



Fate of a climate-driven colonisation: Demography of newly established populations of the limpet *Patella rustica* Linnaeus, 1758, in northern Portugal

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ABSTRACT

Even though a large number of studies linking changes in species distributions to global warming have been published in the last decades, the long-term success of invasions or range shifts has rarely been evaluated. The intertidal limpet *Patella rustica* Linnaeus, 1758, is a warm-water species whose changes in distribution have been related to the recent warming off northern Portugal. Here we analyse the effects of the severe winter of 2008/2009 on the demographic structure of *P. rustica*, with the objectives of reassessing its geographical distribution and testing the mechanisms underlying the establishment of range limits. In addition, three decades of sea surface temperature were analysed, providing information on the thermal context contemporaneous to the distributional changes. Despite the cold winter of 2008/2009, the abundance of *P. rustica* increased in the study area, showing that the previously reported changes on the distribution of this species were not ephemeral. The demographic analyses suggested that even though early life stages are probably affected by extreme low winter temperatures, adults are less sensitive, with important consequences for the resilience of marginal populations and the fluctuations of distributional ranges. These results emphasise the importance of considering the demographic consequences of thermal stress when trying to understand and forecast the effects of climate change on biogeography and biodiversity.

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1. Introduction

A large number of studies linking changes in species distributions to global warming have been published in the last decades (Parmesan and Yohe, 2003; Parry et al., 2007; Root et al., 2003 and references within). Besides the direct effects that such changes have on regional and global biodiversity (Pereira et al., 2010), range shifts can also be used as early warning systems for the impacts of global warming (Helmuth et al., 2006). Changes in the geographic ranges and abundances of marine species, which seem to be occurring at one order of magnitude faster than terrestrial range shifts (Sorte et al., 2010), have been particularly well documented, for both the Atlantic and the Pacific (e.g., Berke et al., 2010; Edwards and Richardson, 2004; Hawkins et al., 2008; Helmuth et al., 2006; Hilbish et al., 2012; Jones et al., 2010, 2012; Kirby and Beaugrand, 2009; Lima et al., 2006, 2007a; Perry et al., 2005; Southward et al., 1995; Wethey and Woodin, 2008; Wethey et al., 2011). Owing to the geographic scales at which climate drives species distributions (Pearson and Dawson, 2003), many of

the analyses relating shifts in the geographic ranges of marine species with changes in climate are done at national or continental scales. Logistical limitations and budgetary constraints related to such large-scale surveys mean that the collected data can be poor in details (e.g., lacking basic information such as the reproductive status of the individuals or the demographic structure of the populations). In addition, large-scale studies typically rely on a restricted number of surveys (as low as one), rendering analyses to the comparison of a few distributional “snapshots”, which may conceal temporal variations essential to the understanding of the dynamics of such complex phenomena. Consequently, the ecological success of invasions or range shifts (i.e., establishment of permanent populations, increases in abundance, or even range extension beyond the initial colonisation, Sorte et al., 2010) has rarely been assessed (but see Gilman, 2006; Lima et al., 2006; Mieszowska et al., 2007; Wethey et al., 2011; Zacherl et al., 2003).

An essential feature of age-structured populations is the “storage effect” (Chesson, 1983; Warner and Chesson, 1985), in which adults persist during periods of low recruitment (Beukema, 1979, 1992; Dekker and Beukema, 1999; Strasser et al., 2001). The storage effect can cause long term changes in geographic ranges after extreme events that increase recruitment beyond range edges, or may dampen changes after temporary local sterility at the range edges induced by climate.

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Because of the storage effect, relic populations can persist long after the events that led to their establishment. Many intertidal species have life spans sufficiently long to reflect storage effects in their age structure. Examples include the decades-old, solitary and reproductively sterile *Semibalanus balanoides* in parts of NW Spain, which are the few remaining survivors of dense populations that existed there in the 1960s to 1980s (Wetthey and Woodin, 2008). These individuals do not reproduce, but they persist because of the storage effect associated with low adult mortality. The storage effect therefore has lasting and potentially misleading influences on the interpretation of biogeographic data because the distributions we see today are not necessarily the result of today's conditions, rather they are the product of the past, with a time scale dependent upon the life span and age structure of the populations. Thus, in order to forecast the effects of climate change on biogeography and biodiversity, we need models that incorporate the storage effect.

