© Sociedad Española de Malacología ——————— Iberus, 25 (1): 57-75, 2007

The southern limit of distribution of *Patella vulgata*

El límite sur de distribución de *Patella vulgata*

João Paulo CABRAL*[1] and José SIMÕES**

Recibido el 20-XI-2006. Aceptado el 23-IV-2007

ABSTRACT

Samples of *Patella vulgata* were collected along the Portuguese continental and the southern Spanish coast. Specimens were identified using shell and radula characteristics. *Patella vulgata* was abundant at sites north of the river Douro whereas, to the south, its abundance decreased markedly. *Patella vulgata* was not observed at Portinho da Arrábida; however, near Cape São Vicente, at Ponta Ruiva and Telheiro, the species was again abundant. Passing Cape São Vicente, the species became scarce. The last significant population was observed at Ingrina, and the last specimen at Rocha. It was proposed that these sites constitute the present day limit of distribution of *P. vulgata*, replacing Odeceixe, reported in the literature fifty years ago. The distribution of *P. vulgata* is not a simple function of the maximum or minimum seawater surface temperature, but appears to depend directly on the temperature in May, the species being absent when the temperature is higher than *ca.* 18°C.

Two hypotheses were formulated to explain the influence of seawater temperature in May on the distribution of *P. vulgata*:

1. Inhibition of the beginning of gametogenesis due to high temperature stress during the resting period.
2. Death of the spat due to high temperature stress, with concomitant failure of the settlement of new generations on the substrates. In addition, the absence of upwelling waters in the eastern part of the Algarve coast could hinder the larval stage of *P. vulgata*, and severe competition with *Patella intermedia* and *Patella ulyssiponensis* could prevent the establishment of those few individuals of the spat that survived. Tonel, Mareta, Martinhal, Barranco and Ingrina sites are candidates to be used as reference points to follow future changes in seawater surface temperature.

RESUMEN

Muestras de *Patella vulgata* fueron recogidas a lo largo de la costa continental Portuguesa y de la costa sur de España. Los ejemplares fueron identificados utilizando las características de la rádula y de la concha. *P. vulgata* es abundante en las localidades al norte del río Duero. Hacia el sur, la abundancia disminuye acusadamente. No se observó *P. vulgata* en Portinho da Arrábida pero, cerca de Cabo San Vicente, en Ponta Ruiva y Telheiro, la especie se vió nuevamente en abundancia. Pasando el Cabo San Vicente, la especie vuelve a ser escasa. La última población significativa fue observada en Ingrina, y el último ejemplar en Rocha. Se propone que éstas localidades constituyen actualmente el límite sur de la distribución de *P. vulgata*, en substitución de Odeceixe, indicado en la bibliografía hace cincuenta años. La distribución de *P. vulgata* no es una función simple de la

* University of Oporto, Center of Marine and Environmental Research (CIIMAR) and Faculty of Sciences, Rua do Campo Alegre, 1191, 4150-181 Porto, Portugal. E-mail: jpcabral@fc.up.pt
** Casa do Grande Sul, Cerro Gordo, 8400-550 Carvoeiro LGA, Portugal.
[1] Author for correspondence.

temperatura máxima o mínima del agua de mar, sino que parece depender directamente de la temperatura del agua en Mayo. La especie no aparece cuando la temperatura sobrepasa *ca.* 18°C.
Dos hipótesis se han formulado para explicar la influencia de la temperatura del agua de mar en la distribución de *P. vulgata*:
1. Inhibición del desarrollo de la gónada, causado por stress de altas temperaturas durante el periodo de reposo en el inicio del proceso.
2. Muerte de los juveniles, causado por stress de altas temperaturas, con el subsiguiente fracaso del establecimiento de nuevas generaciones en el substrato. Adicionalmente, la ausencia de *upwelling* en la costa oriental del Algarve puede perjudicar el estadio larval de *P. vulgata* y la competencia severa con *Patella intermedia* y *Patella ulyssiponensis* puede evitar el establecimiento de los pocos juveniles que hubieran podido sobrevivir. Tonel, Mareta, Martinhal, Barranco y Ingrina parecen localidades idoneas para ser utilizadas como puntos de referencia al objeto de seguir futuras alteraciones en la temperatura del agua de mar.

KEY WORDS: *Patella vulgata*; AVHRR, SST, limpets.
PALABRAS CLAVE: *Patella vulgata*; AVHRR, SST, lapas.

INTRODUCTION

Mapping the geographical distribution of a mollusc, specially its boundary limits, is important, since it gives information about ecological conditions that allow good growth and reproduction of individuals, but also about conditions that are not favorable for the species' survival.

Continental Portugal, at the confluence between the Atlantic and the Mediterranean, displays a rich interplay between the northern and southern flora and fauna of Europe. Indeed, the presence, on our rocky shores, of four *Patella* species, one northern (*Patella vulgata* Linné 1758), two southern (*Patella rustica* Linné 1758 and *Patella ulyssiponensis* Gmelin 1791), and one with an intermediate character (*Patella intermedia* Murray in Knapp 1857) (Christiaens, 1973; CLEMAM, 2002), attest and illustrate this convergence of influences.

The paper by Fisher-Piette and Gaillard (1959) on the distribution of limpets along the Iberian and Moroccan coasts established Odeceixe, on the southwest coast of continental Portugal, as the southern limit of distribution of *P. vulgata*. Almost half a century after this work, we felt that it was worth and opportune to re-analyze the issue of the southern limit of this species. Marine and coastal environments have changed substantially, seawater temperature is rising. These factors might have changed the distribution of *P. vulgata* since the 1950s. There is at present a considerable amount of detailed data on environmental variables, such as atmospheric and seawater temperatures. We are now in a better position to formulate hypothesis on factors involved in the southern limit of distribution of this northern *Patella* species. The aims of this investigation were therefore twofold. Firstly, to determine, in detail, the present day southern limit of distribution of *P. vulgata*, updating the information of Fisher-Piette and Gaillard (1959), and complementing the recent studies of Boaventura (2000), Boaventura, Ré, Fonseca and Hawkins (2002a) and Santos (2000). Secondly, to explain or formulate hypothesis on the main factors involved in determining the southern limit of distribution of *P. vulgata*.

MATERIAL AND METHODS

Sampling was carried out along the Portuguese continental coast, from the far northern to the far southern rocky

