St. Guénolé, 31 – Trévignon, 32 – Pte. Pen Men, 33 – Port-Louis, 34 – Quiberon, 35 – Pte. Kerbihan, 36 – Pte. Croisie, 37 – St. Michel Chef Chef, 38 – Pte. St. Gildas, 39 – Yeu, Pte. But, 40 – Yeu, Pte. Tranche, 41 – Croix de Vie, 42 – Les Sables d’Olone, 43 – Phare Balenes, 44 – Phare Chassiron, 45 – Royan, 46 – Courdouan, 47 – L’Amelie, 48 – Montalivet, 49 – Lancanau, 50 – Arcachon, 51 – Mimizan, 52 – Contis, 53 – Vieux-Boucau, 54 – Capbreton, 55 – Boucau, 56 – Biarritz, 57 – Cabo Higuer, 58 – San Sebastian, 59 – Zarauz, 60 – Zumaya, 61 – Deba, 62 – Bermeo, 63 – Barrica, 64 – Urdiales, 65 – Santoña, 66 – Noja, 67 – Santander, 68 – Cabo Menor, 69 – Ubiarco, 70 – San Vicente de la Barquera, 71 – Llanes, 72 – Ribadesella, 73 – Lucas, 74 – Perlora, 75 – Candas, 76 – Salinas, 77 – San Juan, 78 – Luarca, 79 – Navia, 80 – Cangas de Foz, 81 – Ribadeo, 82 – San Ciprian, 83 – Vivero, 84 – Espasante, 85 – Cobas, 86 – Carnoedo, 87 – La Coruña, 88 – Sta. Cristina, 89 – Arteijo, 90 – Malpica, 91 – Lage, 92 – Mugia, 93 – Finisterre, 94 – Muro, 95 – Corrubedo, 96 – Grove, 97 – Punta Corbeiro dos Castros, 98 – San Miguel de Oia, 99 – Bayona, 100 – Cabo Sillero, 101 – La Guardia, 102 – VP Âncora, 103 – Montedor, 104 – Viana Castelo, 105 – Vila do Conde, 106 – Leixões, 107 – Aguda, 108 – Espinho, 109 – Aveiro, 110 – Cabo Mondego, 111 – Buarcos, 112 – Leirosa, 113 – Nazaré, 114 – S. Martinho Porto, 115 – Cabo Carvoeiro, 116 – Peniche, 117 – Azenhas do Mar, 118 – Cascais, 119 – Cabo Espichel, 120 – Sesimbra, 121 – Sines, 122 – VN Milfontes, 123 – Odeceixe, 124 – Sagres, 125 – Lagos, 126 – Armação de Pêra, 127 – Rota, 128 – Trafalgar, 129 – Punta Paloma, 130 – Punta Malabata, 131 – Tanger, 132 – Cap Spartel, 133 – Arcila.

Table 1 Summary of the independent variables used in the CART modelling of *Patella rustica* distribution

Environmental variables	Acronym	Unit of measurement	Considered periods	Statistics	Temporal resolution	Spatial resolution (raw data)
Sea surface temperature	SST	°C	1950–1959 1991–2000	Mean, minimum and maximum during winter, summer, and reproduction	Monthly	4 km
Near surface air temperature	NSAT	°C	1950–1959 1991–2000	Mean, minimum and maximum during winter, summer, and reproduction	Monthly	10 min
Cloud cover	CC	%	1950–1959 1991–2000	Percentile 25, 50, 75	Monthly	10 min
Precipitation	PP	%	1950–1959 1991–2000	Percentile 25, 50, 75	Monthly	10 min
Sea surface salinity	SSS	‰	1958–1959 1991–2000	Percentile 25, 50, 75	Monthly	10 min
Wave power	WP	kW	1985–2001	Mean	–	Approximately 100 km

by a group of lines radiating from each coastal point with a 7.5° bearing step between them. Lines were trimmed when reaching the coastline. For each one of the remaining lines, wave parameters from the corresponding directional sector were selected and used to estimate the wave power observed in coastal location over that specific direction. Wave power (P) in kW was defined as $P = nE1.56T$ where $n = 0.5$, T = mean significant wave period (in seconds) and E (energy in Joules) = $1/16 \rho g H$ where ρ = seawater density (1020 kg m^{-3}) g = acceleration due to gravity (9.8 m s^{-2}) and H = mean significant wave height in metres. For each coastal location, total wave power was computed as the sum of all converging partial estimates from the different directions, weighted by the percentage of time waves were observed in each direction. The online wave data were only available for the period between 1985 and 2001 and records were summarized in statistics relative to that 16-year period without the possibility to extract specific years or months, which forced the use of the whole data set. As a consequence, the parameter WA was considered static (i.e. not varying from the 1950s to 1990s), which may not be entirely true (see Davies & Johnson, 2006).