The present study focused on the dynamics of the recently established populations of the Lusitanian limpet *Patella rustica*, Linnaeus, 1758, in northern Portugal. The distribution of this subtropical species encompasses the rocky coast from Mauritania in the south (Fischer-Piette and Gaillard, 1959) to Capbreton, France, in the north (Lima et al., 2007b), including the Mediterranean basin (Sá-Pinto et al., 2010). During the majority of the 20th century, *P. rustica* was absent from approximately 280 km of coast in northern Portugal. Multiple settlement episodes in the late 1990s, however, culminated in the complete bridging of the historical distributional gap in the early 2000s (Lima et al., 2006). In a retrospective analysis of the historical SST patterns off northern Portugal, Lima et al. (2006) suggested that *P. rustica*'s pre-1990s distributional gap was set by summer/late autumn cold sea surface temperature (SST) either causing reproductive failure or inhibiting juvenile development. The same study suggested that the beginning of the colonisation was most likely facilitated by the warm summer/autumn of 1997, featuring an extraordinary weak upwelling and elevated SST off northern Portugal. Bioclimatic modelling (Lima et al., 2007b; Xavier et al., 2010) confirmed the strong association between the abundance of the species and SST during its reproductive season, and forecasted an increase in the density of the populations in northern Portugal throughout the 21st century in response to the projected rise in temperature. However, by 2005, densities in northern Portugal were still at least one order of magnitude lower than those from historical stable populations in central and southern portions of Portugal (Lima et al., 2006), casting doubts as to whether other climatic factors could be limiting population growth.

Despite several decades of average global temperature increase (Hansen et al., 2006; IPCC, 2007; Lima and Wetthey, 2012), the 2005/2006, 2008/2009 and 2009/2010 winters were associated with extreme low SST in the Bay of Biscay (Wetthey et al., 2011) and with severe cold events over Eurasia (Hansen et al., 2010). Cold spells have previously been shown to have catastrophic effects on intertidal populations on NE Atlantic (Crisp, 1964). In contrast, summer SST were particularly warm in 2003, 2006, 2009 and 2010 (Wetthey et al., 2011). This alternation between warm summers and cold winters offered a unique opportunity to test two contrasting biogeographic hypotheses, following the framework suggested by Wetthey et al. (2011) building on the ideas proposed by Hutchins (1947). In the specific case of *P. rustica*, if the pre-1990s distributional gap was set by reproductive failure or intolerance of larvae/juveniles to summer cold, then, in 2010 the newly-established adult populations should not have declined, regardless of the previous cold winters. If, on the other hand, the historical distributional gap was set by low winter temperatures (causing mortality of adults or juveniles), then, in 2010 the newly-established adult populations should have declined severely as a result of the previous cold winters. Newly-established populations could even have become extinct, owing to the relatively low densities observed in 2005 (Lima et al., 2006). This study is aimed primarily at testing the above mentioned biogeographic hypotheses, reassessing the distributional range and demographic structure of the recently established populations of *P. rustica* in northern Portugal. In order to provide the climatic context

of the historical demographic changes, three decades of SST (1982–2010) were analysed.

2. Material and methods

In the spring of 2010, size-frequencies and population densities of *P. rustica* were surveyed in 13 intertidal locations along the Portuguese coast (Fig. 1). Locations were the same sites surveyed by Lima et al. (2006) in 2003 and 2005, including seven rocky shores within the historical distribution gap in northern Portugal and six rocky shores within the historical range. Fieldwork was done by the authors of the original study, aided by the original field notes, insuring that the same areas within each shore were re-visited. In accordance with the original surveys, sampling occurred during spring tides and was limited to approximately 3 h on each shore.

Within the historical distribution range (central and southern locations), densities were estimated using 0.25 m² quadrats haphazardly placed in the high-intertidal. Due to the high densities of limpets, and to avoid bias toward larger size classes, size-frequency data were collected by measuring all specimens within each quadrat. The maximum length of each limpet was measured with digital callipers and rounded to the nearest millimetre. In the early 2000s, when colonisation had just started in the former distributional gap, densities were so low that the usage of quadrats was impractical and hence all observed individuals were measured (Lima et al., 2006). In order to obtain comparable results, the same sampling procedure was followed in this study. Densities were then calculated by dividing the number of sampled individuals by the total sampled area, obtained from Google Earth aerial imagery. Variation in length-frequency data between pairs of sampling dates was assessed independently for each location, using two-sample Kolmogorov–Smirnov tests with Bonferroni correction. The same size classes adopted by Lima et al. (2006), i.e., juveniles being those individuals