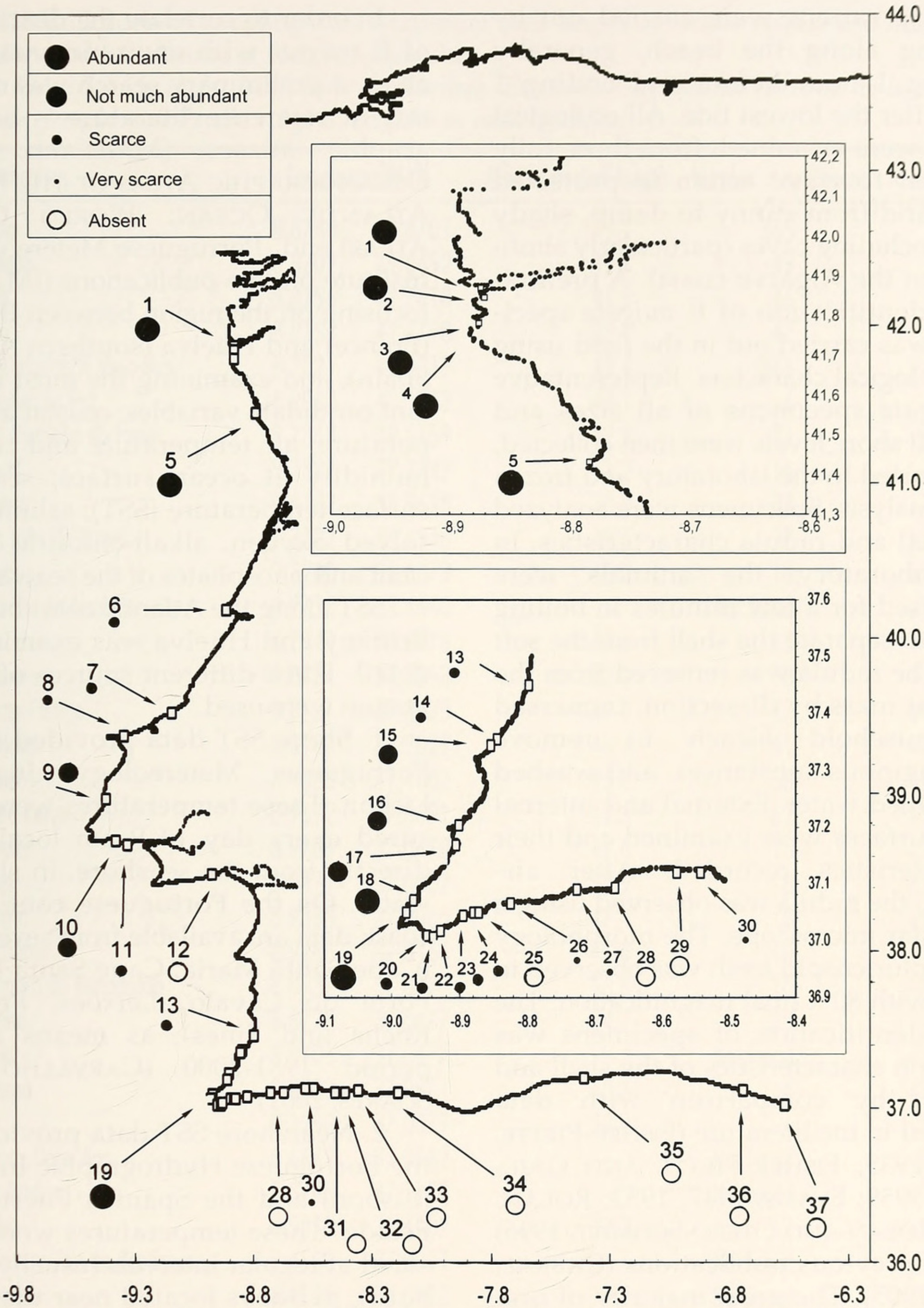


Figure 1. Localization of sampling sites on the Portuguese continental coast (#1 - #35) and in the Huelva region (#36 - #37). Abundance of *Patella vulgata* at each sampling site.

Figura 1. Localización de las localidades de muestreo en la costa continental portuguesa (#1 - #35) y en la costa de la región de Huelva (#36 - #37). Abundancia de Patella vulgata *en cada localidad de muestreo.*

shores. In addition, three beaches with rocky substrates in the southern coast of Portugal (the pontoon of Vila Real de Santo António) and Spain (the collapsed towers of Torre del Oro and Torre de la Higuera) were examined. The identification and localization of all studied sites is presented in Figure 1 and Table I. Only beaches accessible by walking were examined. Rocky zones between beaches only accessible by boat were not surveyed.

Observations were carried out by walking along the beach, generally starting 1 hour before and ending 1 hour after the lowest tide. All ecological niches were examined, from those fully exposed to wave action to protected sites, and from sunny to damp, shady sites, including caves (particularly abundant on the Algarve coast). A preliminary identification of *P. vulgata* specimens was carried out in the field using conchological characters. Representative *P. vulgata* specimens of all sizes and from all shore levels were then collected, transported to the laboratory and frozen until analysis. Specimens were analyzed for shell and radula characteristics. In the laboratory, the animals were immersed for a few minutes in boiling water to separate the shell from the soft part. The radula was removed from the visceral mass by dissection, immersed in household bleach to remove mucilaginous substances, and washed in distilled water. External and internal shell surfaces were examined and their characteristics recorded. After air-drying, the radula was observed using a binocular microscope. The morphology of the pluricuspid teeth was observed in detail with 80 x final magnification. The final identification of specimens was based on characteristics of the shell and radula, by comparison with data reported in the literature (FISHER-PIETTE, 1934, 1935; FISHER-PIETTE AND GAILLARD, 1959; EVANS, 1947, 1953; ROLÁN, 1993; ROLÁN AND OTERO-SCHMITT, 1996) and in previous publications (CABRAL, 2003, 2005). The great majority of preliminary identifications were confirmed after examining the radula. The abundance of *P. vulgata* was then estimated for each sampling site using the following classification: 1. Abundant, if many individuals were present, and evenly distributed. 2. Not very abundant, if more than 25 individuals were observed, but these were not regularly distributed. 3. Scarce, if only 5 - 25 specimens were found in the survey. 4. Very scarce, if less than 5 individuals were observed. 5. Absent, if no specimen was observed.

In order to correlate the distribution of *P. vulgata* with environmental variables, a preliminary search was carried out in reference literature – oceanographic atlases (MAILLARD, 1986; OCEANOGRAPHIC ATLAS OF THE NORTH ATLANTIC OCEAN; WORLD OCEAN ATLAS) and Portuguese Metereological Institute on-line publications (IM, 2006), focusing on the region between Brittany (France) and Huelva (southern Atlantic Spain), and examining the most important candidate variables: coastal air temperature; air temperature and relative humidity at ocean surface; seawater surface temperature (SST); salinity, dissolved oxygen, alkali-chloride coefficient and phosphates of the seawater.

SST along the Atlantic coast between Brittany and Huelva was examined in detail. Three different sources of information were used.

1. Shore SST data provided by the Portuguese Metereology Institute, Lisbon. These temperatures were measured every day, at 9 am local time, directly from the seashore, in shallow water. On the Portuguese continental coast, data are available from seven sites (Cape Santa Maria, Cape Santa Marta, Forte do Cavalo, Leixões, Peniche, Rocha and Sines), as means of the period 1981-2000 (CARVALHO AND SOARES, 2001).

2. Nearshore SST data provided by the Portuguese Hydrographic Institute (Lisbon) and the Spanish Puertos del Estado. These temperatures were measured at regular intervals (usually every hour), in buoys located near the coast, and are displayed as monthly means. For the Portuguese continental coast, data are available from three buoys (Faro, Leixões and Sines), but spanning very different periods:

- Faro, from 2000 to 2004, with most years complete
- Leixões, from 1998 to 2004, but most years were incomplete.
- Sines, from 1996 to 2004, with most years complete.

The raw information was purchased from the Hydrographic Institute. For the Spanish Atlantic coast, data are avail-

Table I. Identification of sampling sites. Maximum shell length of *Patella vulgata* and number of analyzed specimens collected at each sampling site.
Tabla I. Identificación de las localidades de muestreo. Extensión longitudinal máxima de la concha y número de ejemplares de Patella vulgata *recogidos en cada localidad.*

#	Identification	Coordinates:W/N		Maximum shell length	Number of specimens	Near AVHRR #
1	Ínsua	-8.8740	41.8701	49.7	365	-1
2	Moledo	-8.8702	41.8452	39.7	49	+1
3	Arda	-8.8756	41.7818	41.9	46	+2
4	Afife	-8.8754	41.7798	39.7	42	+2
5	Aguçadoura/A Ver-o-Mar	-8.7821	41.4319	49.4	366	+14
6	Figueira da Foz	-8.9060	40.1773	41.1	6	+62
7	São Martinho do Porto	-9.1369	39.5159	42.9	21	+85
8	Baleal	-9.3382	39.3742	41.2	16	+88
9	Ericeira	-9.4182	38.9648	38.9	33	+100
10	São João do Estoril	-9.3722	38.6940	49.6	27	+113
11	Oeiras	-9.3240	38.6773	45.9	18	+114
12	Portinho da Arrábida	-8.9715	38.4840	-	Not found	+126
13	Odeceixe	-8.7944	37.4478	43.5	15	+167
14	Amoreira	-8.8434	37.3553	42.2	18	+171
15	Monte Clérigo	-8.8521	37.3423	47.9	27	+171
16	Bordeira	-8.8987	37.2022	45.3	41	+177
17	Amado	-8.9036	37.1682	45.0	56	+177
18	Ponta Ruiva	-8.9672	37.0691	52.3	62	+182
19	Telheiro	-8.9781	37.0478	49.5	15	+182
20	Tonel	-8.9471	37.0082	55.9	8	+187
21	Mareta	-8.9383	37.0065	47.4	8	+187
22	Martinhal	-8.9266	37.0166	41.8	10	+188
23	Barranco do Benaçoitão	-8.8937	37.0421	56.6	10	+188
24	Ingrina	-8.8778	37.0477	44.7	25	+188
25	Zavial	-8.8705	37.0477	-	Not found	+189
26	Salema	-8.8233	37.0661	43.6	4	+190
27	Luz	-8.7250	37.0879	22.9	1	+192
28	Lagos - Dona Ana	-8.6679	37.0932	-	Not found	+194
29	Três Irmãos	-8.5763	37.1199	-	Not found	+195
30	Rocha	-8.5410	37.1182	32.2	2	+196
31	Carvoeiro-Vale de Centianes	-8.4503	37.0911	-	Not found	+199
32	Marinha	-8.4109	37.0912	-	Not found	+199
33	Armação de Pera	-8.3534	37.1019	-	Not found	+200
34	Olhos d'Água	-8.1912	37.0905	-	Not found	+205
35	Vila Real de Santo António	-7.4092	37.1770	-	Not found	+222
36	Torre del Oro	-6.7349	37.0941	-	Not found	+237
37	Torre de la Higuera	-6.5623	37.0071	-	Not found	+241

able from two buoys (Bilbao and Gijón), for March to November, 2004, and downloaded from the Puertos del Estado site (www.puertos.es).

