REVIEW

Latitudinal gradients in *Scrobicularia plana* reproduction patterns, population dynamics, growth, and secondary production

Tiago Verdelhos[1,2,*], P. G. Cardoso[1], M. Dolbeth[1,2], M. A. Pardal[2]

[1]Institute of Marine Research (IMAR), Department of Life Sciences, University of Coimbra, 3004-517 Coimbra, Portugal
[2]Centre for Functional Ecology (CFE), Department of Life Sciences, University of Coimbra, Apartado 3046, 3001-401 Coimbra, Portugal

ABSTRACT: The bivalve *Scrobicularia plana* is a dominant species in terms of biomass and productivity in intertidal soft-substrate benthic communities along the NE Atlantic area. As such, it constitutes an important link in the food web and as a human food source, with high commercial and economic value. Several studies have suggested the existence of latitudinal variation in the ecological patterns of the species along its geographic distribution range. In the present study, a review and a comparison among previous studies on this species were performed. The resulting patterns of reproduction, population dynamics, growth and secondary production were analysed, and possible relationships between latitude and *S. plana*'s ecological patterns and life strategies assessed. Results suggest the existence of different life strategies, depending on temperature, latitudinal gradient and local habitat conditions. Higher-latitude populations usually exhibit low abundance values, shorter reproduction periods and a 'slower' lifestyle, with lower growth rates ($0.1 < k < 0.2$, where k is a growth coefficient), extended lifespan and lower productivity. Areas between 40 and 45° N seem to present optimal ecological conditions, with the highest abundance values registered, longer reproduction periods, 'faster' growth ($0.3 < k < 0.8$) and higher productivity, while further south, populations showed lower abundance, productivity and growth rates.

KEY WORDS: Latitude · *Scrobicularia plana* · Ecological patterns

INTRODUCTION

Scrobicularia plana is a long-living selective deposit-feeder bivalve that is both eurythermal and euryhaline, and inhabits intertidal soft bottoms with abundant organic matter (Hughes 1970a, Guelorget & Mazoyer-Mayère 1983, Essink et al. 1991, Sola 1997, Guerreiro 1998, Casagranda & Boudouresque 2005, Verdelhos et al. 2005). It is considered one of the dominant species of intertidal soft-substrate in estuaries, lagoons and bays along the NE Atlantic coast (Hughes 1970a, Bachelet 1982, Casagranda & Boudouresque 2005, Dolbeth et al. 2005, Verdelhos et al. 2005, Cardoso et al. 2008), showing a wide geographic distribution, from Norway (60° N) to the Mediterranean and West Africa (14° N).

Moreover, this species is an important link in the food chains of these ecosystems, playing an important role in the diet of wading birds, crabs and benthic fish (Hughes 1969, 1970b, Bachelet 1982, Guelorget & Mazoyer-Mayère 1983, Casagranda & Boudouresque 2005, Langston et al. 2007). There is

increasing commercial interest in it as a human food resource with potential economic and social value (Rodríguez-Rúa et al. 2003, Langston et al. 2007).

Scrobicularia plana studies ranging from the UK and the Wadden Sea to Tunisia have focused on reproduction (Paes-da-França 1956, Hughes 1971, Worrall et al. 1983, Sola 1997, Guerreiro 1998, Rodríguez-Rúa et al. 2003, Raleigh & Keegan 2006, Mouneyrac et al. 2008), population dynamics (Hughes 1970a, Guelorget & Mazoyer-Mayère 1983, Essink et al. 1991, Sola 1997, Guerreiro 1998, Casagranda & Boudouresque 2005, Verdelhos et al. 2005), individual growth (Green 1957, Hughes 1970a, Bachelet 1981, Guelorget & Mazoyer-Mayère 1983, Sola 1997, Guerreiro 1998, Verdelhos et al. 2005) and secondary production (Hughes 1970b, Bachelet 1982, Guelorget & Mazoyer-Mayère 1983, Sola 1997, Guerreiro 1998, Casagranda & Boudouresque 2005, Verdelhos et al. 2005), and these studies suggest the existence of latitudinal variations.