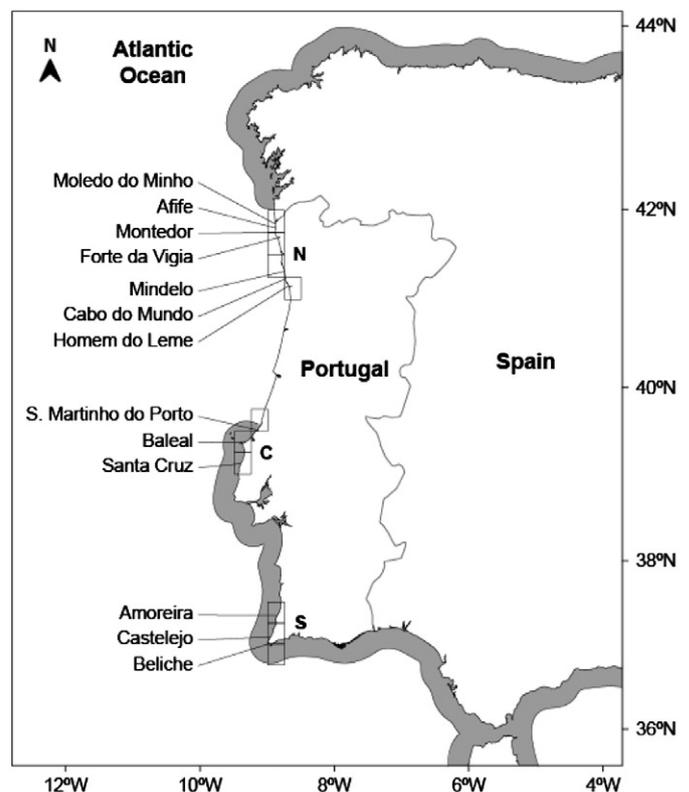


Fig. 1. Study area. The grey shading shows the historical (pre-1997) range of *Patella rustica* in western Iberia, bearing a distributional gap in northern Portugal. Coastal 0.25° pixels for which SST data were retrieved are shown along the coastline. N, C and S stand for northern, central and southern Portugal, respectively.

with less than 13 mm in length and large adults those larger than 28 mm were adopted for interpreting the results.

Sea surface temperature (SST) data with a spatial resolution of 0.25° were obtained from the US National Climatic Data Center at <http://www.ncdc.noaa.gov/oa/climate/research/sst/oi-daily.php> (Reynolds et al., 2007). AVHRR (Advanced Very High Resolution Radiometer) data encompassing nearly three decades were available. Daily files (from January 1, 1982 to December 31, 2010) encompassing the study area were imported into R 2.12 (R Development Core Team, 2011), and SST data were retrieved for the coastal pixels spanning the regions ($n=4, 3$ and 3 for northern, central and southern Portugal, respectively, see Fig. 1). For each pixel, daily standardised anomalies were calculated as the difference between each day's SST and the corresponding monthly average across all years, divided by the corresponding monthly standard deviation. In addition, average anomalies were calculated on a yearly basis, separately for the reproductive season of *P. rustica* (July–November, Ribeiro et al., 2009) and for the rest of the year (December–June). Since a preliminary analysis of the data revealed high similarity among temperatures retrieved within each region, within-region averages were used.

3. Results

Between 2005 and 2010, densities of *P. rustica* increased significantly within the historical distributional gap in northern Portugal (paired t -test = 2.23, $df=6$, $p<0.05$, see Fig. 2). Increases ranged from 1.5 fold at Homem do Leme to 8.8 fold at Moledo do Minho. For example, while in 2005 the entire population of *P. rustica* at Moledo do Minho did not exceed 109 individuals and was restricted to a small number of rocky outcrops, in 2010 more than 950 limpets were observed across the entire shore. Despite such striking increases in abundance, in none of the sampled northern locations did limpet densities exceed 2.5 individuals m^{-2} , which is still far less than the minimum abundance observed in central or southern Portugal both in 2003 or 2010 (61 limpets m^{-2}). Also, changes in population sizes did not alter the large-scale density pattern previously reported by Lima et al. (2006), since there was still a clear south–north decreasing cline in population densities in 2010 (Pearson's correlation between location and density $r=0.90$, $df=11$, $p<0.05$, see also Fig. 3). Even though historical southern populations were not surveyed in 2005, densities did not change significantly between 2003 and 2010 (paired t -test = 1.18, $df=5$, $p>0.05$, see also Fig. 3).

The analysis of the length–frequency histograms revealed differences between the demographic evolution of the populations from (i) locations in northern Portugal, colonised before 2003; (ii) locations in northern Portugal, colonised between 2003 and 2005; and (iii) historical populations from central and southern Portugal (Fig. 2). In 2003, only four locations from the southern portion of the gap had been colonised (Montedor, Mindelo, Cabo do Mundo and Homem do Leme) but at that time populations were already mostly composed of adults. In contrast, historically stable populations in central and southern Portugal had a juvenile percentage of 6.9 ± 3.2 (Table 1). By 2005, and after at least one additional successful recruitment event, *P. rustica*'s densities had increased at the four previously colonised shores (Table 1). Still, these alterations were not strong enough to significantly change the population structure observed in the first survey in 2003 (non-significant Kolmogorov–Smirnov tests, see also Fig. 2). In 2005, *P. rustica* was also found at three additional locations (Moledo do Minho, Afife and Forte da Vigia), entirely bridging the distributional gap in northern Portugal (Table 1). In 2010, populations from the southern part of the former distributional gap had significantly different length–frequency structures compared to 2005 (significant Kolmogorov–Smirnov tests, Fig. 2). In 2010, these southern gap populations were characterised by a higher proportion of larger (and likely older) individuals, by a lower proportion of juveniles (<13 mm) and by a larger size of the modal class compared to 2005 (see Fig. 2 and Table 1). In contrast, and with the exception of