3. Nearshore SST data estimated from the AVHRR (Advanced Very High Resolution Radiometer) on board the NOAA series polar orbiting satellites. The AVHRR measures emitted and reflected radiation in two visible and three infrared channels. SST estimates use the infrared channels information,

calibrated with in situ determinations measured using moored and drifting buoys (SMITH, VAZQUEZ, TRAN AND SUMAGAYSAY, 1996). AVHRR measures the ocean's «skin» temperature, corresponding to the uppermost millimeter of the ocean (SMITH *ET AL*., 1996). Buoys measure the temperature of the underlying mixed layer, the ocean's «bulk» temperature (SMITH *ET AL*., 1996). The ocean skin temperature can be as much as 0.7°C cooler than the bulk temperature, due to evaporation or radiative cooling (SMITH *ET AL*., 1996). However, since AVHRR measurements are calibrated using buoys' determinations, the final estimate resembles more closely a bulk temperature estimate than a skin temperature estimate (SMITH *ET AL*., 1996). Data were downloaded from the AVHRR Pathfinder v5 data set, at http://poet.jpl.nasa.gov, as monthly means, from 1985 to 2004, with nighttime retrieval. Each pixel corresponds to a square with a 4 km side. Data were first downloaded in sets corresponding to squares with 1° longitude x 1° latitude. The closest, or the two pixels closer to the coast were then selected, and the other values discarded. This procedure resulted in 350 SST pixels along the northern French and Spanish coast, and 243 SST pixels along the Portuguese and southern Spanish coasts (Fig. 2). Two sets of data were built. One set, with mean maximum (August) and mean minimum (February) SST for the period 1984-2004, along the entire set of pixels (-350 to +243). Another set, with monthly means for the year 2000, along the Biscay coast, and from Galicia to the furthest pixel +243. One of the limitations of the AVHRR measurements is cloud cover, which results in several absences of estimates, especially in winter months. For the calculation of maximum and minimum means, only pixels with more than 50% determinations were used. For comparison between shore or buoys SST determinations, and AVHRR SST estimates, those pixels closest to the shores or buoys were chosen, and were for, Cape Santa Maria, Cape Santa Marta, Forte do Cavalo, Leixões, Peniche, Rocha and Sines, pixels +211, +112, +123, +21, +90, +196 and +114, respectively, and for the buoys of Faro, Leixões, Sines, Bilbao and Gijón, pixels, +211, +18, +145, -169 and -111, respectively. These three sources of information on the SST have advantages and limitations. Shore and buoys data were available only at a few sites along the examined coast, and were particularly scarce in the Portuguese and Spanish southern coast. Both sources are expected to be accurate, since determinations were carried out with measuring instruments. Shore data were determined on the beach (only once a day), but buoys were near the coast (several readings per day). AVHRR data are continuous along the studied coast, but the values are estimates, with several months missing due to cloud cover, and measured pixels were near the coast, not on the shore.

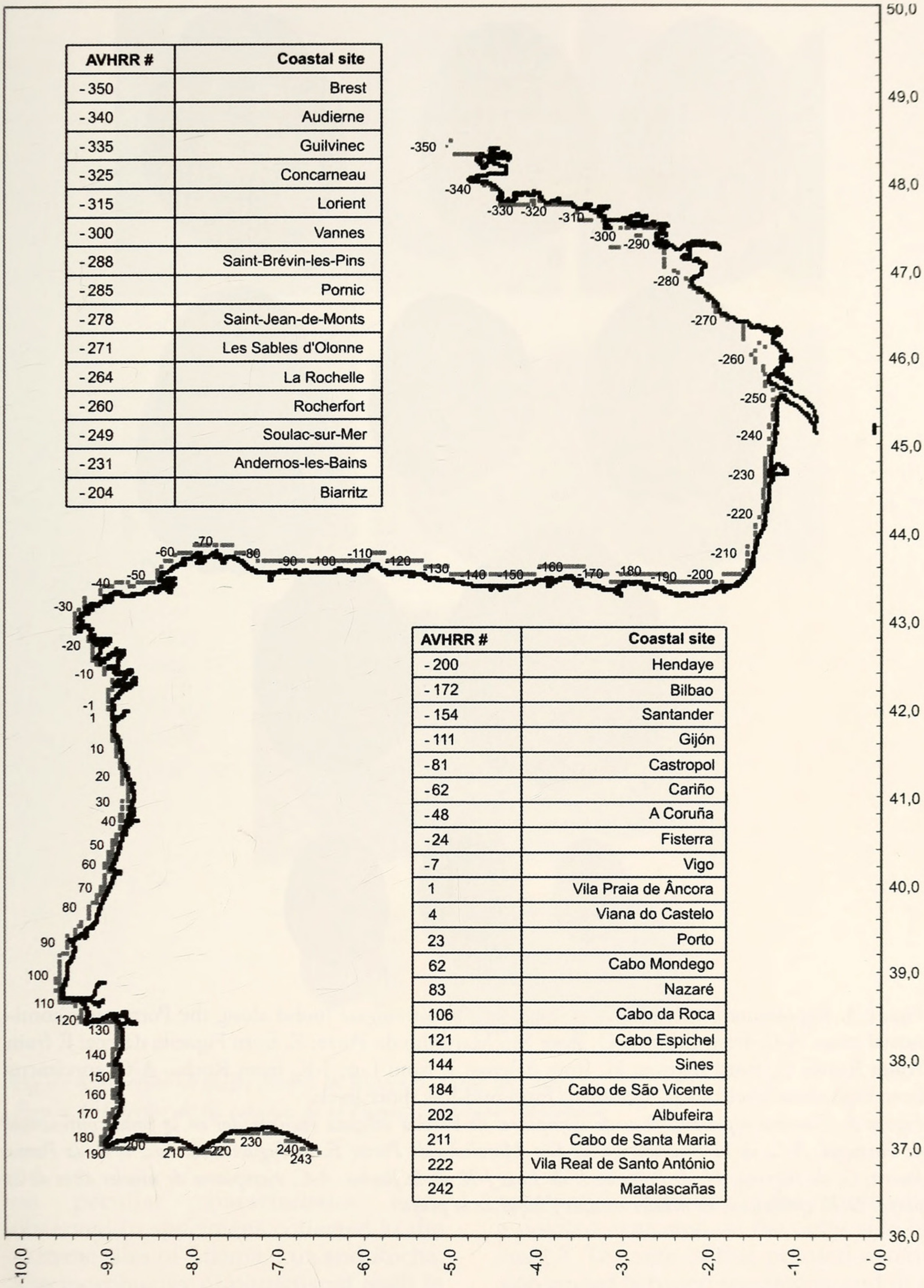
In order to correlate the distribution of *P. vulgata* with the geology of the Portuguese continental coast, the rocks of the sampling sites were identified using reference literature (CARTA GEOLÓGICA DE PORTUGAL).

To test if the slope and intercept of the regression lines were significantly different from one and zero, respectively, the procedure of ZAR (1984) was used. Significance level was set at 0.05.

RESULTS

I Distribution, abundance and size of *P. vulgata*

P. vulgata shells are shown in Figures 3 and 4, including the four specimens collected from the extreme far sites of Salema, Luz and Rocha (Figs. 3, 4, H-K). Shells had an ellipsoidal, slightly eccentric base. Shell conicity was variable, but shells were usually neither very flat nor very tall. The margin of the shell was entirely or slightly indented. The external surface was smooth at the apex, with spaced discreet ribs below. Shells from high shore levels were usually bare (Figs. 3, 4, A-C), but those from mid and low shore levels were completely



AVHRR #	Coastal site
-350	Brest
-340	Audierne
-335	Guilvinec
-325	Concarneau
-315	Lorient
-300	Vannes
-288	Saint-Brévin-les-Pins
-285	Pornic
-278	Saint-Jean-de-Monts
-271	Les Sables d'Olonne
-264	La Rochelle
-260	Rocherfort
-249	Soulac-sur-Mer
-231	Andernos-les-Bains
-204	Biarritz

AVHRR #	Coastal site
-200	Hendaye
-172	Bilbao
-154	Santander
-111	Gijón
-81	Castropol
-62	Cariño
-48	A Coruña
-24	Fisterra
-7	Vigo
1	Vila Praia de Âncora
4	Viana do Castelo
23	Porto
62	Cabo Mondego
83	Nazaré
106	Cabo da Roca
121	Cabo Espichel
144	Sines
184	Cabo de São Vicente
202	Albufeira
211	Cabo de Santa Maria
222	Vila Real de Santo António
242	Matalascañas

Figure 2. Localization of the AVHRR pixels used to estimate nearshore SST, from Brittany (France) to Huelva (Spain). Representative mainland coastal sites near the AVHRR pixels are displayed.

Figura 2. Localización de los pixels AVHRR utilizados para estimar la SST cerca de la costa, desde Bretaña (Francia) hasta Huelva (España). Se muestran localidades representativas de la costa cerca de los pixels AVHRR.