Latitudinal gradients for bivalves are well established, focusing either on biodiversity (Crame 2000, 2002, Rex et al. 2000, Roy et al. 2000a) or on growth rate, body size and lifespan (MacDonald & Thompson 1988, Hummel et al. 1998, Roy et al. 2000b). However, bivalve populations seem to be influenced not by latitude *per se*, but by several environmental variables — e.g. temperature, seasonality, precipitation and ecosystem energy flux. These parameters co-vary with latitude and interact with each other, influencing recruitment success, survival and growth rates, controlling primary production and consequently the food supply in the ecosystem (Macpherson 2002, Willig et al. 2003, Angilletta & Sears 2004, Giangrande & Licciano 2004).

A general latitudinal trend in temperature is observed along the European coast, with temperature decreasing with increasing latitude (www.worldweather.org). Temperature seems to play an important role in *Scrobicularia plana* population dynamics, controlling reproduction patterns (Hughes 1971, Worrall et al. 1983, Sola 1997, Rodríguez-Rúa et al. 2003, Raleigh & Keegan 2006, Mouneyrac et al. 2008), survival and mortality (Hughes 1969, Guelorget & Mazoyer-Mayère 1983, Essink et al. 1991), growth rates (Bachelet 1981), and consequently secondary production. Different temperature patterns may then result in different life strategies along the geographic range of a species (Hughes 1971, Bachelet 1981, 1982, Essink et al. 1991, Sola 1997, Clarke 2003, Rodríguez-Rúa et al. 2003).

Studying the variation in population dynamics and strategies along a latitudinal gradient is a good approach to increase our knowledge of a species throughout its biogeographic range. A thorough review of previous studies on *Scrobicularia plana* along a wide range of its distribution, from the UK and the Wadden Sea (~55° N) to Southern Europe and the Mediterranean (~36° N), may allow us to assess distinct ecological patterns for different populations of this species.

The main goals of the present study were to analyse differences in (1) reproduction periods, (2) population dynamics, (3) growth rates and (4) secondary production of *Scrobicularia plana*, by comparing these results among populations along a latitudinal gradient and to assess possible relationships between latitude and *S. plana*'s ecological patterns and strategies. We expect to be able to extract relevant information from these relationships that may be useful to other approaches on population studies, such as modelling, a useful tool to understand the dynamics and responses of a population to both natural and anthropogenic stressors, as well as to make predictions for future scenarios (Anastácio et al. 2009).

MATERIALS AND METHODS

An extended bibliographic search was done, and published data on 25 *Scrobicularia plana* were collected from several studies performed between 1930 and 2008 (Table 1), focusing on reproduction, population dynamics, growth and secondary production of *Scrobicularia plana* populations from the Western European and Mediterranean coasts, along a latitudinal gradient (56 to 36° N) (Fig. 1).

Temperature data were collected from www.worldweather.org, in order to assess the existing temperature latitudinal gradient and to compare its patterns. Here, we use average monthly minimum and maximum temperature values (climate normals from 1971 to 2000) for the Wadden Sea, Ireland, UK (Wales and Cornwall), North France (Loire region), Gulf of Biscay (Gironde region, France and San Sebastian, Spain), Portugal (Coimbra, Lisbon and Alentejo), the Mediterranean (Marseille, France and Tunisia) and South Spain (Cádiz).

