



Recent changes in the distribution of a marine gastropod, *Patella rustica* Linnaeus, 1758, and their relationship to unusual climatic events

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ABSTRACT

Aim Recent colonization of northern Portuguese shores by *Patella rustica* Linnaeus, 1758, led to the bridging of a historical gap in the distribution known since the 1900s. Long-term oceanographic data collected over the last half-century were examined in order to detect possible mechanisms for the observed change in its distribution.

Location This study was carried out along the entire Portuguese coastline, from 41°50' to 37°06' N. Time-series of hydrographical variables (sea surface temperature and salinity) were derived for the Atlantic coast of the Iberian Peninsula.

Methods Abundance and size-frequency distributions of the newly observed limpet populations were compared with those from well-established populations in southern Portugal. Anomalies were computed for sea surface temperature (1950–2000) and sea surface salinity (1958–2001) data, covering the whole Atlantic coast of the Iberian Peninsula. An upwelling index (1967–2005) was derived for a single location within the distributional gap of *P. rustica*. Split moving window analysis was performed to detect significant discontinuities in hydrographical data sets.

Results *Patella rustica* has gradually been expanding in northern Iberia, and in the late 1990s the historical gap in distribution in northern Portugal was bridged. Size-frequency distribution differed between historical and recent populations, the latter lacking small-sized individuals. At the same time, several anomalous oceanographic events occurred off the Portuguese coast and were probably related to this expansion.

Main conclusions Although sea surface temperature might be a major determinant of the reproductive success of *P. rustica* and hence its dispersal potential, it is more likely that a coincidence of several factors occurring in the late 1990s provided exceptional conditions that allowed the geographical expansion of this species.

Keywords

Biogeography, climate change, dispersal, *Patella rustica*, Portugal, sea salinity, sea temperature, upwelling.

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INTRODUCTION

Recent ecological literature reflects concerns with anthropogenic global climate change (Southward *et al.*, 1995; Stensen

et al., 2002; Walther *et al.*, 2002; Parmesan & Yohe, 2003; Root *et al.*, 2003) and has provided insights into the causes of species range limits and shifts in response to changing climatic conditions (Sagarin *et al.*, 1999; Sagarin & Gaines, 2002a;

Zacherl *et al.*, 2003). Keeping records of alterations in the environment and creating predictive models that enable the detection of variations in climate is one of today's primary aims in ecology (Lewis, 1999; Hawkins *et al.*, 2003; Hiscock *et al.*, 2004).

Changes in the distribution and abundance of several marine species on the eastern coasts of the Atlantic and Pacific oceans have been particularly well documented over the last decades. Consistent responses to climate change have been described at different trophic levels for both sessile and pelagic assemblages (Southward *et al.*, 1995; Holbrook *et al.*, 1997; Sagarin *et al.*, 1999; Wethey, 2002; Beaugrand & Reid, 2003; Borges *et al.*, 2003; Hawkins *et al.*, 2003; Zacherl *et al.*, 2003; Genner *et al.*, 2004; Hiscock *et al.*, 2004; Paine & Trimble, 2004). In contrast to pelagic systems, intertidal communities are ideal for studying climate-driven community changes because the constituent species are typically long-lived, less influenced by short-term factors and respond more readily to multi-decadal periods of environmental variability (Barry *et al.*, 1995; Southward *et al.*, 1995). In addition, their ranges are roughly one-dimensional and easily defined as the coastal endpoints. Therefore, conspicuous, easily identified, slow moving or sedentary rocky shore species are some of the best candidates to monitor climate changes (Lewis, 1996, 1999; Sagarin & Gaines, 2002b; Hiscock *et al.*, 2004).

Because alterations of the environment affect a series of physiological factors that act on population-level processes, it is thought to be more important to understand the mechanisms that influence population dynamics and the synchrony between climatic oscillations and species life cycles, instead of studying only the physiological limitations of individuals (Holbrook *et al.*, 1997; Zacherl *et al.*, 2003; Hagberg *et al.*, 2004). Thus, quantitative approaches like studies of the populations dynamics of newly established populations are encouraged (Kolar & Lodge, 2001), and may indicate which processes determine the success or failure of a particular shift or invasion (Zacherl *et al.*, 2003; Genner *et al.*, 2004), allowing more successful prediction of the patterns of invasive species.

The Portuguese coast is particularly well suited for the study of the putative effect of climate warming on species distribution for several reasons. First, the clear north–south orientation of the coastline is the most appropriate for this type of analysis (Rivadeneira & Fernández, 2005). Second, it is characterized by particular hydrographical features, with a cooler northern region affected by both upwelling and rainfall leading to a higher volume of river run-off and a much warmer southern region with a strong Mediterranean influence (Sánchez & Relvas, 2003; Santos *et al.*, 2004; Peliz *et al.*, 2005). Third, this is a contact region between warm- and cold-water species, where both northern and southern boundaries of several organisms can be found (Fischer-Piètte, 1959, 1963; Fischer-Piètte & Gaillard, 1959; Ardré, 1970; Santos, 2000; Boaventura *et al.*, 2002). Finally, shifts in species distribution have been described since the 1950s, not only for this particular stretch of coastline but also for the Iberian Peninsula (Fischer-Piètte & Forest, 1951; Fischer-Piètte, 1957a,b, 1960;

Fischer-Piètte & Kirsch, 1957; Ardré, 1971; Santos, 2000; Pereira *et al.*, 2006).