Figure 3. Representative shells of specimens of *Patella vulgata* found along the Portuguese continental coast. A-C, from Ericeira; D, from São Martinho do Porto; E, from Figueira da Foz; F, from Ponta Ruiva; G, from Ingrina; H, from Salema; I, from Luz; J-K, from Rocha. A-C, specimens from high shore levels. D-K, specimens from mid-low shore levels.
Figura 3. Conchas representativas de ejemplares de Patella vulgata *encontrados en la costa continental de Portugal. A-C, de la Ericeira; D, de São Martinho do Porto; E, de Figueira da Foz; F, de la Ponta Ruiva; G, de Ingrina; H, de Salema; I, de Luz; J-K, de la Rocha. A-C, ejemplares de niveles altos de la playa. D-K, ejemplares de niveles medios y bajos de la playa.*

covered with algae (Figs. 3, 4, D-K). Almost all shells had a silvery head scar, in the interior. A few specimens showed a whitish-silver head scar. Below the head scar, most specimens had alternating dark and orange/yellow/green rays, but a few specimens were almost totally yellow (Fig. 4C) or dark (Fig. 4D). The most notorious and constant characteristics of *P. vulgata* shells were the smooth external surface at the apex and the silvery interior head scar. No consistent morphological trend was observed in specimens from north to south, and

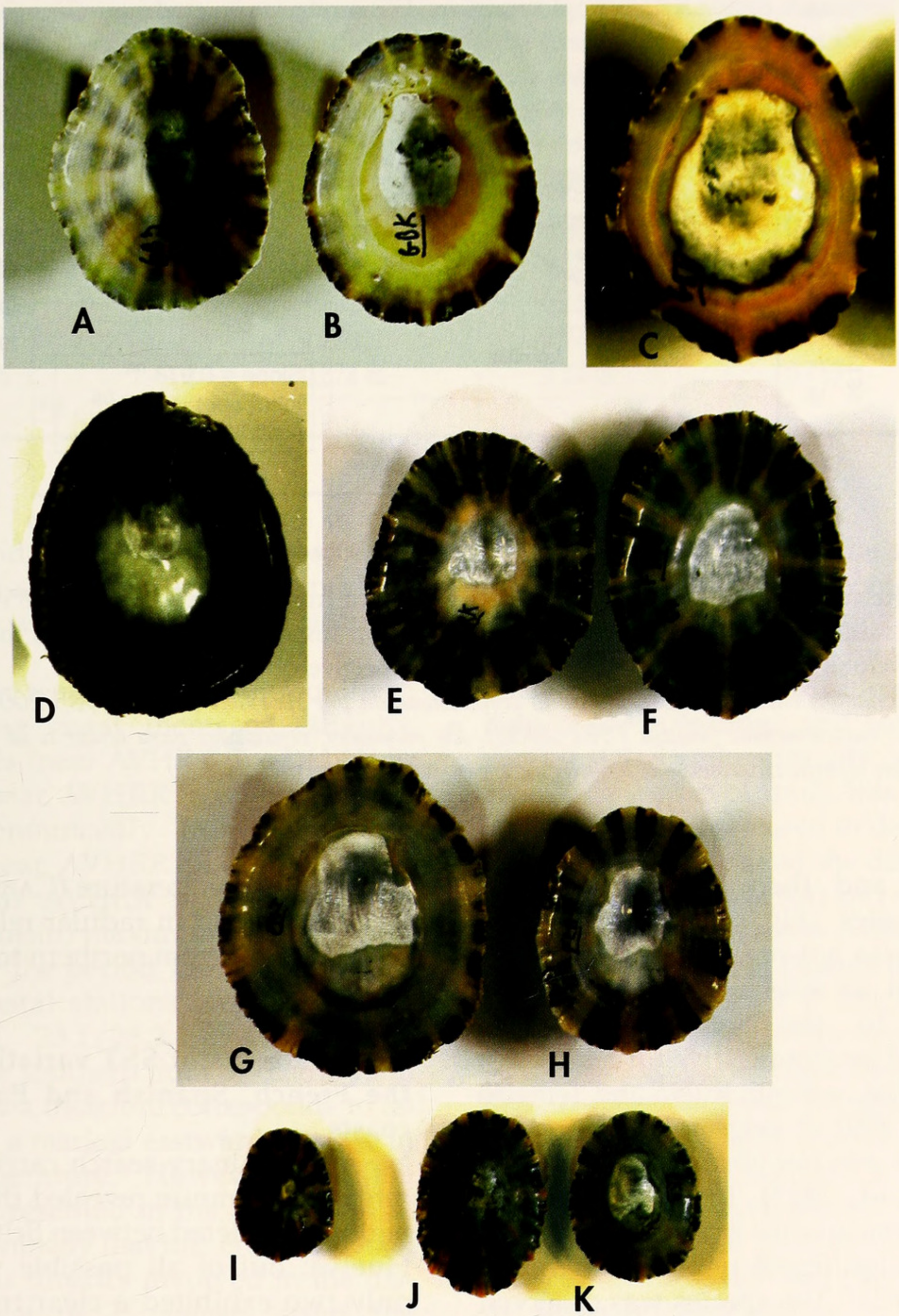


Figure 4. Interior of shells shown in Figure 3. Same localities.
Figura 4. Interior de las conchas de la Figura 3. Mismas localidades.

no peculiar characteristics were observed in specimens collected at the extreme sites of Salema, Luz and Rocha. The morphology of pluricuspid teeth in the radula was similar to the types reported in the literature (FISHER-PIETTE, 1934, 1935; FISHER-PIETTE AND GAILLARD, 1959; EVANS, 1953; HAWKINS, WATSON, HILL, HARDING, KYRIAKIDES, HUTCHINSON AND NORTON, 1989; CABRAL, 2003). The most notorious and constant characteristic of the radula was a pointed extension on the outer side of cusp 3. The size of this pointed extension varied between specimens, and in a few, was very reduced, but was always present, including in specimens collected at the extreme sites of Salema, Luz and Rocha.

The abundance of *P. vulgata* showed a generally decreasing trend from northern to southern sites, till Cape São

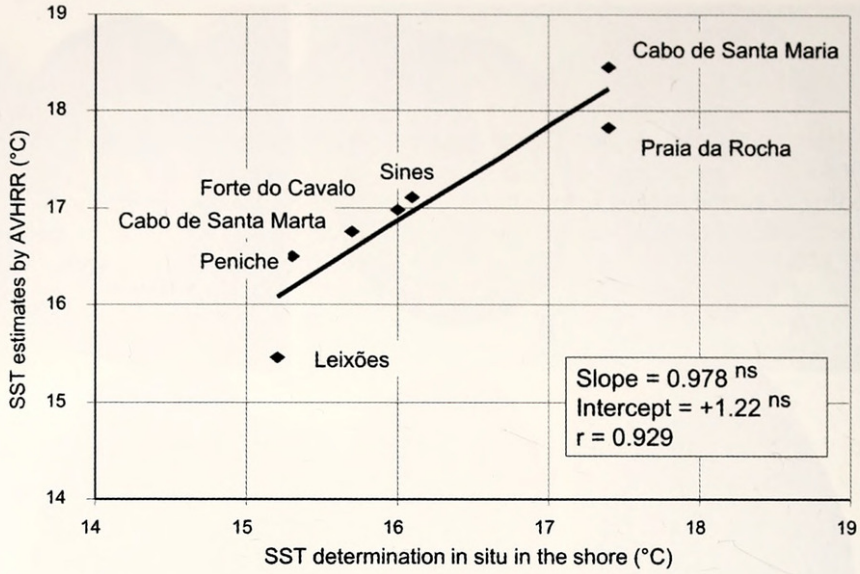


Figure 5. Relationship between nearshore SST estimated from AVHRR (means 1985-2004) and shore SST measured by instruments (means 1981-2000). Insert, results for testing if the slope and intercept were significantly different from 1 and 0, respectively.
Figura 5. Relación entre la SST cerca de la costa estimada por AVHRR (media 1985-2004) y la SST medida por instrumentos (media 1981-2000). En recuadro, resultados para testar si la pendiente y ordenada son significativamente diferentes de 1 y 0, respectivamente.

Vicente, and then from western to eastern sites (Fig. 1). However, this pattern was not regular. *P. vulgata* was abundant at sites north of the river Douro. To the south, abundance decreased pronouncedly, but near Cape São Vicente, at Ponta Ruiva and Telheiro (#18 and #19), *P. vulgata* was abundant. *P. vulgata* was not observed at Portinho da Arrábida (#12). Passing Cape São Vicente, the species became scarce, and the last significant population was at Ingrina (#24). The species was observed even to the east, at Salema, Luz and Rocha, but only very few specimens were observed.

Maximum shell size varied between sites (Table I), and no trend was observed from northern to southern sites. Even at the far extreme site of Salema (#26), shells reached considerable dimensions. Only at Luz and Rocha (#27 and #30), shells were small, but not minute. Therefore there was no correlation between abundance and maximum size of *P. vulgata* along the Portuguese continental coast. The relative size of radula to shell length was usually in the range 1.5-2.0. Similar values have been reported in the literature (Cabral, 2003, 2005). No trend in radular relative size was observed from northern to southern sites.