We found studies on the reproduction and gametogenic cycle of *Scrobicularia plana* from Ireland (Raleigh & Keegan 2006), the UK (Hughes 1971, Worrall et al. 1983), France (Mouneyrac et al. 2008), Spain (Sola 1997, Rodríguez-Rúa et al. 2003) and Portugal (Paes-da-França 1956, Guerreiro 1998), which focused on gonad development, breeding cycle and recruitment.
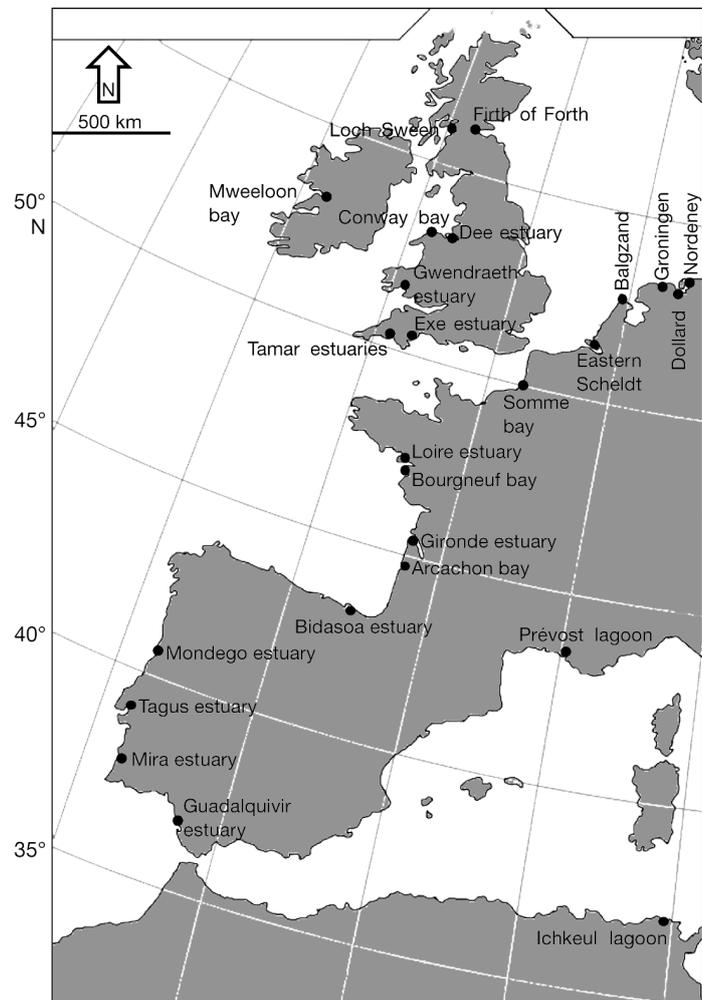
Table 1. *Scrobicularia plana*. Studies found in our extended bibliographic search, listed from north to south. m² values = core area; na = not available