Moledo do Minho, all populations from the northern portion of the former gap (Afife, Montedor, and Forte da Vigia) displayed the same demographic structure in 2010 as they had in 2005 (non-significant Kolmogorov–Smirnov tests, Fig. 2), despite the high increase in number of individuals (Table 1).

From 1982 to 2010, SST anomalies observed off northern Portugal (i.e., in the area of the historical distributional gap) were correlated with anomalies in central and southern regions (Pearson's correlations of 0.94 and 0.85 and root mean square errors of 0.34 °C and 0.53 °C, respectively). Similar to the pattern obtained from ICOADS data (Lima et al., 2006), Reynolds et al. (2007) data also showed a ~13 month-long positive anomaly off northern Portugal between 1997 and 1998 (white arrow in Fig. 4). During this period, there were no anomalies less than 0 °C, indicating that all temperatures were higher than the reference period average (Fig. 4). This anomaly was correlated with the onset of the colonisation in northern Portugal by *P. rustica* in the late 1990s (Lima et al., 2006). Since then, strong positive anomalies occurred in 2002, 2004 and 2006 but were less prominent than the 1997/1998 event. On the other hand, there were sporadic cold anomalies along the study area since the late 1990s, especially in 2002, 2007, 2008/2009 and 2010, with the winter negative anomaly in 2008/2009 being the strongest in the dataset – all temperatures were more than 1 °C lower than the reference period average (see the black arrow in Fig. 4).

Average SST anomalies in northern Portugal are shown in Fig. 5 separately for the July–November and December–June periods. After the colonisation in 1997, most years were characterised by positive anomalies during summer and late autumn (Fig. 5A), when *P. rustica*'s gonads develop, mature, and individuals spawn (Ribeiro et al., 2009). Mean anomalies for that season exceeded 0.5 °C in 1999, 2003 and in 2006, which was the historical maximum since 1982. There was only a single negative anomaly lower than -0.5 °C (2007). For the period between December and June, the pattern was variable after 1997, with yearly alternations between cold and warm anomalies. The only average anomalies higher than 0.5 °C occurred in 1998, 2008 and 2010. On the other hand, the winter of 2009 was the coldest since the settlement of *P. rustica*'s populations in northern Portugal in 1997, with an average SST anomaly of -0.7 °C.

4. Discussion

The intertidal communities from north-western Iberia are singular from a biogeographic perspective since their species composition is distinct from the surrounding regions. Numerous cold-water animal and algae species, common in north-western France or south-western Britain, also occur in distributional pockets along northern Portugal and Galicia, in north-western Iberia (e.g., Araújo et al., 2009; Ardré, 1971; Lima et al., 2007a, 2009; van den Hoek and Donze, 1967; Wetthey and Woodin, 2008). On the other hand, many warm-water organisms are absent from northern Portugal even though their distributions range from northern Africa and Mediterranean Sea to the Bay of Biscay, in south-western France (e.g., Ardré, 1971; Fischer-Piette, 1959; Lima, 2010; Lima et al., 2006, 2007a; van den Hoek and Donze, 1967; Wetthey and Woodin, 2008). *P. rustica* was a clear example of the latter until the late 1990s, when its distributional gap in northern Portugal started to contract.

The present study validates the observations made in the early 2000s (Lima et al., 2006, 2007b), which, at that time, suggested that the colonisation of northern Portugal by *P. rustica* was not an ephemeral phenomenon. In fact, both the spatial and the temporal scales of the distributional changes here described (~280 km and ~13 years) are quite distinct from transient, small-scale fluctuations previously reported for marginal populations of intertidal species on the Iberian Peninsula (e.g., Fischer-Piette, 1955, 1956, 1957; Fischer-Piette and Prenant, 1957). Together with the evidence that other warm-water species such as the pulmonate gastropods *Onchidella celtica* and *Siphonaria*