II Patterns of SST variation along the French, Spanish and Portuguese coasts

A preliminary search carried out in reference literature revealed that for the region considered between Britanny and Huelva, out of all possible variables, only two exhibited a clear trend from north to south till Cape São Vicente, and then from west to east – the air temperature along the coast and ocean surface, and the sea surface temperature (SST).

The relative humidity of air at the ocean surface displayed no significant trend in this region. Salinity of seawater at the surface decreased slightly along the Brittany coast, Bay of Biscay, and the northern and central Portuguese coast due to the output of fresh water from large rivers in these regions, but from the southern coast of Portugal to southern Spain, water salinity was constant. Dissolved oxygen and the alkali-chloride coefficient were constant between

Table II. Regression analysis of nearshore SST estimated by AVHRR versus measured by instruments in buoys. Tests if the slope is significantly different from 1 and the intercept from 0.
Tabla II. Análisis de regresión de la SST cerca de la costa estimada por AVHRR versus medida por boyas. Muestra si la pendiente es significativamente diferente de 1 y la ordenada diferente de 0.

Site/Buoy	Slope	Intercept	r
Bilbao	1.02 ns	-0.39 ns	0.987*
Gijón	1.15 ns	-3.12 ns	0.963*
Leixões	1.23 s	-3.23 s	0.872*
Sines	1.22 s	-2.97 s	0.934*
Faro	0.874 ns	2.77 ns	0.753*

(*)$P < 0.001$

Galicia and southern Spain. Phosphates decreased slightly until the central Portuguese coast, but were then constant to the south.

The air temperature in the southern Portuguese coast increased, slightly from Sines (near AVHRR pixel +144) to Sagres (near AVHRR pixel +184), and then pronouncedly from Sagres to Rocha (near AVHRR pixel +196) and Faro (near AVHRR pixel +211). The August mean/maximum air temperatures (for the period 1961/71-1990) for these coastal stations were 19.0/21.4, 20.2/23.4, 23.1/28.2, 23.4/28.8 (IM, 2006). The southern limit of distribution of *P. vulgata* therefore corresponds to an area with a marked eastward increase in air temperature. However, for the reasons presented in the discussion, it seemed unlikely that this environmental factor was directly involved in the disappearance of *P. vulgata* from the western Algarve coast.

In order to test the involvement of the SST in the southern limit of distribution of *P. vulgata*, this variable was examined in detail, using three sets of data from three different sources. Significant correlations were found at all comparisons between AVHRR and nearshore or buoys data, and for most of the comparisons, the slope and intercept of the regression line were not significantly different from 1 and 0, respectively (Fig. 5, Table II), indicating that these three sources of information gave comparable results. However, for both Leixões and Sines buoys, the slope and intercepts were significantly higher than 1 and lower than 0, indicating either an under-estimation by the buoys or an over-estimation by the radiometer. In light of these findings, and considering the fine detail and continuity of AVHRR data in the region of study, this source of information was explored in detail.

Firstly, we examined the distribution of the maximum (August) and minimum (February) SST along the Atlantic coast between Brittany and Huelva (Fig. 6). In August, SST was high in Bay of Biscay, decreasing until the northwestern corner of the Iberian peninsula in Galicia, and then increasing until Huelva, at first slightly until Cape São Vicente area, and then pronouncedly eastwards to Huelva region. The region between Cape Finisterre (near AVHRR pixel -24) and Cape São Vicente (near AVHRR pixel +184) is, in summer, affected by a vigorous upwelling regime, driven by strong northerly winds associated with the northward displacement of the Azores high-pressure cell and the weakening of the Iceland low (FERREIRA, 1984, 1986, 2005; RELVAS AND BARTON, 2002, 2005). Between April-May and September-October, cold, less saline and nutrient-rich subsurface waters emerge at the surface, near the coast in this region, lowering the SST (FERREIRA, 1984, 1986, 2005; FIÚZA, HAMANN, AMBAR, DÍAZ DEL RIO, GONZÁLEZ AND CABANAS, 1998; RELVAS AND BARTON, 2002, 2005). On occasions, water upwells on the west coast, extends

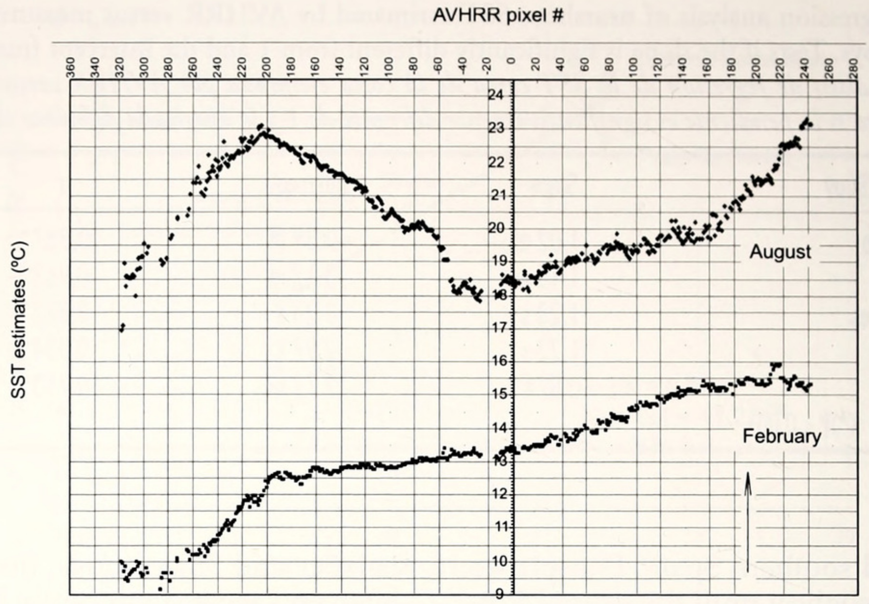


Figure 6. Maximum (August) and minimum (February) nearshore SST estimated from AVHRR (means for 1985-2004) between Brittany and Huelva. The localization of the pixels is presented in Figure 2. Only pixels with more than 10 values are represented. The arrow indicates the end of distribution of *Patella vulgata*.
Figura 6. SST cerca de la costa, máxima (Agosto) y mínima (Febrero), estimada por AVHRR (medias 1985-2004) desde Bretaña (Francia) hasta Huelva (España). La localización de los pixels está representada en la Figure 2. Solamente pixels con más de 10 valores están representados. La flecha indica el final de la distribución de Patella vulgata.

around Cape São Viente, eastward along the Algarve shelf (FERREIRA, 1984, 1986, 2005; RELVAS AND BARTON, 2002, 2005). The intensity and frequency of these upwellings decreases from west to east along the Algarve south coast (RELVAS AND BARTON, 2002, 2005). The upwelling phenomenon explains the relatively low SST along the western coast of the Iberian peninsula, in August, shown in Figure 6. Considering the distribution of *P. vulgata* observed in the present work, and the data reported in the literature indicating the presence of this species on the French and northern Spanish coast, including Bay of Biscay, it became clear that neither the maximum nor the minimum SST per se could explain the distribution of *P. vulgata*. Maximum SST in Bay of Biscay were higher then in Salema – Rocha (AVHRR pixels +190 - +196), where the last specimens of *P. vulgata* were observed. Minimum SST in eastern Algarve and Huelva (where *P. vulgata* was not observed) were not higher than in the region of Salema – Rocha.

Guided by the published information on the life cycle of *P. vulgata*, in particular the study of PEÑA, YAGÜE AND IBÁNEZ (1987) showing, for Bay of Biscay, a correlation between the gonadal stages and SST three months before, we examined the monthly distribution of the SST, in Bay of Bascay and from Galicia to Huelva, for the year 2000 (Fig. 7). Data for February and August agreed with previous observations for the 1985-2004 means. The upwelling phenomenon is evident between May and September, with a relatively low SST along the west coast of the Iberian peninsula, as referred above. When comparing the distribution of *P. vulgata* and each of the monthly graphs, we found a close similarity between the distribution of the SST in May and the occurrence/absence of *P. vulgata* along the coast. The species occurs for SST lower than ca. 18°C. In Bay of Biscay and along the coast up to Salema – Rocha (AVHRR pixels +190 - +196), the SST was lower than this value, except the AVHRR pixels +120 - +130, which slightly exceeded this value. Re-