Location	Latitude	Source	Study focus	Sampling	Collection method
Firth of Forth (Scotland)	56° 20' N	Stephen (1930) (in Hughes 1970a)	Macrofauna		na
Loch Sween (Scotland)	55° 57' N	Raymont (1955) (in Hughes 1970a)	Macrofauna		na
Norderney (Wadden Sea)	53° 42' N	Michaelis (1987) (in Essink et al. 1991)	Population dynamics	Seasonal (1976–1985)	1 mm sieve
Groningen (Wadden Sea)	53° 23' N	Essink et al. (1991)	Population dynamics	Seasonal (1969–1988)	1 mm sieve
Dollard (Wadden Sea)	53° 20' N	Essink et al. (1991)	Population dynamics	Seasonal (1974–1988)	1 mm sieve
Dee estuary (Wales)	53° 19' N	Stopford (1951) (in Sola 1997)	Ecological survey		na
Conway Bay (Wales)	53° 15' N	Hughes (1970a,b, 1971)	Population dynamics; reproduction; growth; production	Oct 1967 for survey study; monthly (Nov 1966–Nov 1967); monthly (Dec 1966–Dec 1967) for reproductive cycle study	0.25 m² (depth 30 cm); 1 m² (depth 30 cm), to collect adults; 0.25 m² (depth 5 cm), sieve 1.59 mm to collect spat; adult collection for reproductive cycle study
Mweeloon Bay (Ireland)	53° 13' N	Raleigh & Keegan (2006)	Gametogenic cycle	Monthly (Feb–Sep 1996; Jan–Sep 1997)	Adults collected (>22.4 mm)
Balgzand (Wadden Sea)	52° 53' N	Beukema (1989) (in Essink et al. 1991)	Population dynamics	Seasonal (1969–1988)	1 mm sieve
Eastern Scheldt (Wadden Sea)	51° 46' N	Craeymeersch et al. (1988) (in Essink et al. 1991)	Population dynamics	Seasonal (1983–1985)	1 mm sieve
Gwendraeth estuary (Wales)	51° 43' N	Green (1957)	Growth	Seasonal (1954–1955)	1 m² (depth 30 cm), 6 mm and 1 mm sieve
Exe estuary (Cornwall, UK)	50° 39' N	Holme (1949) (in Hughes 1970a)	Macrofauna		na
Tamar estuaries (Cornwall, UK)	50° 25' N	Warwick & Price (1975) (in Sola 1997)	Production		na
		Worrall et al. (1983)	Physiological ecology; gametogenic cycle	6 wk interval (Jan 1977–Jul 1979)	Adults collected
Somme Bay (English Channel, France)	50° 14' N	Ducrotoy (1987) (in Essink et al. 1991)	Population dynamics	Seasonal (1981–1987)	1 mm sieve
Loire estuary (Loire, France)	47° 10' N	Robineau (1986) (in Essink et al. 1991)	Population dynamics	Seasonal (1981–1983)	1 mm sieve
Bourgneuf Bay (Loire, France)	47° 00' N	Mouneyrac et al. (2008)	Gametogenic cycle	Apr 2005–May 2006	Adults collected
Gironde estuary (Gironde, France)	45° 30' N	Bachelet (1981, 1982)	Growth; production	Monthly (Jan 1976–Feb 1978)	0.25 m² (depth 30 cm), 1 mm sieve; 12 cm², 500 µm sieve
Arcachon Bay (Gironde, France)	44° 50' N	Bachelet (1981, 1982)	Growth; production	Monthly (Jan 1977–Jan 1978)	0.25 m² (depth 30 cm), 1 mm sieve; 12 cm², 500 µm sieve
Bidasoa estuary (San Sebastian, Spain)	43° 50' N	Sola (1997)	Population dynamics; reproduction; growth; production	Monthly (Feb 1987–Dec 1990)	0.1 m² (depth 25 cm), 1 mm sieve for population dynamics; 10 cm² (depth 2 cm), 200 µm sieve for recruitment study; adult collection for reproductive cycle study
Prévost lagoon (Marseille, France)	43° 00' N	Guelorget & Mazoyer-Mayère (1983)	Population dynamics; growth; production	Monthly (Oct 1983–Dec 1984)	0.1 m² (depth 30 cm), 1 mm sieve
Mondego estuary (Coimbra, Portugal)	40° 07' N	Verdelhos et al. (2005)	Population dynamics; growth; production	Monthly (Jan 1993–Dec 2000)	5–10 replicates of 0.14 m² core (depth 25 cm), 500 µm sieve

Table 1 (continued)

Location	Latitude	Source	Study focus	Sampling	Collection method
Tagus estuary (Lisbon, Portugal)	38° 50' N	Guerreiro (1998)	Population dynamics; reproduction; growth; production	Monthly (Apr 1986– Oct 1987)	0.25 m² (depth 25 cm), 1 mm sieve; adults collected for gametogenic cycle study
Mira estuary (Alentejo, Portugal)	37° 43' N	Guerreiro (1998)	Population dynamics; reproduction; growth; production	Monthly (Apr 1986– Oct 1987)	0.25 m² (depth 25 cm), 1 mm sieve; adults collected for gametogenic cycle study
Ichkeul lagoon (Tunisia)	37° 10' N	Casagranda & Boudouresque (2005)	Population dynamics; production	Monthly (Jul 1993– Apr 1994)	3 replicates of 0.18 cm² core (depth 20 cm), 300 µm sieve
Guadalquivir estuary (Cádiz, Spain)	36° 30' N	Rodríguez-Rúa et al. (2003)	Gametogenic cycle	Monthly/fortnightly (Jun 1999–May 2000)	Adults (23–58 mm) were collected

Fig. 1. *Scrobicularia plana*. Study sites on the western European and Mediterranean coasts

Scrobicularia plana population dynamics has been studied both in long-term sampling programmes and for shorter periods since the mid-20th century, in estuaries, lagoons and bays along the Atlantic European coast and the Mediterranean Sea (Hughes 1970a, Guelorget & Mazoyer-Mayère 1983, Essink et al. 1991, Sola 1997, Guerreiro 1998, Casagranda & Boudouresque 2005, Verdelhos et al. 2005). Information on recruitment, survival and mortality, density changes and population structure was used in the present study to compare several populations along the distribution range and in different geographic areas.