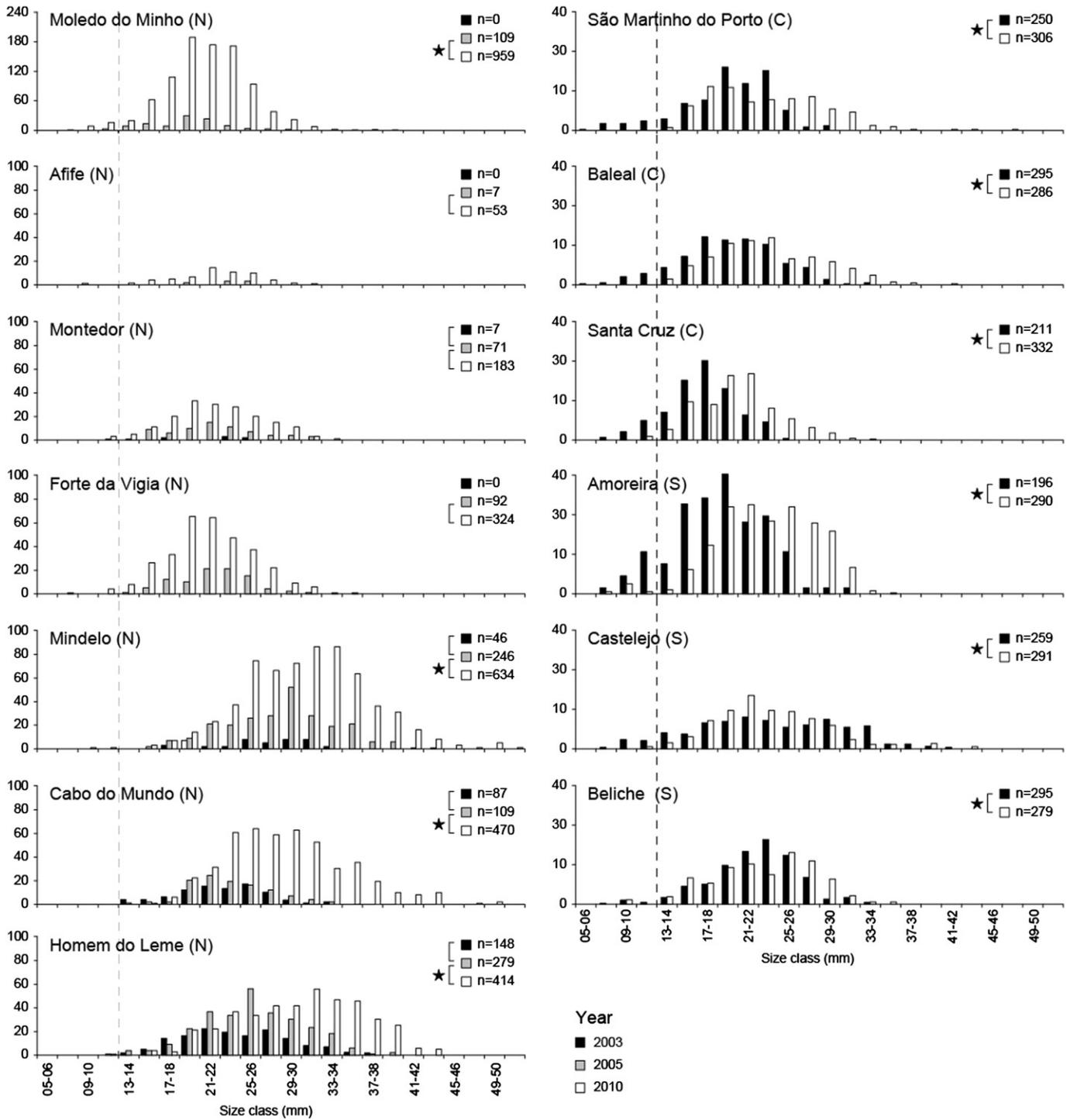


Fig. 2. Length–frequency distribution and number of *Patella rustica* sampled in 2003 (black bars), 2005 (grey bars) and 2010 (white bars) in northern (N), central (C) and southern (S) Portugal. Northern locations (within the historical distributional gap) are on the left. Note that the scale of the y-axes varies among graphs. Vertical lines denote a size of 13 mm, used to distinguish between juveniles and adults. Stars denote pairs of populations with significantly different size structures after two-sample Kolmogorov–Smirnov tests, which were performed on pairs connected by the square brackets.

pectinata (Lima, 2010) and the algae *Sargassum flavifolium* and *Asparagopsis armata* (Araújo et al., 2009; Lima et al., 2007a) are also bridging their distributional gaps in northern Portugal, these findings are compatible with the hypothesis that a large-scale driver (such as climate change) is influencing the biogeographic patterns in the area (Pearson and Dawson, 2003; Pearson et al., 2002).