Modelling approach

Classification and Regression Trees (CART) (Breiman *et al.*, 1984) are one of the currently available climate envelope approaches. Traditionally applied to fields such as medical diagnosis, meteorology, plant physiolo-

gy, soil sciences and wildlife management, they have recently been used to successfully model terrestrial (e.g. Vayssières *et al.*, 2000; Edwards *et al.*, 2006; Fronzek *et al.*, 2006) and marine species distributions (De'ath & Fabricius, 2000; DeVantier *et al.*, 2006; Friedlaender *et al.*, 2006).

For the purposes of the current study CART models were selected primarily because they are relatively immune to multicollinearity (Breiman *et al.*, 1984; Jackson & Bartolome, 2002; Karels *et al.*, 2004), and the data set incorporated 20 potentially correlated predictor variables. Other advantages included the possibility of output response variables with more than two levels, the robustness regarding possible outliers and nonnormal distributions of variables (Breiman *et al.*, 1984) and the capacity to determine complex interactions among explanatory variables without the need to specify them *a priori* (Vayssières *et al.*, 2000; Rouget *et al.*, 2001). Additionally, these analyses are easy to interpret (De'ath & Fabricius, 2000) because they provide a hierarchical view of the relationships between species and environmental variables, allowing the identification of those which are the most correlated with the presence of species (Vayssières *et al.*, 2000).

Homogeneity of groups was assessed by the Gini purity index (Breiman *et al.*, 1984). Because the maximal tree is usually overfitted to training data, a computational step to constrain the tree to its best size is required to avoid the problem of overfitting (Araújo & Guisan, 2006). Overfitted models tend to perform exceptionally well on the training data because they fit

the idiosyncrasies and noise in the data set used to build the model, in addition to the generic relationships between independent and response variables. Thus, a balanced model including sufficient complexity to uncover subtle effects and interactions but not compromising predictive power should be chosen. A common approach in tree-based techniques is to freely allow the maximum growing process and then prune the over-branched tips of the tree (Breiman *et al.*, 1984; De'ath & Fabricius, 2000; Questier *et al.*, 2005). The initial tree was allowed to attain the maximum size and then pruned using the mode of 50 repeated 10-fold cross-validations (see Breiman *et al.*, 1984; De'ath & Fabricius, 2000 for details). For the cross-validation, the data set was divided in 10 parts and each subset was removed in turn, being used as a test sample against predictions based on the remaining 90% of data. This technique is similar but more robust than jack-knifing, as it gives a better reflection of its performance on new data (Fielding & Bell, 1997). The average error rate was plotted in relation to the tree size and the best size for the tree was chosen as the smallest having an error rate within one SE of the minimum (De'ath & Fabricius, 2000).

The predictive power of the model was evaluated using the area under curve (AUC) obtained from the receiver operator characteristic (ROC) plot. AUC is a reliable measure of model performance because it is largely unaffected by the data prevalence, (i.e. the proportion of study sites naturally occupied by the species (Manel *et al.*, 2001; McPherson *et al.*, 2004; Vaughan & Ormerod, 2005). Because the output of CART is categorical, ROC curves were derived by recursive partitioning (Cook & Goldman, 1984; Rauber-tas *et al.*, 1994). Even though it has been traditionally used to measure the degree to which a classifier can discriminate between two classes, its extension to a multiclass classification may be done by computing a series of binary AUCs for each class vs. all the others (called one- vs. -all approach or OVA). Thus, each one of these binary comparisons has its own AUC, measuring how well each class is identified by the model (Patel & Markey, 2005).

The model was evaluated by feeding it with climatic and oceanographic data from the 1990s, when the distributional gap was bridged, to hindcast the contemporary distribution of *P. rustica* along the NE Atlantic coast. The output was subsequently compared with the real distribution and abundance of *P. rustica* assessed in the 2002–2003 and 2006 surveys.