Individual growth of *Scrobicularia plana* has been calculated in several previous works, either based on successive growth ring distances in the shell, or by estimating and tracking cohorts in size frequency distributions over successive sampling dates, and the resulting empirical data were adjusted to mathemat-

ical equations. Green (1957) estimated growth for an *S. plana* population in the Gwendraeth Estuary (Wales) based on growth rings, by constructing a curve using a series of shells. Hughes (1970a) fitted data on distances between growth rings with a Ford-Walford method, plotting the shell length at one winter ring (L_t) against the shell length at the next winter ring (L_{t+1}):

$$L_{(t+1)} = L_t \times (1 - e^{-k}) + L_\infty \times e^{-k} \qquad (1)$$

where L_∞ is the theoretical maximum size (asymptotic length), k is the rate at which growth rate decreases with age and t is time.

Hughes (1970a) also plotted the data from Green (1957) by the same Ford-Walford method, obtaining similar results. In the Prévost lagoon (France), growth was estimated by applying a simple mathematical model on size frequency distribution data (Guelorget & Mazoyer-Mayère 1983). Bachelet (1981), Sola (1997) and Guerreiro (1998) used a von Bertalanffy equation to calculate L_t, based on growth rings and size frequency distributions. This equation is one of the most frequently used methods for growth estimation of molluscs, and it allows us to compare growth curves calculated for different populations:

$$L_t = L_\infty \times (1 - e^{-k \times (t - t_0)}) \qquad (2)$$

where L_∞ is asymptotic length, t_0 is the hypothetical age when $L_t = 0$, and k is the growth constant.

In the present study, we fitted data from the Mondego estuary population to the same growth model, through cohort recognition. In addition, we adjusted the von Bertalanffy model to the published results of Green (1957), Hughes (1970a) and Guelorget & Mazoyer-Mayère (1983), calculating the parameters k and L_∞ from the Ford-Walford plot, as in Bachelet (1981). The estimated equation curves were analysed, and the parameters (k, L_∞) resulting from these studies were compared for different *Scrobicularia plana* populations along the latitudinal gradient.

Results were then analysed along the latitudinal gradient, and adjusted to mathematical equations using TableCurve 2D v. 5.01 software. Temperature and spawning data were fitted to simple regression equations: $y = ax + b$, describing a linear relationship with latitude.

Mean population abundance and individual length at Year 2 were fitted to a Gaussian equation, describing a normal distribution variation along latitude.

Data from different studies on secondary production of *Scrobicularia plana* were also analysed and compared. Different cohort-based methods were used to calculate secondary production: (1) removal summation method (Hughes 1970b, Bachelet 1982, Sola 1997, Guerreiro 1998, Casagranda & Boudouresque 2005), where production is computed as the change in biomass from time t to time $t + 1$, over the cohort time period (sum of the standing stock gain) plus the mortality due to predation, among others (biomass eliminated), over the same period; (2) increment summation method (Bachelet 1982, Sola 1997, Guerreiro 1998, Verdelhos et al. 2005), where production is computed as the change in biomass from time t to time $t + 1$, over the cohort time period, due to the growth increases of all the members of the population; and (3) instantaneous growth method (Guerreiro 1998), where production is also derived from the growth increments of all the members of the population, which are added for the study period, but a growth rate is computed. These different methods have been assumed to provide similar evaluations of secondary production, and are among the most accurate (Dolbeth et al. 2005). Results from Hughes (1970b) were converted from calories to grams, and results in dry weight (DW) in Guelorget & Mazoyer-Mayère (1983) were converted to ash-free dry weight (AFDW) by Bachelet (1982).