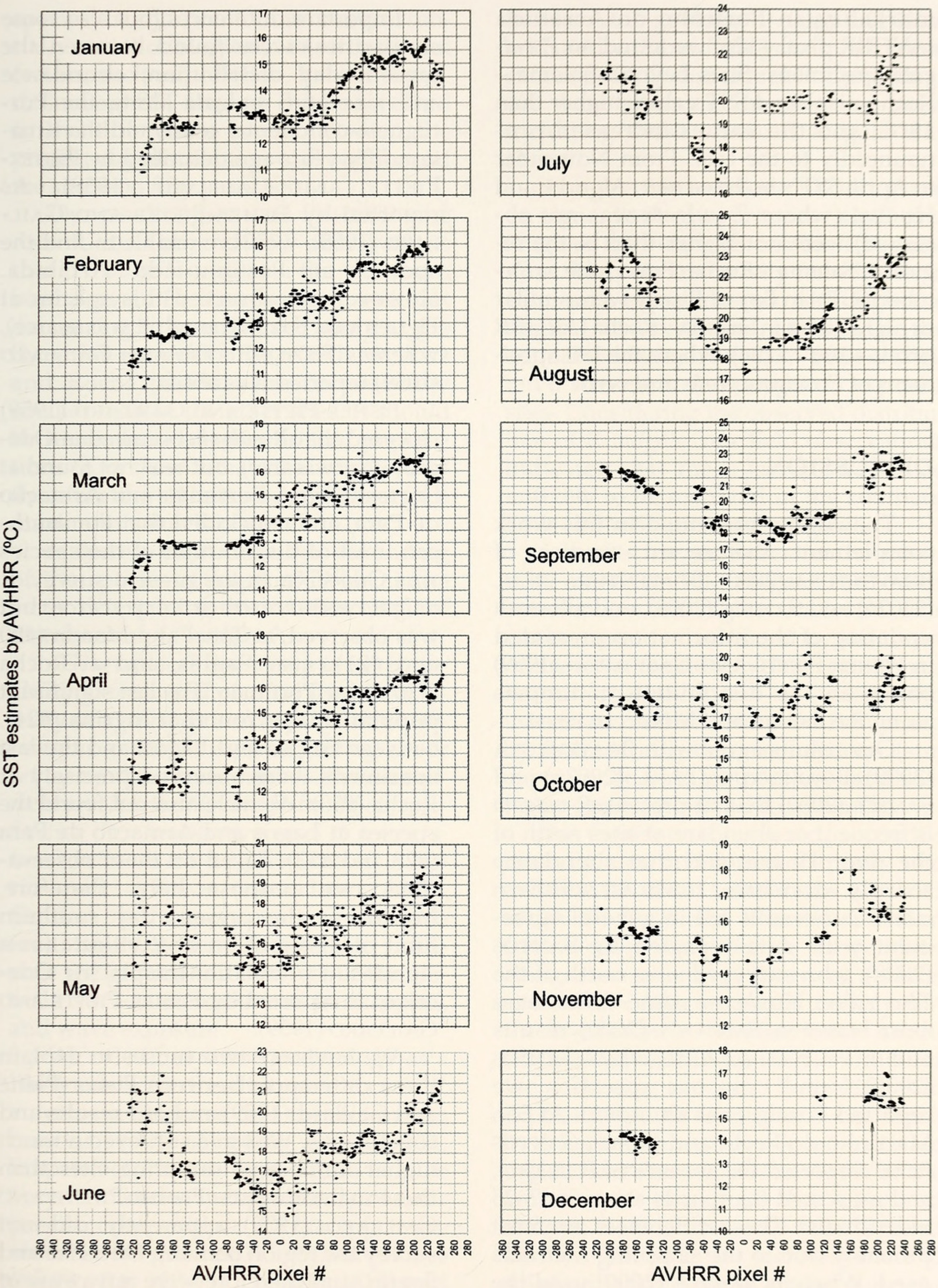


Figure 7. Monthly nearshore SST estimated from AVHRR (for the year 2000), for Bay of Biscay, and from Galicia to Huelva. The localization of the pixels is presented in Figure 2. Missing values were not available in the AVHRR Pathfinder v5 database. The arrow indicates the end of distribution of *Patella vulgata*.

Figura 7. SST cerca de la costa, media mensual, estimada por AVHRR (para el año 2000), para el Golfo de Vizcaya, y desde Galicia hasta Huelva. La localización de los pixels está representada en la Figure 2. Los valores no representados no estaban disponibles en la base de datos del AVHRR Pathfinder v5. La flecha indica el final de la distribución de Patella vulgata.

markably, in Portinho da Arrábida (AVHRR pixel +126) we found no *P. vulgata* specimens. Sites beyond Salema – Rocha displayed SST values higher than 18°C, and the values increased pronouncedly to the east. From November to April, SST's in the eastern Algarve and Huelva (where *P. vulgata* was not observed) were not higher than in the region of Salema – Rocha. From June to October, SST's in Bay of Biscay were similar or higher than in Salema – Rocha (AVHRR pixels +190 - +196), where the last specimens of *P. vulgata* were observed.

DISCUSSION

The results presented in this work complement the recent studies of BOAVENTURA (2000), BOAVENTURA *ET AL.* (2002a) and SANTOS (2000), and allow an updating of the information presented in FISHER-PIETTE AND GAILLARD'S (1959) paper on the distribution of limpets along the Iberian and Moroccan coast.

Our results agree with BOAVENTURA (2000), BOAVENTURA *ET AL.* (2002a) and SANTOS (2000) that, at present, *P. vulgata* is frequent or abundant at sites north of the river Douro, and that abundance sharply decreases towards southern sites. Our results are in general agreement with data reported by SANTOS (2000), who surveyed sites north of the Tejo river. However some differences exist between SANTOS'S (2000) results and our survey. At Afife, where SANTOS (2000) found only one specimen, we reported *P. vulgata* as abundant. At São Martinho do Porto and Baleal, SANTOS (2000) reported the absence of *P. vulgata*, and we scored the species as scarce (5-25 individuals). These differences are most probably due to the sampling methods used. Whereas SANTOS (2000) used the transect method, we have made searches by walking along the site, covering therefore a much wider area. BOAVENTURA (2000) and BOAVENTURA *ET AL.* (2002a) only reported mean abundances for the north, centre and south sites, and therefore a detailed comparison with the present work is not possible.

Important differences (but also some similarities) were found between the present day distribution, abundance and size of *P. vulgata* along the Portuguese continental coast, and the situation fifty years ago described by FISHER-PIETTE AND GAILLARD (1959). As reported by FISHER-PIETTE AND GAILLARD (1959), we were unable to find the species at Portinho da Arrábida. However, we observed this species at Figueira da Foz (although it was scarce), whereas FISHER-PIETTE AND GAILLARD (1959) reported it as absent.

FISHER-PIETTE AND GAILLARD (1959) reported that *P. vulgata* occurred at Odeceixe (very scarce), but was not found at Sagres, Lagos, Portimão and Armação de Pera, and concluded that the southern limit of distribution of the species was Odeceixe. In the present survey, *P. vulgata* was scarce or very scarce, but was observed, at Tonel and Mareta (#20 and #21), near Sagres, and at Rocha (#30), near Portimão. The last significant population was found at Ingrina (#24), between Sagres and Lagos, and the last specimens were observed precisely at Rocha (#30). We have also not found the species at Lagos and Armação de Pera (#28 and #33). Based on these observations, we propose here, therefore, Ingrina as the present day southern limit of distribution of *P. vulgata* (as a significant population), replacing Odeceixe, as reported by FISHER-PIETTE AND GAILLARD (1959).

We envisage two causes to explain these differences between Fisher-Piette and Gaillard (1959) and our results and conclusions. We have surveyed a much higher number of sampling sites than these malacologists. FISHER-PIETTE AND GAILLARD (1959) apparently did not survey the region between Odeceixe and Sagres, and therefore were not aware of Amoreira, Monte Clérigo, Bordeira, Amado, and specially, Ponta Ruiva and Telheiro (#18 and #19), which, at present, have abundant *P. vulgata* populations. The region between Sagres and Lagos was also not studied, and this is precisely, at present, the most important zone in the southern limit of distribution of this species. In addition to this cause, essentially methodological, environmental factors, such as pollution, habitat degradation and SST changes can be involved in the differences found between the present day distribution of *P. vulgata* and the situation fifty years ago.

Our results agree with FISHER-PIETTE AND GAILLARD'S (1959) observations that *P. vulgata* reaches the southern boundary of distribution without decreasing in size. Indeed, only at the three far extreme sites of Salema, Luz and Rocha, shells were considerably smaller than in the other sites. It should be remembered, however, that populations from these sites were minute, and therefore the statistical significance of a maximum value is restricted.

Is there a main cause for the ending of the species at Ingrina? What is the factor determining this southern limit of distribution of *P. vulgata*?

«*Geographical limits may be set by inability to withstand physical conditions directly or to compete successfully where efficiency is somewhat impaired; or they can be set by a failure in the reproductive/recruitment process; the higher sensitivity of reproductive then somatic processes to temperature conditions has long been known in marine species*» (BOWMAN AND LEWIS, 1977). Guided by these concepts, we considered, firstly, general factors that influence the growth and survival of the animals, such as the substrate, food supply, and wave exposure.