Results

A total of 122 locations for which data were available from the 1950s were revisited during the 2002–2003

survey, enabling abundance and distribution to be mapped (Fig. 2a and c). In the 40-year period between the two surveys, the most remarkable changes were: (i) the bridging of the distributional gap in northern Portugal (Lima *et al.*, 2006); (ii) a global increase in abundance in NW Iberia (Galicia) and on some southern Portuguese shores; and (iii) no extension of the northern boundary of the range at Capbreton, although an increase in abundance was also observed in this region.

The final model, selected and pruned after cross-validation, could be represented as a five leaf tree explaining 94% of data variance for the distribution during the 1950s (Fig. 3). Scores of the AUC obtained from ROC plots for test data were 0.93 for category class 0 (absent), 0.99 for category 1 (rare) and 0.92 for category 2 (abundant), which according to Swets (1988) and Zweig & Campbell (1993) indicates excellent classification accuracy. From the variety of climate data fed into the model, SST and NSAT were selected as determinant factors of the distribution of *P. rustica*. The first data partition, based solely in the observed value of the average NSAT of the coldest month during the reproductive period, explained nearly 38% of data variation and was responsible for identifying the break, which corresponds to the northern boundary of the distribution. The remaining cases were generally explained by the average SST of the coldest winter month, average NSAT and average SST. Nearly half of misclassifications occurred within the distributional gap in Northern Portugal. In this area, the model erroneously predicted the presence of *P. rustica* at two locations where the species had not been observed (Cabo Mondego and Buarcos). It also predicted the existence of limpets at high densities at Vila do Conde, a location where Fischer-Pi ette & Gaillard (1959) reported only a single individual during their 1950s survey. In addition, the model overestimated the abundance in three locations in the southern part of the studied distribution (Sesimbra, Rota and Tangier). In one locality in northern Spain (Santander) the predicted abundance was misclassified as rare, while in reality it was abundant (Fischer-Pi ette & Gaillard, 1959). Nevertheless, globally the model performed quite well, because the main distributional features such as the northern range limit, the existence of a distributional gap in northern Portugal and the region of low abundance in north-western Iberia were correctly modelled (Fig. 2b).

When the model was fed with environmental data from the 1991–2000 period, scores of the AUC were 0.78 for category class 0 (absent), 0.45 for category 1 (rare) and 0.95 for category 2 (abundant). In particular, the model correctly hindcasted the bridging of the historical gap in Northern Portugal and also the observed increase in densities at Galicia (NW Iberia) and at the



Fig. 2 Abundance of *Patella rustica* along the studied area. Circles represent rocky shore locations and squares represent seawall constructions. White stands for absent, grey represents rare and black means abundant. (a) Historical abundance. (b) Abundance modelled for the 1950s. (c) Contemporary abundance. (d) Model output for 1990s.

current northern limit of the species range (Capbreton). However, it overestimated the densities inside the former distributional gap and more importantly, failed in identifying the actual northern limit of the species range, because it predicted the species presence (although at low densities) in all locations between Capbreton and Ile d'Oléron and further north, between Pointe de Kerbihan and Pointe de Lervily. A new survey made in 2006, from Capbreton towards the Cotentin Peninsula (in the English Channel), revealed

that the predicted northern expansion of the species range had not occurred.

Discussion

The CART model suggested that the distribution of *P. rustica* during the 1950s was highly correlated with temperature. According to the model output, the distribution of this species along the European Atlantic coast could be accurately explained by air and sea