Extreme temperature events provide unique opportunities for testing the mechanisms responsible for setting biogeographic limits (Crisp, 1964; Firth et al., 2011; Wetthey et al., 2011). In the present

study, the observation of an increase in the abundance of *P. rustica* in northern Portugal despite the unusually cold winter of 2009 suggests that extremely cold winters do not have a severe effect on the survival of the adults. Also, the fact that all populations in northern Portugal showed multiple adult length-classes across all surveys means that, at least during several consecutive years, these populations experienced regular self-recruitment and/or received multiple larval inputs from neighbouring populations (e.g., Mieszowska et al., 2007). The current abundance decrease towards the north may thus indicate that the

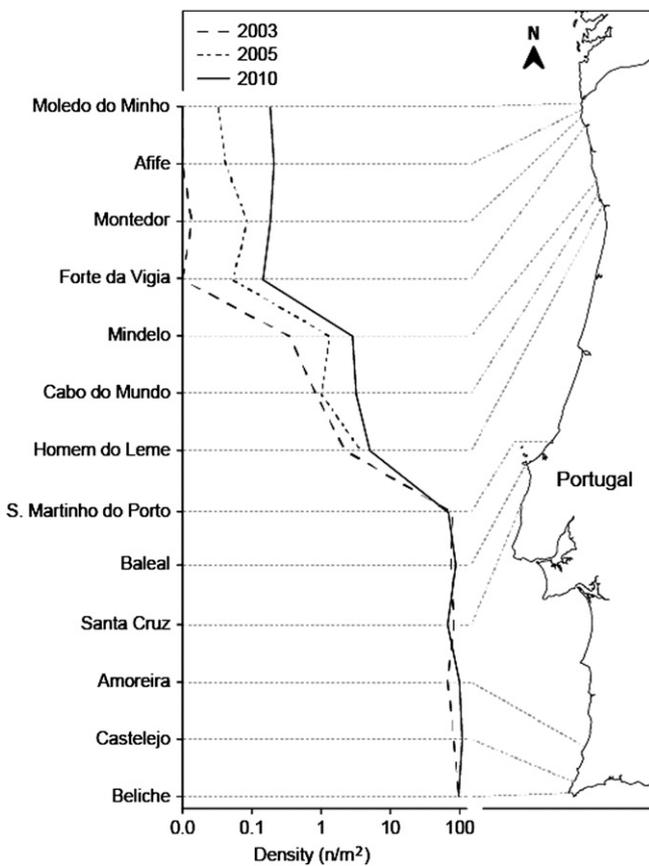


Fig. 3. Map of northern Portugal (the historical distribution gap) showing the geographical cline in density of *Patella rustica* (in number of individuals m^{-2}) in 2003, 2005 and 2010. There are no data for central and southern locations in 2005.

primary source of larval inputs is from central and southern Portugal, or that a geographic gradient in local self-recruitment has amplified the abundance cline initially established in 2003 (Lima et al., 2006). Unfortunately, a recent study using data from five microsatellites and mtDNA markers failed in detecting any structure in the populations of *P. rustica* in NW Iberia, being therefore unable to identify the origin of the colonisers (Ribeiro et al., 2010) and so this question remains open.

The growth of a given population is tightly related to its demographic structure: while a population with a high percentage of juveniles has the potential to increase in size, a population dominated by old individuals tends to decline (Purves et al., 1998). Because during

the last decade the populations of *P. rustica* in northern Portugal have apparently been lacking young individuals, one would expect them to decline, but they have been growing since 2003. Two non-exclusive hypotheses may be advanced to explain this paradox. First, it is possible that small juveniles may exploit different microhabitats, for example dwelling in crevices, inside empty barnacle shells or underneath mussel byssal threads (as described for *Patella vulgata*, Lewis and Bowman, 1975), thus becoming inconspicuous. The validity of this hypothesis is however, questioned by the clear lack of larger juveniles (Fig. 2), which would be harder to miss in the field surveys. A second hypothesis is that the observed population structures were strongly influenced by events which prevented recruitment immediately before the surveys. Several intertidal species have been shown to develop age structures strongly skewed towards large classes when juvenile cohorts die of exposure to harsh environmental conditions or predation pressures and only occasionally a high number of individuals survive, becoming “dominant year groups” (Connell, 1972). In marginal populations, irregular age structures missing year classes and displaying biases towards old animals arise when the environmental conditions cause an inability to repopulate, but do not cause adult mortality (Lewis et al., 1982). On their turn, deficiencies in re-population result in lower densities and therefore increase growth rates and larger maximum body sizes (Lewis et al., 1982). These are the demographic traits displayed by *P. rustica* in northern Portugal. Therefore, and despite the evidence for regular recruitment during the majority of the last decade (there are no gaps on the adult cohorts), the small number of juveniles observed in northern Portugal since the beginning of the surveys suggests that recruitment failure may be common within the former distributional gap. In addition, recruitment failure seems to have extended to the totality of the study area, since there was a clear lack of juveniles along the entire Portuguese coast in 2010, including central and southern locations, which may have been a demographic response to the cold winter of 2008/2009.