The geographical distribution of *Patella rustica* Linnaeus, 1758, ranges from the Mediterranean to the Atlantic coast of the Iberian Peninsula and northern Africa, including the Macaronesian Islands (Ridgway *et al.*, 1998). In the Atlantic, its southern limit is speculated to occur further south than Mauritania, whilst its northern limit is located at the French Basque Country (Fischer-Piètte, 1955; Crisp & Fischer-Piètte, 1959). Within this range there is a well-documented gap. Hidalgo (1917) placed it between the locations of Nazaré (Portugal, 39°36'16" N, 9°05'08" W) in the south, and La Coruña (NW Spain, 43°22'54" N, 8°26'23" W) in the north. Although the work of Nobre (1940) provides no information regarding the northern boundary of this species, he identified São Pedro de Moel (39°45'34" N, 9°01'58" W) as the northern limit of *P. rustica* in Portugal.

The works of Fischer-Piètte (1955) and Fischer-Piètte & Gaillard (1959) still remain the most comprehensive accounts of the distribution and abundance of patellid limpets on the Atlantic coast of the Iberian Peninsula. According to these authors, during the 1950s *P. rustica* was still largely absent from northern Portugal (surprisingly, one individual was found at Vila do Conde, 41°21'05" N, 8°45'21" W). From its northern geographical boundary in Biarritz (south-west France) toward La Coruña, densities were described as progressively decreasing. However, they observed new populations in Galicia (north-west Spain), with limpets occurring in low densities only at very exposed locations. After a detailed review of Hidalgo's (1917) work, Fischer-Piètte & Gaillard (1959) concluded that they were observing an on-going expansion of *P. rustica* in the northern part of the distributional gap.

More recent data, based on multiple surveys carried out between 1993 and 1998 over the entire Portuguese coast (Santos, 2000), confirmed the southern boundary of the distributional gap in central Portugal (São Martinho do Porto, 39°30'43" N, 9°08'33" W). In 1996, S. J. Hawkins (pers. obs.) spotted a single *P. rustica* at Moledo do Minho. Despite continuous sampling in the area since 1993, it was only in the winter of 2002 that several individuals (> 20) were recorded at Homem do Leme (Porto), within the historical gap. A subsequent survey revealed that the species was already present at very low densities in several shores north of Porto.

This study describes the recent bridging of the 280 km distributional gap of *P. rustica* in northern Portugal. Density and size-frequency distribution of the newly observed populations were compared with those from well-established southern populations, and long-term hydrographical data were used both to demonstrate the gap area as one with anomalous oceanographic conditions and to formulate alternative hypotheses to explain the recent change in the geographical distribution of this species. Plausible hypotheses, like changes in upwelling regimes, sea surface temperature or coastal current patterns are discussed, and a testable explanatory model is suggested.

MATERIAL AND METHODS

On the Atlantic coasts of Europe and North Africa, *P. rustica* is normally found in the upper eulittoral zone (usually above mean high water neap) of exposed rocky shores. Although other limpet species (*Patella vulgata* Linnaeus, 1758 and *Patella depressa* Pennant, 1777) also occur in this zone, *P. rustica* is easily identified by the characteristic black spots that ornament its shell. This feature can be observed even in small (c. 5 mm) animals, so juvenile identification does not pose any problems. In addition, *P. rustica* has a strong preference for vertical walls or very steep surfaces and, at least on the Portuguese coast, is seldom found outside this habitat.

During February 2003, density and size-frequency surveys of *P. rustica* were carried out in two different regions. The first encompassed recently colonized locations within the distributional gap of *P. rustica* in northern Portugal, whilst the second included historically inhabited areas in central and southern Portugal. In each region, six shores were visited (Fig. 1). Within the gap area, the southern half consists mainly of large stretches of sandy shores, interspersed with a few rocky shores that do not provide suitable habitat for *P. rustica* (no rocky substrate above mean tide level). An initial survey was done over the entire area, but the species was only found in the northern half of the gap, which is mainly rocky. Since the

recent colonization of northern Portugal could be an on-going process rather than a single event, sampling was repeated in February 2005 for the northern shores.

On the southern shores, the density of limpets was estimated using several haphazardly placed 50 × 50 cm quadrats. Due to the high density of limpets, and to avoid bias toward larger size classes, size-frequency data were collected by measuring all limpets within each quadrat. The maximum length of each limpet was measured with digital callipers and rounded to the nearest millimetre. Because low-water spring tides occur in the early morning (07:00–09:00), sampling time was roughly limited to 3 h on each shore. At northern locations, in order to obtain comparable values of density, a 3-h survey was also undertaken. However, because densities were very low, all individuals observed were counted and measured. Length-frequency histograms were built for each sample using 2 mm size classes.