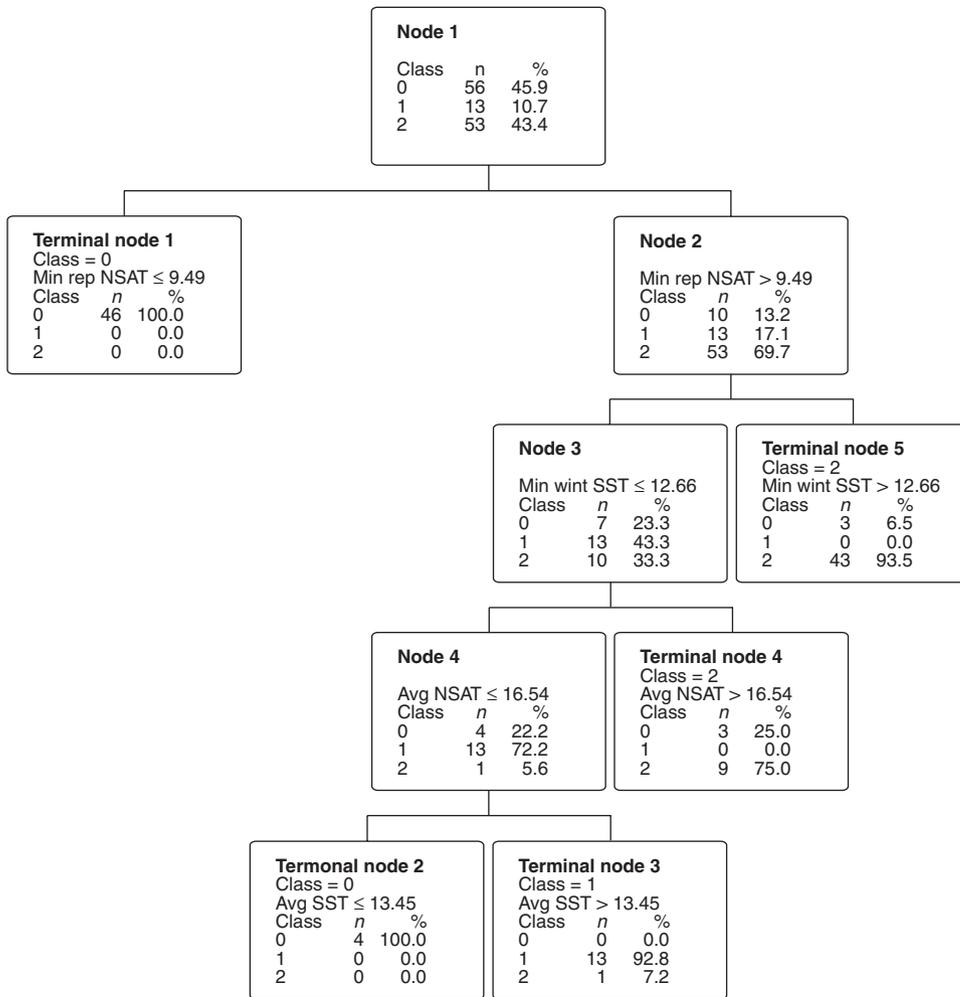


Fig. 3 Decision tree of the CART model built using historical (1950s) survey data. At each partition, the value of the splitting variable is shown. Information featured in the nodes includes the node identification, the level of the predicted response and the value of the split variable associated with that node. Finally, the number and percentage of cases for each level of the predicted response is also displayed. 0 stands for absent, 1 for rare and 2 for abundant. Climatic variables refer to the period of 1950–1959. Min rep NSAT, mean NSAT value of the coldest month during reproductive season; min wint SST – mean SST value of the coldest month during winter; avg NSAT – mean NSAT value during the 10-year period; avg SST – mean SST value during the 10-year period.

temperature patterns, especially during the reproductive (autumn) and initial growth (winter) periods. The model correctly excluded *P. rustica* from locations where temperature was too low, such as most of the French Atlantic coast and in the historical distributional gap in Northern Portugal, where upwelling has a dominant cooling effect on the sea temperature, at least during some periods of the year (Peliz *et al.*, 2002, 2005). On the other hand, regions characterized by a warmer climate such as the Southern Portuguese coast and the Bay of Biscay were correctly modelled as having high densities of *P. rustica*.

The use of the climate envelope with contemporary environmental conditions correctly predicted the bridging of the gap and the increase in densities in Northern

Spain. This suggests that some of the factors used in the model do determine, to some extent, the distribution of *P. rustica*, at least in this section of the range. Both events are probably connected, constituting an ongoing expansionary episode whose onset was already noticed by Fischer-Pi ette & Gaillard (1959). Yearly abundance reassessments made from 2003 to 2006 clearly showed that the number of individuals from the new populations in this area is still increasing (F. P. Lima, unpublished data). The recent expansion of *P. rustica* observed in Northern Portugal, which led to the collapse of a long-term distributional gap in the late 1990s, was coincident with sea surface anomalies recorded over the last decade off the Portuguese coast (Lima *et al.*, 2006). The current patterns observed off the Portuguese coast