Thus, although data suggest that adults are relatively unaffected by the extreme low winter temperatures such as those observed in 2008/2009, early life stages (either larvae or juveniles) are probably more sensitive, as indicated by the widespread lack of juveniles seen in the 2010 surveys. In this context it is important to consider the population storage effect, by which the increased environmental tolerance of adults allow them to persist during periods of low recruitment (Lewis, 1986; Warner and Chesson, 1985). The storage effect increases the resilience of the populations, which may persist long after the events that led to their establishment (e.g., Southward, 1967; Southward et al., 1975; Wetthey and Woodin, 2008; Wetthey et al., 2011). This means that warm-water species, which are limited by cold

Table 1
Density (limpets m^{-2}), percentage of juveniles (less than 13 mm) and modal class with minimum and maximum sizes (mm) of *Patella rustica* sampled at each location during 2003, 2005 and 2010 surveys. Sample sizes (n) are shown in parentheses. – indicates the absence of the species. Locations not visited are indicated with n.a. Data from 2003 and 2005 are from Lima et al. (2006).

Site	2003			2005			2010			
	Density (n)	% Juv (<13 mm)	Modal class (min–max)	Density	% Juv	Modal class (min–max)	Density (n)	% Juv (<13 mm)	Modal class (min–max)	
North	Moledo do Minho	–	–	<0.01 (109)	2.8	19 (12–30)	0.04 (959)	2.8	20 (8–39)	
	Afife	–	–	0.01 (7)	14.3	25 (10–25)	0.05 (53)	0.0	22 (13–31)	
	Montedor	<0.01 (7)	0.0	24 (17–26)	0.01 (71)	1.4	21 (12–32)	0.04 (183)	3.3	21 (9–33)
	Forte da Vigia	–	–	–	0.01 (92)	0.0	22 (13–31)	0.03 (324)	1.5	21 (8–36)
	Mindelo	0.09 (46)	0.0	29 (17–43)	0.46 (246)	0.0	29 (16–42)	1.19 (634)	0.3	31 (9–51)
	Cabo do Mundo	0.26 (87)	0.0	22 (13–34)	0.32 (109)	0.0	22 (14–34)	1.40 (470)	0.0	26 (16–49)
	Homem do Leme	0.89 (148)	0.0	22 (13–37)	1.67 (279)	0.4	25 (12–39)	2.48 (414)	0.2	35 (12–44)
Centre	São Martinho do Porto	76.1 (250)	8.8	20 (4–30)	n.a.	n.a.	65.6 (286)	0.0	19 (13–48)	
	Baleal	63.2 (295)	7.6	18(5–34)	n.a.	n.a.	81.2 (306)	0.0	21 (13–42)	
	Santa Cruz	89.7 (211)	10.4	17 (7–25)	n.a.	n.a.	72.8 (332)	1.2	19 (11–33)	
South	Amoreira	61.0 (196)	7.1	20 (11–31)	n.a.	n.a.	102.0 (290)	1.0	21 (10–35)	
	Castelejo	81.2 (259)	6.2	22 (8–42)	n.a.	n.a.	112.4 (291)	0.7	22 (11–43)	
	Beliche	97.6 (295)	1.0	23 (7–34)	n.a.	n.a.	99.6 (279)	0.0	26 (13–35)	