To test for non-independence between size structure and location a chi-square test was used. Limpets were divided into three length classes: < 13 mm, 13–28 mm and > 28 mm. The choice of the interval to represent non-reproductive (juvenile) stages was problematic because size at sexual maturity is unknown for *P. rustica*. The upper limit of 12 mm was based on the assumption that it would be similar to the value already known for *P. depressa* (Guerra & Gaudêncio, 1986; P. A.

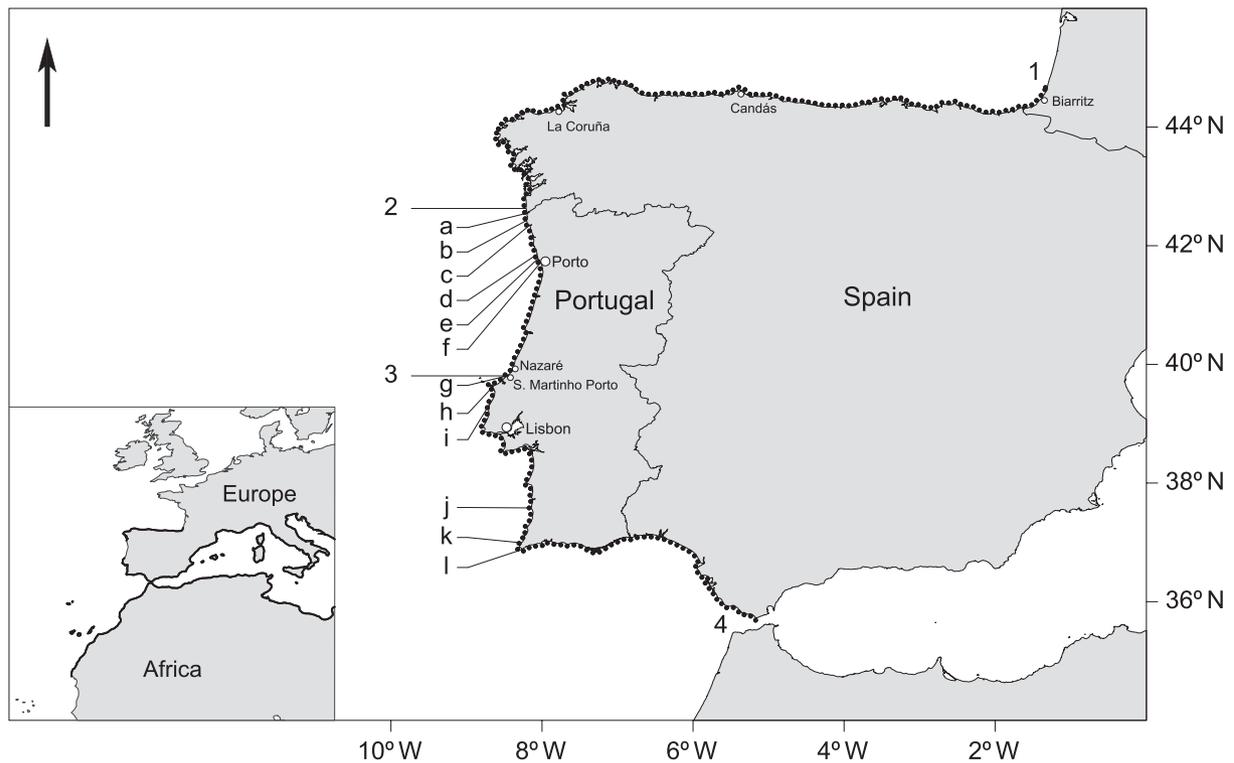


Figure 1 Study area. 1, Biarritz (northern limit of *P. rustica* distribution). The coastline between 2 (Baiona) and 3 (São Martinho do Porto) is the historical gap in northern Portugal. 4, Strait of Gibraltar. Locations visited: (a) Moledo do Minho, (b) Montedor, (c) Forte da Vigia, (d) Mindelo, (e) Cabo do Mundo, (f) Homem do Leme, (g) São Martinho do Porto, (h) Baleal, (i) Santa Cruz, (j) Amoreira, (k) Castelejo and (l) Beliche. Hydrographical coastal sampled points are represented as black circles. Inset figure shows known distribution of *P. rustica* prior to recent expansion.

Ribeiro, unpubl. data), which displays a largely overlapping Atlantic distribution.

Sea surface temperature (SST) along the Atlantic coast of the Iberian Peninsula, from January 1950 to December 2000, was derived from *in situ* raw data obtained from the International Comprehensive Ocean–Atmosphere Data Set (ICODAS; Woodruff *et al.*, 1988). To avoid bias due to different daytime measurements, only data from 12:00 were used. Point data were imported into the GRASS Geographical Information System (GRASS Development Team, 2005) and transformed into raster maps with a spatial resolution of 4×4 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).

Sea surface salinity (SSS) data, with an average resolution of 0.5° latitude \times 0.5° longitude cells, were extracted from the 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 were imported into GRASS GIS. Data were available for the period between January 1958 and December 2001.