in the autumn/winter are part of a wider and well-known system called 'Navidad' which affects the Atlantic European continental slope (Pingree & Le Cann, 1992). During winter, a warm water stream flows northward along the east coast of Portugal and Spain. It then splits into two streams, one flowing directly to northern France and the British Isles, and the other moving eastward, following the Spanish coastline, and turning north along the French coast. This stream is tightly correlated with the North Atlantic Oscillation Index (NAO). An extremely negative winter NAO Index was observed during 1996 and 1998, enhancing poleward flow and an anomalous winter warming along the coast of the Bay of Biscay (Pingree & Le Cann, 1992; Garcia-Soto, 2004). Therefore, because the observed changes in the distribution of *P. rustica* are likely to be related with increases in temperature (either from air or sea), a similar expansion was anticipated in Southern France, where an analogous warming trend was observed (Koutsikopoulos *et al.*, 1998). Hence, it was interesting to notice the absence of such a phenomenon. The only evidence of a tendency for expansion in the northern portion of the range was the huge increase in densities observed in the two northernmost locations (Boucau and Capbreton) when compared with the data from Fischer-Pi ette & Gaillard (1959). However, this evidence is fairly weak, because in these locations the building of coastal defences largely expanded the area of suitable habitat, thus confounding the effect of any other factor, such as environmental changes due to sea or air temperature increase.

The model failed to predict the correct northern range boundary on the Western French coast (Capbreton), extending the 'suitable habitat' for *P. rustica* as far north as Pointe de Lervily. This probably indicates that although both air and sea temperatures could be nowadays favourable to the presence of the species, some other factor, or even a combination of factors are hampering the expansion. It is possible that *P. rustica* is already present in locations north of Capbreton, but at densities which hindered its detection even by experienced observers. This is very unlikely considering the effort of the fieldwork, with more than 50 locations visited between Capbreton and Royan. In addition to the few rocky shores, all artificial coastal defences were also surveyed. It is also possible that certain variables not accounted in the model have a strong limiting influence on survival and/or expansion of this species. For example, recent work suggests that marine populations may be less open than originally thought (Bohonak, 1999; Cowen *et al.*, 2000; Levin, 2006) and that sea currents can potentially constitute insurmountable barriers to species with a dispersive larval stage, constraining their ranges even when there is suitable

habitat beyond those barriers (Gaylord & Gaines, 2000). The situation becomes even more complicated when effects of dispersal barriers are confounded with effects of physiological limitations imposed by steep clines in climatic factors such as sea temperature, because they usually co-occur in space (Zacherl *et al.*, 2003). The ocean circulation in the Bay of Biscay has been studied by numerous authors (Koutsikopoulos *et al.*, 1998; Bardey *et al.*, 1999; Puillat *et al.*, 2004; Planque *et al.*, 2006), who pointed out several hydrographical fronts, upwellings, eddies and low salinity plumes from the rivers Loire and Gironde as being responsible for strong discontinuities in oceanic and coastal waters. Thus, these factors may represent considerable dispersal barriers for *P. rustica*.

Another hypothesis could be related with the limited larval dispersal potential of *P. rustica*. Even assuming that oceanographic barriers are not obstructing larval transport, a limited dispersal ability coupled with the lack of suitable habitat may pose a serious problem to expansion, as reported previously by Crisp (1958) for the barnacle *Elminius modestus*. The 200 km of coastline between Capbreton and Royan are mainly sandy and, therefore, do not allow larval settlement. The ability to traverse such a gap depends on the existence of a sufficiently long larval stage, able to survive during the transport towards the north, and even so, favourable currents must exist during larval drift. In the Bay of Biscay, the current flow over the continental slope was determined as having a characteristic northward velocity of 5 cm s^{-1} during the winter, and probably reversing during the summer (Aken, 2002). Spawning is thought to happen during the autumn (Ibanez *et al.*, 1986) but unfortunately very little is known regarding ocean circulation in this region during that season. However, and considering an average travelling speed of 5 cm s^{-1} , larvae would need more than 45 days to traverse the sandy coastline, a prohibitive period for a species whose planktonic stage lasts approximately 6 days (P. A. Ribeiro, unpublished data). If this is the main factor limiting the species expansion, why has it not prevented the recent colonisation of several locations in Northern Portugal, leading to the collapse of the historical 280 km gap? Coastal currents off the Portuguese coast display a stronger northward component during the reproductive period of *P. rustica*, with mean velocities of $15.1 \pm 4.4 \text{ cm s}^{-1}$ (Martins *et al.*, 2002). In 6 days, this current may transport larvae for distances of up to 100 km, which is enough to cover the largest sandy stretch of coastline.