We ruled out substrate geology as a likely cause for the disappearance of *P. vulgata* in Algarve for the following reasons. 1. In sampling sites #1-#34, limpets occurred throughout on hard or very hard rocks, independently of their precise composition. *Patella* spp. were observed on granites (#1-#5), limestones (#6-#8, #16, #19-#34), basalts (#17) and sanstones (#10, #11). However, limpets were not found in very soft rocks such as marls and soft clays present in sampling sites #6 and #8. 2. In sampling sites #19-#34 (corresponding to the southern area of distribution of *P. vulgata*), limestone was the dominant substrate, and no appreciable difference was observed between the geology of sampling sites with and without *P. vulgata*. In addition, *P. intermedia*, *P. rustica* and *P. ulyssiponensis*, were abundant in all these sites, including those where *P. vulgata* was absent.

Limpets are herbivorous and graze on algae. Lack of appropriate algal coverage of the substrate can limit populations. Limpets are usually found both in calm and exposed sites, although the degree of exposure influences the animals' density. *P. vulgata* prefers sheltered sites, but also occurs on exposed sites. Considering the observed distribution of *P. vulgata*, our field observations indicated that these factors were also unlikely to be involved in the southern limit of distribution of *P. vulgata*.

Limpets are molluscs of the intertidal zone, and *P. vulgata* can occur between low and high shore levels. This environment is dominated by the direct influence of the tidal cycles. The animals are alternatively out of water and immersed, and therefore are influenced by both atmospheric conditions (sun exposure and air temperature) and seawater composition and temperature.

We therefore considered, secondly, these factors, and found that only two exhibited a clear trend from north to south till Cape São Vicente, and then from west to east – the air temperature along the coast and at the ocean surface, and the SST. We consider it unlikely that the first factor is involved in the southern limit of distribution of *P. vulgata* for the following reasons. Both high sun exposure and air temperature can result in dehydration, which beyond a certain threshold value, results in death of the animal. At Ingrina, the observed animals were located on a fully exposed surface. The animals were exposed to solar radiation almost all day long. At sites to the east of Rocha, we searched all ecological niches on the shores, including shady areas and caves, where the animals were never exposed to direct sunlight. No specimen was found. Although air temperature on the south coast increases markedly from west to east, it seemed unlikely that at Ingrina, dehydration stress was lower than in a cave of Carvoeiro or Marinha, for instance. If sun exposure and air temperature were determinant factors in the distribution of *P. vulgata*, ongoing to the limit of distribution, we would have expected to find the animals in an increasingly sheltered and shady environment, a pattern which was not observed. We therefore considered this factor no further in our research.

Thirdly, we studied in detail the variation of the SST between Bay of Biscay and Huelva region, and found a close relation between May means and the observed distribution of *P. vulgata*. Since reproduction and the life cycle of *P. vulgata* are directly dependent on seawater temperature, we analyzed data reported in the literature on this issue.

In the northern Portuguese coast, gonads are inactive from May to July. Ripening of the gametes begins in August. Spawning begins in September-October, is at maximum in November-January, and then decreases. In April-May, the gonads are again in the neuter resting condition (GUERRA AND GAUDÊNCIO, 1986). According to BOWMAN AND LEWIS (1986), the main spawning time displays a north/south gradient, being in the summer in northern Europe (July-August in Norway, August-October in Scotland), and in the winter in northern Iberia. Published information confirms this rule. ORTON, SOUTHWARD AND DODD (1956) studied the breeding cycle at several sites in the British Isles, from Aberdeen in the north to Plymouth in the south, and found that maximum gonad development occurred in August-September at northern sites, and in September-October, at southern sites. At Robin Hood Bay, on the north-east coast of England, BOWMAN AND LEWIS (1977) reported maximum gonad index in October-November. In Bantry Bay, on the southwest coast of Ireland, THOMPSON (1980) found maximum gonad index in September-January. On the south coast of England, EVANS (1953) observed full reproduction in late autumn-early winter. At the Orkney Islands, BAXTER (1983) reported spawning occurring in December-February. At Saint Malo (France), FISCHER-PIETTE (1948) found maximum gonad development in October-January. On the Basque coast, IBÁÑEZ AND FELIÚ (1983) and FELIÚ AND IBÁÑEZ (1984) observed reproduction in November-January. On the coasts of Bay of Biscay, PEÑA *ET AL.* (1987) found maximum gonad development in October-December. It is therefore plausible that in the south coast of Portugal, the maximum gonad index is reached in December-January or slightly later.

The larval cycle is brief. Sex cells, spermatozoa and eggs, are discharged into the sea. One day after fertilization, the animals are pelagic trochophores; in two-three days, they are early veligers; in four-five days, torsion is completed, and at nine days, they have reached 0.2 mm length and become sedentary veligers, starting metamorphosis (DODD, 1957; CHOQUET, 1968; LEWIS AND BOWMAN, 1975; BOWMAN AND LEWIS, 1977). The definitive shell then replaces the larval early shell (CHOQUET, 1968). After settlement and until the production of a calcified shell (with ca. 0.7 mm length), spat is very sensitive to low and high temperatures, desiccation, and rough seas, and therefore is only found in protected, damp and shady habitats (JONES, 1948; BOWMAN AND LEWIS, 1977, 1986). This critical period can vary between six weeks and five months (BOWMAN AND LEWIS, 1986). In northern Portugal, juveniles are visible to the naked eye only in late October (GUERRA AND GAUDÊNCIO, 1986).

How can the SST in May affect directly the breeding cycle of *P. vulgata*? We envisage two hypotheses. The first is related to the maintenance of the breeding cycle, and the second to the settlement of the juveniles.

In May, gonads are in full resting condition. To the east of Ingrina – Rocha (AVHRR pixels +188 - +196), nearshore SST was higher than 17.5°C (Fig. 7). All western sites, up to Bay of Biscay, display lower SST values (Fig. 7). It is conceivable that the beginning of the resting period demands a threshold limit of temperature, above which subsequent development of sex cells in the gonad will be inhibited.

In May, spat resulting from last phase of reproduction is at a critical phase of sensitivity to high temperature stress. To the east of Ingrina – Rocha (AVHRR points +188 - +196), nearshore SST increases pronouncedly with longitude (Fig. 7). It is possible that these higher temperatures eliminate the spat, and therefore no new generation is able to establish itself on the substrates. In May, nearshore SST in Bay of Biscay is only slightly lower than in Ingrina – Rocha (Fig. 7). However, in this region, reproduction is presumably earlier, and therefore, spat is older, and more resistant to temperature stresses.

A third cause may also be operating and acting synergistically with the first two, this is competition between *P. vulgata*, *P. intermedia* and *P. ulyssiponensis*. These two latter species occur in high densities at all sites (except #35 - #37) where *P. vulgata* was not observed. It is possible that a few individuals of the spat survived, but did not succeed in establishing themselves on the substrate. This interpretation is supported by results reported by Boaventura (2000) and Boaventura, Fonseca and Hawkins (2002b). In an experimental study carried out in a northern shore of the Portuguese coast on the competition between *P. intermedia* and *P. vulgata*, it was found that both species, in increased densities, showed higher mortality, and reduced size, weight and gonad development. The addition of *P. intermedia* to *P. vulgata* populations and vice versa had results similar to increasing the density of each species. It was concluded that inter- and intraspecific competition were occurring amongst *P. intermedia* and *P. vulgata*.

In summer, on some occasions, upwelled waters extend around Cape São Vicente and reach the Lagos-Rocha area, but rarely spread beyond this point (Ferreira, 1984, 1986, 2005; Relvas and Barton, 2002, 2005). This region corresponds to the southern limit of distribution of *P. vulgata*. Upwelled waters are cold (and responsible for the relatively low SST along the west coast of the Iberian Peninsula in summer, as already discussed) but are also very nutrient-rich. It is conceivable that these nutrients are important for the larval stage of *P. vulgata*, and their lowering in the eastern side of the Algarve coast can also contribute to the absence of this species in this area.

According to Bowman and Lewis (1986), spawning is triggered when the SST drops below the critical value of 12°C. Results presented here indicate that this level, if it exists, is certainly higher than this value. The minimum nearshore SST in the region of Ingrina – Rocha (AVHRR points +188 - +196) where the last specimens were observed were higher than 15°C (Fig. 6).

If SST is the main factor involved in the distribution of *P. vulgata*, and considering the ongoing alteration in the climate and increase in the air and ocean temperatures, Tonel, Mareta, Martinhal, Barranco e Ingrina sites, being on the limit of tolerance of the species, are candidates to be used as indicators to follow future changes in SST.

ACKNOWLEDGEMENTS

We are especially indebted to Dr. Denise Brum Ferreira (University of Lisbon) and Dr. Paulo Relvas (University of Algarve) for helpful discussions and comments on the manuscript.

BIBLIOGRAPHY

Baxter, J. M., 1983. Annual variations in soft-body dry weight, reproductive cycles and sex ratios in populations of *Patella vulgata* at adjacent sites in the Orkney Islands. *Marine Biology*, 76: 149-157.