The resulting set of 612 (51 years \times 12 months) SST and 528 (44 years \times 12 months) SSS maps was stored in GRASS GIS as monthly layers and sampled along the Iberian coastline at regularly spaced points, 10 km distant from each other and 2 km offshore. The resulting data for each physical parameter were combined to build a table with each row denoting a geographical location and each column a month/year combination. Monthly standardized anomalies were computed by subtracting from each value the monthly mean across all years and dividing it by the monthly standard deviation. To identify significant hydrographical time-series discontinuities on the recently colonized area, split moving window (SMW) boundary analysis (Ludwig & Cornelius, 1987; Cornelius & Reynolds, 1991) was carried out for SSS and SST anomalies from the area

between $39^\circ 30'$ and $41^\circ 54'$ N. This technique has been successfully applied to time-series of both biological and physical variables (Beaugrand & Reid, 2003; Beaugrand, 2003, 2004). Because the SMW outcome may vary as a function of window size, three window sizes were used (12, 24 and 48 months). Only results simultaneously detected by the three windows were considered.

A monthly based upwelling index for the location of $41^\circ 00'$ N, $10^\circ 00'$ W (off Porto) and from January 1967 to March 2005 was provided by the Pacific Fisheries Environmental Laboratory (PFEL; <http://las.pfel.noaa.gov/las/main.pl>). A 4-month running mean was computed to remove small-scale variation.

RESULTS

In 2003, recently established northern populations consisted of sparsely distributed and isolated individuals (Table 1). Although the 3-h sampling sessions were enough to cover the entire rocky surface of the appropriate high shore at each location, a maximum of 148 limpets was found at Homem do Leme and two shores appeared to completely lack this species, as not one individual was found. A sharp gradient of abundance, with number of individuals decreasing from south to north, was observed. In contrast, on southern shores densities were always higher than 60 individuals per m^2 .

By 2005, all six shores on the northern Portuguese coast had been colonized by *P. rustica*. The total number of limpets in each locality increased several fold after 2003. However, a clear gradient of abundance, with number of individuals decreasing toward the north, could still be observed.

Length–frequency histograms showed a marked difference between recently colonized locations in northern Portugal and southern historically inhabited areas (Fig. 2). A chi-square test revealed no independence between length classes and sampled

Table 1 Density (limpets m^{-2}) and modal class with minimum and maximum sizes (mm) of *P. rustica* sampled at each location during 2003 and 2005 surveys. – indicates the absence of this species in that site and year. Real counts are shown in parentheses. Locations not visited are indicated with n.a.

Site	Geographical location	2003		2005	
		Density	Modal class (min–max)	Density	Modal class (min–max)
Moledo do Minho	$41^\circ 50' 41''$ N, $8^\circ 52' 07''$ W	(0)	–	(109)	19 (12–30)
Montedor	$41^\circ 44' 30''$ N, $8^\circ 52' 37''$ W	(7)	24 (17–26)	(71)	21 (12–32)
Forte da Vigia	$41^\circ 41' 55''$ N, $8^\circ 51' 22''$ W	(0)	–	(92)	22 (13–31)
Mindelo	$41^\circ 18' 37''$ N, $8^\circ 44' 32''$ W	(46)	29 (17–43)	(246)	29 (16–42)
Cabo do Mundo	$41^\circ 13' 17''$ N, $8^\circ 42' 56''$ W	(87)	24 (13–37)	(109)	22 (14–34)
Homem do Leme	$41^\circ 09' 22''$ N, $8^\circ 40' 58''$ W	(148)	22 (13–37)	(279)	25 (12–39)
São Martinho do Porto	$39^\circ 30' 39''$ N, $9^\circ 08' 36''$ W	83 (250)	23 (5–30)	n.a.	n.a.
Baleal	$39^\circ 22' 29''$ N, $9^\circ 20' 21''$ W	98 (295)	20 (5–34)	n.a.	n.a.
Santa Cruz	$39^\circ 08' 02''$ N, $9^\circ 23' 00''$ W	70 (211)	17 (7–25)	n.a.	n.a.
Amoreira	$37^\circ 20' 57''$ N, $8^\circ 50' 47''$ W	65 (196)	20 (8–31)	n.a.	n.a.
Castelejo	$37^\circ 06' 01''$ N, $8^\circ 56' 43''$ W	86 (259)	22 (8–42)	n.a.	n.a.
Beliche	$37^\circ 01' 30''$ N, $8^\circ 57' 48''$ W	98 (295)	23 (7–34)	n.a.	n.a.