Additionally, the construction of a high number of artificial sea defences to protect both the sandy shores and the main city harbours from wave action has most likely increased population connectivity of rocky shore

species on the Portuguese coast. In fact, most sea defences are massive structures hosting typical rocky shore communities (F. P. Lima, unpublished data), where for example it is possible to find intertidal algae (*Porphyra* spp., *Fucus spiralis*), polychaetes (*Sabellaria alveolata*) crustaceans (*Pachygrapsus marmoratus*, *Pollicipes pollicipes*, *Chtamalus montagui* and *Chtamalus stellatus*) and molluscs (*Mytilus galloprovincialis*, *Littorina neritoides*, *Littorina saxatilis*, *Patella depressa*, *Patella vulgata* and *P. rustica*). These artificial reefs have shortened the largest sandy stretches to approximately 50 km, allowing a much easier expansion. On the contrary, along the 200 km rocky hiatus of the French coast, the construction of sea defences was done in a much more subtle way. With the exception of the two seawalls at Boucau and Capbreton, all constructions are small in height and length, unable to accommodate more than a few ephemeral green algae (genus *Ulva* and *Enteromorpha*), a few mussels (*Mytilus* sp.), oysters, and in some rare occasions, a handful of *P. depressa*. These structures clearly lack the typical habitat of exposed vertical walls required by *P. rustica*. Similarly, Gilman (2006) found that the most likely explanation for the determination of the northern range limit of the intertidal limpet *Collisella scabra* in California was an increase in the distance between populations at the range margin, reducing the chances of dispersing larvae to find suitable habitat for settlement, rather than any climatic constraint. Thus, it is possible that the limits of many marine species can remain unchanged even when peripheral habitat conditions become favourable (Crisp & Southward, 1958; Fields *et al.*, 1993).

It has been noted that range expansions, even from those species which eventually become successfully established, are frequently preceded by several failures (Sax & Brown, 2000). In addition, it was shown that species with a similar larval duration to *P. rustica* may take several years to become completely established over an area similar to the one for which the present expansion was anticipated (see Shanks *et al.*, 2003; Siegel *et al.*, 2003, for a review). Therefore, even with present favourable climatic conditions and assuming that some extraordinary events such as storm-strengthened anomalous currents allowed the species to overpass the sandy barrier, the elapsed time for such a large expansion to occur may still be insufficient. In this perspective, the hindcasted northern range expansion is not completely wrong (see Araújo *et al.*, 2005), and might become visible in future years, as long as the sea and air warming phase of the last decades is maintained.

In the light of current results, the hypothesis proposed by Lima *et al.* (2006) that the changes in the geographical distribution of *P. rustica* observed in NW Iberia were largely related to a joint effect of increasing

temperature and alteration in oceanic circulation patterns is reinforced. Therefore, the conceptual model here proposed has the ability to simultaneously explain several spatially independent phenomena, giving it a higher degree of confidence. Nonetheless, because other valid explanations could be advanced, future investigations are still needed in this area. Several recent studies indicate that some organisms have the ability to adapt to different conditions at diverse parts of their range (Sagarin *et al.*, 2006), and also that environmental variables might not be physiologically limiting at all range edges (Helmuth *et al.*, 2006b). Hence, it is even possible that the factors which were until recently limiting the expansion in northern Portugal could be distinct from those currently governing the northern boundary. Nonetheless, the existence of barriers to dispersal, resulting in limited or no connectivity remains the most parsimonious and, thus the most probable scenario. This hypothesis can be tested using a bioclimatic approach coupled with a dispersal simulation model, encompassing information about oceanic currents and habitat availability. This approach would help to definitely solve the question of the relative importance of temperature or transport in establishing limits in the distribution of *P. rustica*. The use of autocorrelation and/or contagion indexes could also be a way to gain some insights on the strength and extension of larval dispersal.

This study also reinforces the idea that intertidal organisms are clearly influenced by both air and water temperature. Although it has already been shown that various aspects of both terrestrial and aquatic climate drive the physiological performance of these species (Helmuth *et al.*, 2006a), the use of a nonlinear modelling technique showed that these factors frequently alternate with one another and with nonclimate-related factors, in determining distributional limits (Helmuth *et al.*, 2006b).

Although the present results partially support previous suggestions that BEMs may be inadequate for making projections of future events, they also suggest that this approach can be of great utility in gaining further insights into the nature of the relationship between the distribution of the species and the environment (Araújo *et al.*, 2005). Therefore, although sometimes bioclimatic envelopes may appear too limited or deterministic, they certainly still have an important role in ecology by helping to effectively work on some explanatory hypothesis, which can subsequently be tested.

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