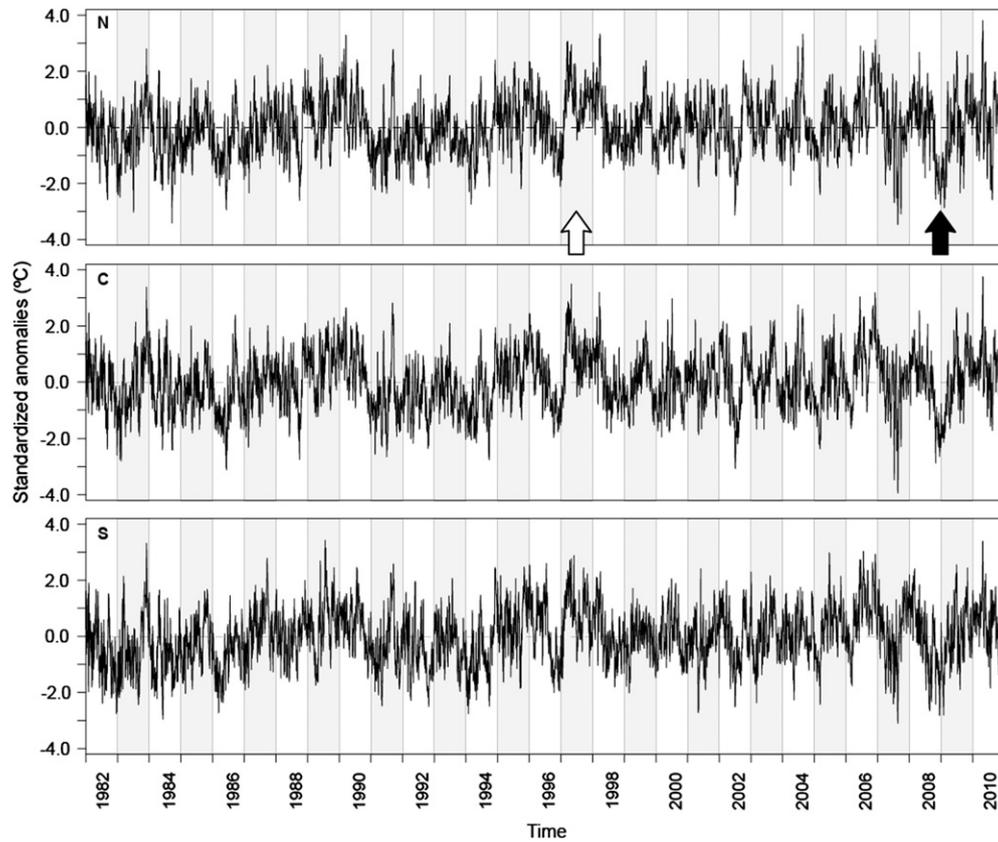


Fig. 4. Standardised SST anomalies for the three studied regions. N, C and S stand for northern, central and southern Portugal, respectively. The white arrow shows the ~13 month-long period previously related with the colonisation of the northern coast by *Patella rustica*, when there were no anomalies less than 0 °C. The black arrow indicates the exceptionally cold winter of 2008/2009 (with no anomalies greater than -1 °C).

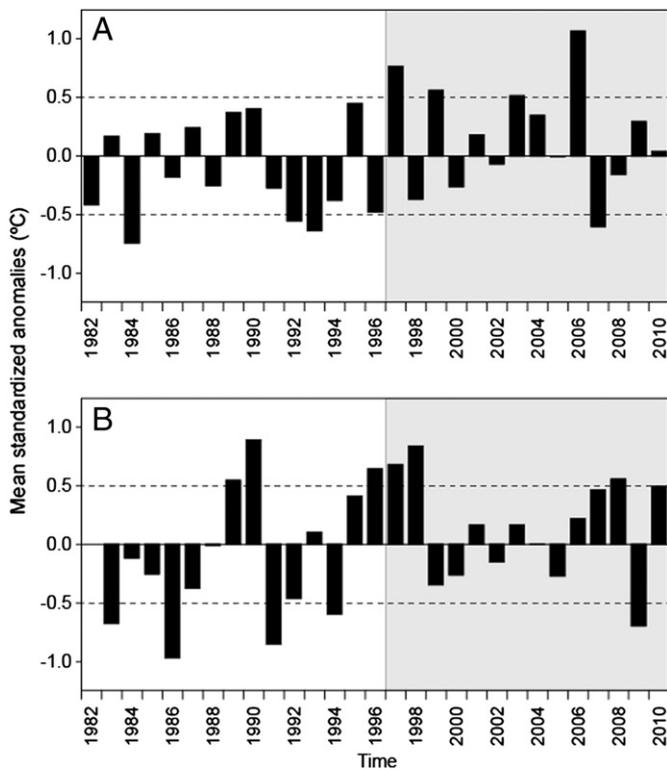


Fig. 5. A) Standardised anomalies between 1982 and 1997 (white background) and between 1997 and 2010 (grey background) calculated for the period between July and November, during *Patella rustica*'s reproductive period. B) Same as in A) but for the rest of the year (December–June).

temperatures causing reproductive failure or inhibiting juvenile development, may expand rapidly in face of warm conditions. Theoretically, and as long as the species has a reasonably long-range dispersal ability (Arrontes, 2005), these expansions are possible even when such favourable periods are transient and interspersed with extreme cold periods causing sterility at range edges. On the other hand, if species whose poleward boundary is set by cold-mediated adult mortality are exposed to relatively small extreme cold events, local extinction at the range margins will reset the expansion process (Canning-Clode et al., 2011; Firth et al., 2011), eventually resulting in a much slower biogeographic response to warming. Thus, the demographic consequences of thermal stress are of great importance when trying to understand and forecast the effects of climate change on biogeography and biodiversity, and may explain some of the disparities observed among biogeographic shifts of similar intertidal species (Lima et al., 2007a). In the specific case of *P. rustica*, it is probable that populations inside the historical gap will keep increasing in density if the recent trends in temperature (Belkin, 2009; Hansen et al., 2010; Lima and Wetthey, 2012) continue in future years, since the current findings suggest that adults of this species are favoured by warm summers and not severely affected by cold winters. The lack of juveniles seen in the 2010 surveys however indicates that this life stage may be sensitive to cold conditions, and reinforces the importance of the storage effect in population expansions.

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