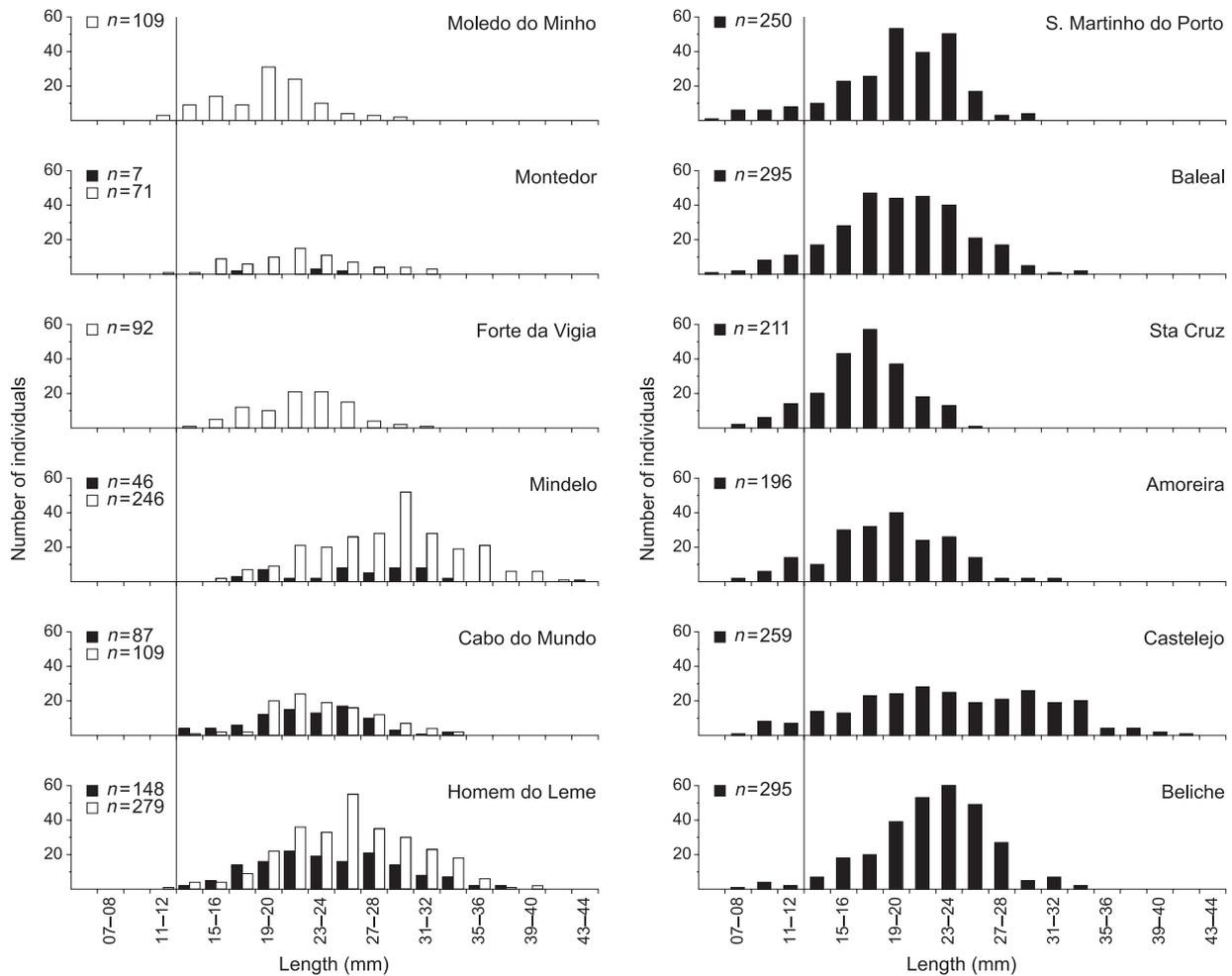


Figure 2 Length–frequency distributions for 2003 (black bars) and 2005 (white bars) surveys. Vertical lines denote a size of 13 mm, used to distinguish between juvenile and adult classes.

locations ($\chi^2 = 105.00$, d.f. = 30, $P < 0.05$), meaning that the population structure was significantly different between sites. All northern populations had fewer small individuals than expected. In 2003 they were composed solely of adults and in 2005 only 0.75% of the observed limpets belonged to the smaller size class. By contrast, populations in the historic portion of the range had a considerably higher frequency of juveniles (7.65%). In 2005, two different patterns in population structure were observed in the newly colonized sites: whilst populations settled before 2003 had a high proportion of adults of more than 28 mm (35.64%), in those populations established in subsequent years this percentage was only 4.41%.

ICOADS monthly mean SST showed a consistent annual pattern throughout the 51-year time-series, with evident seasonality. During winter and spring, a temperature gradient is established along the Iberian coast, from cold waters in Biarritz (south-west France) to the warmer zone in the Strait of Gibraltar (Fig. 3a). However, between summer and autumn the situation is not so linear. Although there is no change in the southern half of the gradient (3–4, Fig. 3a), the northern

half experiences an inversion of the winter/spring pattern as surface waters become warmer (1–2, Fig. 3a). As a result, both extremes of the Iberian coast are warmer than northern Portugal (2–3, Fig. 3a). This colder region between these extremes matched the area from which *P. rustica* was traditionally absent.

SST anomalies were predominantly higher since 1990, with particularly warm sea water temperatures in the autumn, winter and spring during 1997 and 1998. Negative anomalies were almost absent for the last 15 years of the time-series. On the area between 39°30' and 41°54' N, SMW gradient analysis revealed one significant discontinuity in mid-1997 (Fig. 3b). This anomaly corresponds to the abrupt transition between one period of relative normality and another characterized by an unusual increase in SST.