Boaventura, D. M., 2000. *Patterns of distribution in intertidal rocky shores: the role of grazing and competition in structuring communities*. Tese de Doutoramento; Universidade do Algarve, Faro; Portugal.

BOAVENTURA, D., RÉ, P., FONSECA, L. C. AND HAWKINS, S. J., 2002a. Intertidal rocky shore communities of the continental Portuguese coast: analysis of distribution patterns. *Marine Ecology PSZN*, 23: 69-90.

BOAVENTURA, D., FONSECA, L. C. AND HAWKINS, S. J., 2002b. Analysis of competitive interactions between the limpets *Patella depressa* Pennant and *Patella vulgata* L. on the northern coast of Portugal. *Journal of Experimental Marine Biology and Ecology*, 271: 171-188.

BOWMAN, R. S. AND LEWIS, J. R., 1977. Annual fluctuations in the recruitment of *Patella vulgata* L. *Journal of the Marine Biological Association of the U.K.*, 57: 793-815.

BOWMAN, R. S. AND LEWIS, J. R., 1986. Geographical variation in breeding cycles and recruitment of *Patella* spp. *Hydrobiologia*, 142: 41-56.

CABRAL, J. P., 2003. Characterization and multivariate analysis of *Patella intermedia, Patella ulyssiponensis* and *Patella vulgata* from Póvoa do Varzim (Northwest Portugal). *Iberus*, 21: 1-17.

CABRAL, J. P., 2005. Concentrations of metals in *Patella intermedia, Patella rustica, Patella ulyssiponensis* and *Patella vulgata* shells along the Portuguese continental coast. *Bolletino Malacologico*, 41: 23-34.

CARTA GEOLÓGICA DE PORTUGAL, na escala 1/50 000. Serviços Geológicos de Portugal, Lisboa.

CARVALHO, F. AND SOARES, A., 2001. *A temperatura da água do mar em Portugal*. Instituto de Metereologia, Nota Técnica VAM2-2/2001, Lisboa.

CHOQUET, M., 1968. Croissance et longévité de *Patella vulgata* L. (Gastéropode prosobranche) dans le Boulonnais. *Cahiers de Biologie Marine*, 9 : 449-468.

CHRISTIAENS, J., 1973. Révision du genre *Patella* (Mollusca, Gastropoda). *Bulletin du Muséum National d'Histoire Naturelle*, 182: 1305-1392.

CLEMAM. 2002. Check list of European marine mollusca. Downloaded from <http://www.somali.asso.fr/clemam/index.php> on 13/04/2002.

DODD, J. M., 1957. Artificial fertilisation, larval development and metamorphosis in *Patella vulgata* L. and *Patella caerulea* L. *Pubblicazione della Stazione Zoologica di Napoli*, 29: 172-186.

EVANS, R. G., 1947. Studies in the biology of British limpets. I. The genus *Patella* in Cardigan Bay. *Proceedings of the Zoological Society of London*, 117: 411-423.

EVANS, R. G., 1953. Studies in the biology of British limpets – the genus *Patella* on the south coast of England. *Proceedings of the Zoological Society of London*, 12: 357-376.

FELIÚ, D. AND IBÁÑEZ, M., 1984. Sistematica y ecologia del genero *Patella* en la Costa Vasca: III. *Lurralde*, 7: 161-170.

FERREIRA, D. BRUM, 1984. L'upwelling ouest ibérique. Régime et causes aérologiques. *Met Mar*, 123: 4-16.

FERREIRA, D. BRUM, 1986. *Structures thermiques estivales de l'océan au large du Portugal méridional. Évolution et causes aérologiques*. In «Estudos em Homenagem a Mariano Feio», Lisboa, pp. 223-236.

FERREIRA, D. BRUM, 2005. *A Dinâmica do Oceano*. In «Geografia de Portugal. 1. O Ambiente Físico», Círculo de Leitores, Lisboa, pp. 262-288.

FISCHER-PIETTE, M. E., 1934. Remarques de systématique et de biogéographie sur les Patelles des cotes françaises. *Bulletin du Muséum National d'Histoire Naturelle*, 6: 280-285.

FISCHER-PIETTE, E., 1935. Systématique et biogéographie. Les Patelles d'Europe et d'Áfrique du Nord. *Journal de Conchyliologie*, 79: 5-66.

FISCHER-PIETTE, E., 1948. Sur les éléments de prospérité des Patelles et sur leur specificité. *Journal de Conchyliologie*, 88: 45-96.

FISCHER-PIETTE, E. AND GAILLARD, J. M., 1959. Les Patelles, au long des cotes atlantiques ibériques et nord-marocaines. *Journal de Conchyliologie*, 99: 135-200.

FIÚZA, A. F. G., HAMANN, M., AMBAR, I., DÍAZ DEL RIO, G., GONZÁLEZ, N. AND CABANAS, J. M., 1998. Water masses and their circulation off western Iberia during May 1993. *Deep-Sea Research I*, 45: 1127-1160.

GUERRA, M. T. AND GAUDENCIO, M. J., 1986. Aspects of the ecology of *Patella* spp. on the Portuguese coast. *Hydrobiologia*, 142: 57-69.

HAWKINS, S. J., WATSON, D. C., HILL, A. S., HARDING, S. P., KYRIAKIDES, M. A., HUTCHINSON, S. AND NORTON, T. A., 1989. A comparison of the feeding mechanisms in microphagous, herbivorous, intertidal, prosobranchs in relation to resource partitioning. *Journal of Molluscan Studies*, 55: 151-165.

IBÁÑEZ, M. AND FELIÚ, D., 1983. Sistemática y ecología del género *Patella* en la Costa Vasca: II. *Lurralde*, 6: 191-201.

IM, Instituto de Metereologia, 2006. Características do clima da costa de Portugal Continental. Dowloaded from <http://www.meteo.pt/resources/im/pdfs/mari_rc_00_00_II.pdf> on 01/11/2006.

JONES, N. S., 1948. Observations and experiments on the biology of *Patella vulgata* at Port St. Mary, Isle of Man. *Proceedings of the Transactions of the Liverpool Biological Society*, 56: 60-77.

LEWIS, J. R. AND BOWMAN, R. S., 1975. Local habitat-induced variations in the population dynamics of *Patella vulgata* L. *Journal of Experimental Marine Biology and Ecology*, 17: 165-203.

MAILLARD, C., 1986. *Atlas Hydrologigue de l'Atlantique Nord-Est*. IFREMER, Brest.

OCEANOGRAPHIC ATLAS OF THE NORTH ATLANTIC OCEAN, 1967. *Section II. Physical Properties.* U.S. Naval Oceanographic Office, Publication no. 7000, Washington.

ORTON, J. H., SOUTHWARD, A. J. AND DODD, J. M., 1956. Studies of the biology of limpets. II. The breeding of *Patella vulgata* L. in Britain. *Journal of the Marine Biological Association of the U.K.*, 35: 149-170.

PEÑA, J., YAGÜE, M. J. AND IBÁÑEZ, M., 1987. Ciclos reprodutores y variaciones del coeficiente radular de *Patella rustica* y *P. vulgata* (Mollusca: Gastropoda). *Iberus*, 7: 1-10.

RELVAS, P. AND BARTON, E. D., 2002. Mesoscale patterns in the Cape São Vicente (Iberian Peninsula) upwelling region. *Journal of Geophysical Research*, 107(C10): 3164.

RELVAS, P. AND BARTON, E. D., 2005. A separate jet and coastal counterflow during upwelling relaxation off Cape São Vicente (Iberian Peninsula). *Continental Shelf Research*, 25: 29-49.

ROLÁN, E., 1993. *Guía Ecolóxica das Cunchas e Moluscos de Galicia*. Edicións Xerais de Galicia, Vigo, 196 pp.

ROLÁN, E. AND OTERO-SCHMITT, J., 1996. *Guia dos Moluscos de Galicia*. Editorial Galáxia, Vigo, 318 pp.

SANTOS, A. E. F. A. M., 2000. *Intertidal ecology of northern portuguese rocky shores*. Ph. D. Thesis; University of Southampton.

SMITH, E., VAZQUEZ, J., TRAN, A. AND SUMAGAYSAY, R., 1996. Satellite-derived sea surface temperature data available from the NOAA/NASA Pathfinder program. Downloaded from <http://www.agu.org/eos_elec/95274e.html> on 29/09/2005.

THOMPSON, G. B., 1980. Distribution and population dynamics of the limpet *Patella vulgata* L. in Bantry Bay. *Journal of Experimental Marine Biology and Ecology*, 45: 173-217.

WORLD OCEAN ATLAS, 1979. *Volume 2. Atlantic and Indian Oceans.* Ministry of Defence, USSR Navy. Pergamon Press, Oxford.

ZAR, E. J. H., 1984. *Biostatistical Analysis*. Prentice-Hall, New Jersey, 718 pp.