POP-SODA sea surface salinity data also showed strong annual seasonality. Usually, SSS increases in warmer seasons and decreases during winter and spring (Fig. 3c). Even though salinity is generally inversely proportional to latitude, on the northern Portuguese coast it is lower than the surrounding

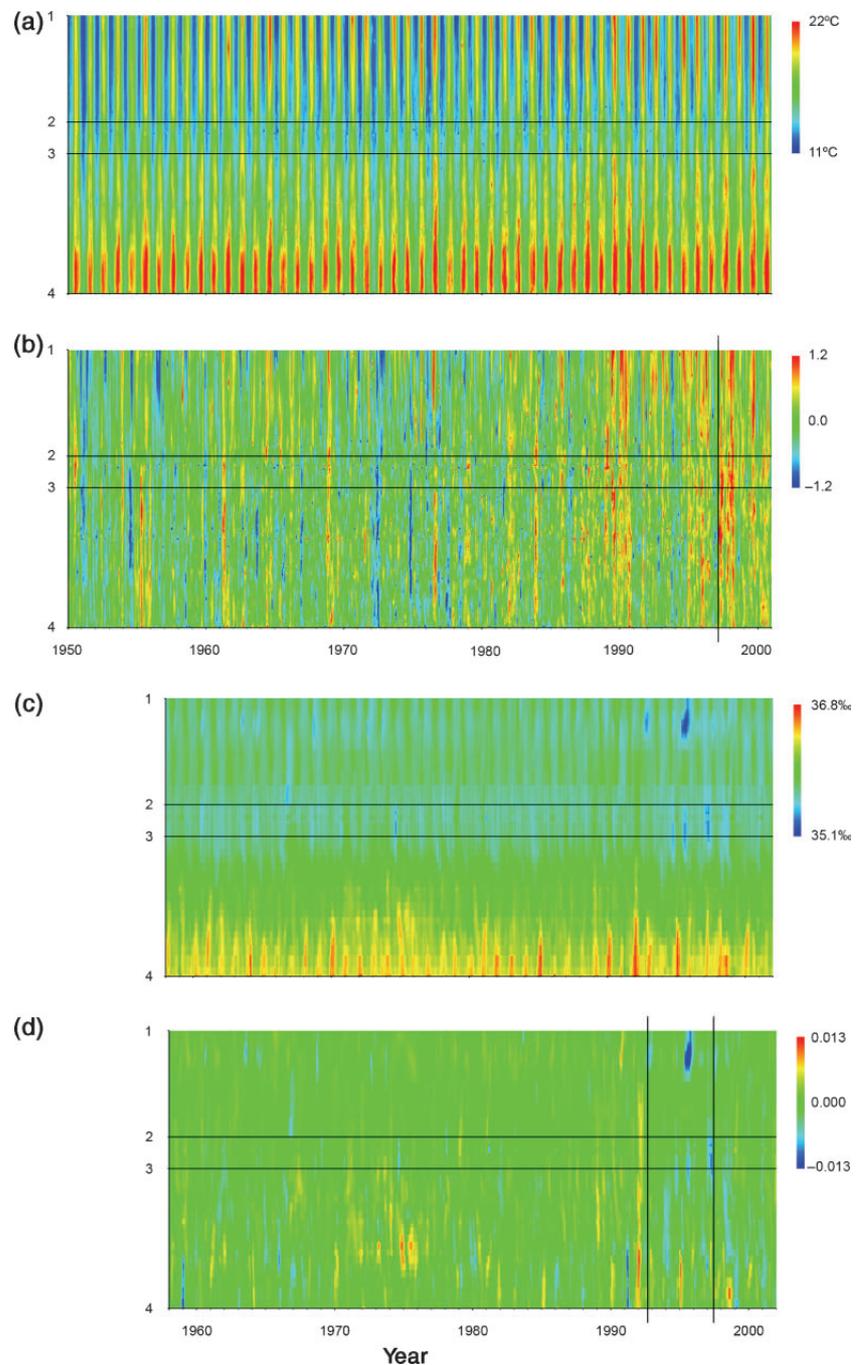


Figure 3 Monthly mean SST (a), SST normalized anomalies (b), SSS (c) and SSS anomalies (d) along the Atlantic coast of the Iberian Peninsula. Horizontal lines (2, 3) limit the historical gap in northern Portugal (see Fig. 1 for locations). Vertical lines correspond to significant SMW results.

areas, reaching values only comparable to those observed in the Bay of Biscay. For the area between $39^{\circ}30'$ and $41^{\circ}54'$ N, SMW gradient analysis revealed two significant discontinuities (Fig. 3d): one in the autumn of 1992 and another in the summer/autumn of 1997. The first anomaly corresponds to a situation where a high-salinity phase that took place in the spring of 1992 ended abruptly and the second denotes a step transition from a period of anomalous low salinity (during the spring of 1997) to a state of relative normality.

Upwelling off the northern Portuguese coast typically occurs from late spring to late autumn (Lemos & Pires, 2004; Peliz *et al.*, 2005). Although this pattern was relatively constant between 1967 and 2005, several anomalous episodes were identified (Fig. 4). The summer upwelling indexes of 1997, 1998 and 1999 were the lowest ever, reaching a historical minimum in 1997. Moreover, the lowest winter upwelling value over the entire time-series was recorded in 1998.

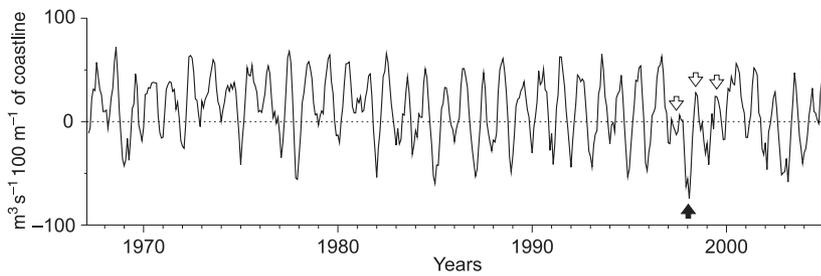


Figure 4 Four-month running mean computed on upwelling index ($\text{m}^3 \text{s}^{-1}$ per 100 m of coastline) for the location of $41^\circ 00' \text{ N}$ $10^\circ 00' \text{ W}$, between January 1967 and March 2005. The black arrow denotes the 1997/98 winter anomaly and white arrows indicate summer minimums from 1997 to 1999.

DISCUSSION

The present results show unequivocally that *P. rustica* has recently colonized the northern Portuguese coast, leading to the bridging of a historical gap in distribution known since the early 1900s. From 2003 onward, there was an increase in the number of colonized locations, and most notably in the number of individuals present at each location. The estimation of the minimum time of colonization based solely on length–frequency data would require knowledge of the growth rates of *P. rustica*. However, this parameter has not yet been assessed and results from growth studies of other *Patella* species are discrepant. For example, Guerra & Gaudêncio (1986) suggest a possible longevity of no more than 4 years for *Patella ulyssiponensis* Gmelin, 1791, *P. depressa* and *P. vulgata* on the Portuguese coast, based on length–frequency analysis. Since these species reach a maximum size of 3–4 cm in the region, growth rates must be relatively high, especially during the early stages of benthic life. In contrast, at higher latitudes (the UK and France) estimated growth rates fall into the range of $1\text{--}5 \text{ mm year}^{-1}$ for *P. vulgata* and *P. depressa*, with a maximum life span of 5–16 years, depending on habitat conditions (Fischer-Pi ette, 1941; Bowman, 1981).

Taking a conservative estimate of 4–6 years for the maximum longevity of *P. rustica*, and given that the largest individuals were observed in some of the northern shores, data from the present work suggest that colonization of the northern Portuguese coast by this species started in the late 1990s. Additionally, the lack of small size classes, when compared with the size–frequency distributions of well-established southern populations (where breeding and recruitment are thought to be more regular and successful) may indicate that populations of *P. rustica* in northern Portugal resulted from sporadic settlement events (Lewis, 1986; Zacherl *et al.*, 2003).

High growth rates of early life stages can explain, in part, the absence of limpets on two northern shores (Moledo do Minho and Forte da Vigia) during the 2003 surveys and their subsequent occurrence in 2005. Yet, a 2-year period seems not to be enough to explain the presence of the largest limpets. It is possible that juvenile limpets use different nursery habitats on northern shores, thus being difficult to observe during their initial life stages. Because in the midshore zone extensive sampling of the mussel/barnacle mosaic and rock pools in the scope of environmental monitoring studies never revealed a

single *P. rustica*, whilst other species of *Patella* were abundant, it is more likely that cryptic habits, like sheltering in crevices in the upper shore, may have rendered these individuals almost impossible to spot.

Finding the factors that maintained the distributional gap until the late 1990s is a first step to understanding the causes of the recent colonization of *P. rustica* in northern Portugal. As previously stated, between $39^\circ 30'$ and $41^\circ 54' \text{ N}$, the Portuguese coast displays oceanographic features that are distinct from the surrounding areas. Considering that the breeding period begins in July and spawning occurs between August and November/December (Ibanez *et al.*, 1986), low temperatures during this phase of the life cycle could have inhibited juvenile development, particularly because immature molluscs are very sensitive to severe conditions during settlement and early life stages (Lewis, 1986). Coincidentally, an increase in average SST was observed on the Portuguese coast during recent decades (Lemos & Pires, 2004; Peliz *et al.*, 2005). Moreover, recent sea surface warming during autumn/early winter, as shown by the analysis of SST anomalies, might have provided temperatures within the limited range suitable for metamorphosis and fast growth, allowing limpets to attain a sufficient size to survive the coming winter. Northern Portuguese populations of *P. rustica* are characterized by low densities and predominance of large individuals, which is typical of populations that fail to reproduce successfully and hence have infrequent recruitment success owing to thermal stress at the northern boundary of their range, because of low temperatures (Lewis *et al.*, 1982; Lewis, 1986; Zacherl *et al.*, 2003).

Apparently, intolerance to low salinity alone is not a plausible explanation for the maintenance of such a long-term gap, since SSS in this area within the historical gap is similar to that observed in the Bay of Biscay, where *P. rustica* has been recorded since the early 1900s. Flow fields often observed in association with biogeographical boundaries have the potential to constrain a species' geographical range, even when suitable habitat is available elsewhere (Gaylord & Gaines, 2000). Therefore, another explanation for the maintenance of the gap would be a deficient larval input resulting from adverse sea currents. Although it was not possible to obtain detailed data on surface currents, it is known that over the continental shelf current intensity and direction are closely related to upwelling intensity and to the development of the Western Iberia Buoyant Plume (WIBP). During negative upwelling periods (downwelling), the predominant southward offshore currents

decrease in intensity and inshore poleward circulation rises in strength (Figueiras *et al.*, 2002; Peliz *et al.*, 2002; Sánchez & Relvas, 2003). The WIBP consists of a low-salinity surface water layer fed by the winter-intensified run-off of several rivers on the northwest coast of Portugal and Spain (Santos *et al.*, 2004). The development of the WIBP results in isolation of inner-shelf waters and strong poleward transport (Peliz *et al.*, 2002, 2005). In years with strong buoyant discharge and weak upwelling, northward coastal transport is enhanced. On the contrary, strong upwelling, reduced river run-off or both, will have the opposite effect (Santos *et al.*, 2004).

Assuming the reproductive period suggested by Ibanez *et al.* (1986), larval release and dispersal will occur when equatorward currents are at their maximum, because in late summer/autumn upwelling is usually strong and river run-off is at its minimum due to the drier summer season. Surprisingly, even though in the last decades hydrographical conditions remained stable, favouring larval drift from Galicia, there is no evidence of successful colonization. It is possible that southern Galician populations are not reproductive and subsist only through repopulation by larvae that arrive from north-west Spain every autumn. In this case, larval drift coupled with larval life span may have limited dispersal toward the south. On the other hand, sporadic observation of isolated individuals within the historical gap (see the Introduction) may indicate that settlement has indeed taken place but is intermittent, or somehow that individuals did not survive to reach adult stages. Although not easily identifiable, this phenomenon is probably more frequent than assumed (Sax & Brown, 2000; Zacherl *et al.*, 2003), and is a more likely explanation for the maintenance of the gap under conditions that favour larval transport from Galicia.

Lower SSS values on the northern Portuguese coast from 1995 onward indicate an increase of the WIBP. In addition, from 1997 to 1999 upwelling was consistently low. These two phenomena combined could have favoured larval transport from central and southern Portugal toward the north. Taking into account that during this period positive SST anomalies could have reduced the thermal pressure on early life stages, it is plausible to assume a scenario where a combination of several oceanographic variables allowed southern larvae to drift northward, settle and survive in such numbers that populations started to develop. The observed decrease in number of individuals toward the north, which was consistent in 2003 and 2005 surveys, also supports the hypothesis that colonization occurred in that direction.

The multi-factor explanation is more plausible than supposing that just one factor was responsible for the observed changes. In many cases, species range limits are determined by the interaction of several factors, including ocean currents, upwelling, salinity, fetch, sea temperature, as well as the type of planktonic development (Crisp & Southward, 1958; Menge, 2000; Zacharias & Roff, 2001; Rivadeneira & Fernández, 2005). By overlapping SST, SSS and upwelling time series it was possible to find a common time window, from the beginning of 1997 to the end of 1998, when it is more likely that the

expansion has taken place. Moreover, 1997 was an exceptionally mild year over Europe, with a winter season characterized by high temperatures and intense rainfall (Dong *et al.*, 2000), and 1998 was the warmest year of the last millennium in the Northern Hemisphere (IPCC, 2001).

As proposed by Lewis (1986), occasional successful settlement may result in a sudden increase in numbers, which then persist conspicuously for several years. In the present case, however, several independent settlement episodes have to be considered, since between 2003 and 2005 the number of individuals increased several fold in colonized sites, and new populations were found. Two explanations are possible and not mutually exclusive: one or more new colonization episodes occurred with larvae that originated from historical locations, or reproduction of the newly established populations was successful, providing larvae that not only settled on the same shores but also expanded to the vicinity. Once critical population size was established self-recruitment would be possible.

The recent colonization described is most likely the corollary of the expansion process observed in Galicia during the 1950s by Fischer-Piëtte & Gaillard (1959), which was also coincident with a warmer period in north-west Europe (see Hawkins *et al.*, 2003 for a review). However, the lack of detailed oceanographic data sets for that time frame in northern Spain make it impossible to correlate their findings objectively with changes in the environment.

A detailed knowledge of the population dynamics of this species, particularly in this geographical region, is essential for a better understanding of the colonization process. Determining the exact extent of the reproductive period, as well as the growth rate and life span of *P. rustica*, will reduce the uncertainties related to the time of colonization. The multi-factor hypothesis presented here describes a sequence of climatic and hydrographical events that ultimately led to the colonization of northern shores. It implicitly assumes that this colonization occurred from the south. Provided that there is a reasonable degree of genetic differentiation between northern and southern populations, this hypothesis can be tested using highly variable molecular markers. Thus, studies on population genetics should help to identify the source of newly established populations of *P. rustica* in northern Portugal and also to determine possible past expansion and/or retraction events in this region.

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