A redundancy analysis (RDA) was applied to the collected and estimated data, in order to evaluate the relationships between *Scrobicularia plana* population dynamics, reproduction and growth parameters, the environmental parameters and latitude. The RDA was chosen after detecting a linear gradient with a detrended correspondence analysis (DCA) performed with the biotic data. All environmental variables were used in a first analysis and their significance was tested with the model forward-selection procedure. A second analysis was performed only with the significant environmental variables. These analyses were performed using CANOCO software (Van den Brink & Ter Braak 1999).

RESULTS

Average monthly temperatures followed the characteristic seasonal pattern of temperate regions, with lower values during winter and increasing towards summer (Fig. 2). A general latitudinal gradient along the European coast and a strong relationship between temperature and latitude were observed (Fig. 3). Northern regions (e.g. Wadden Sea, Ireland and UK) are usually characterised by low temperature values, severe cold winters and mild summers, while with decreasing latitude, temperature increases and southern regions are characterised by
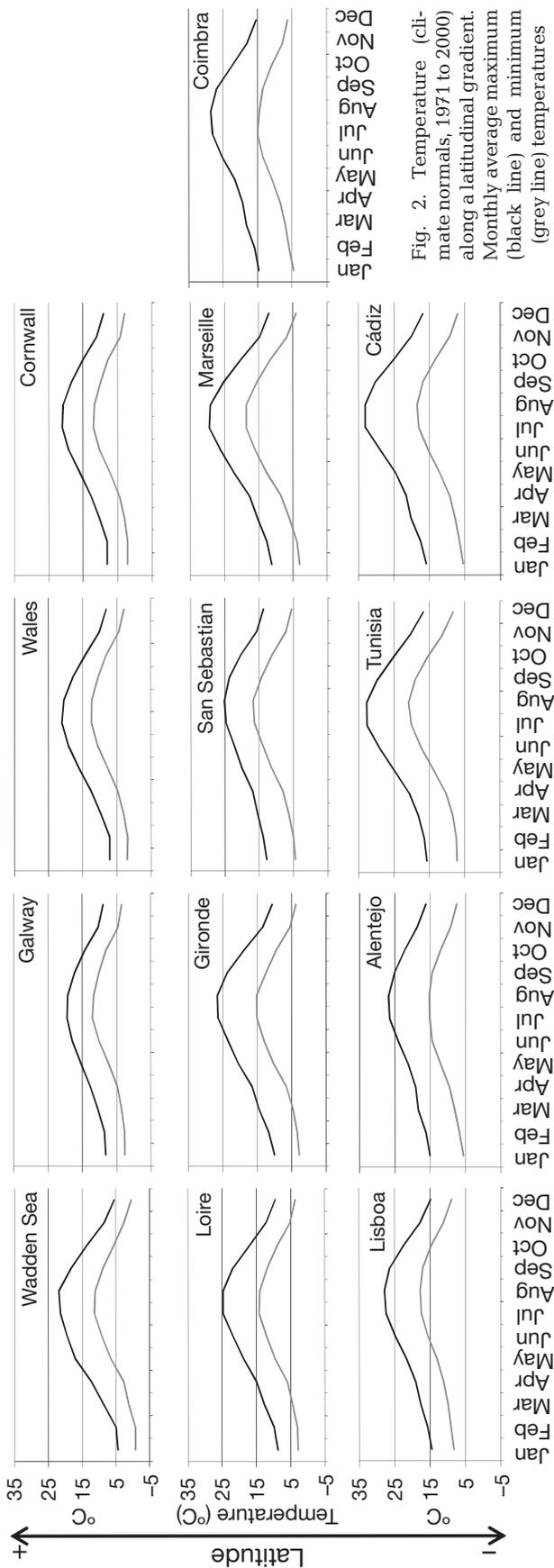
Fig. 2. Temperature (climate normals, 1971 to 2000) along a latitudinal gradient. Monthly average maximum (black line) and minimum (grey line) temperatures

mild winters and hot summers, reaching ~35°C in Tunisia and Cádiz (Spain) (Fig. 2).

Different reproduction patterns along latitude seem quite clear when analysing gonad development, spawning and recruitment periods for *Scrobicularia plana*. In northern populations, gonad development started during spring and spawning periods were usually short, lasting 2 or 3 mo during summer (vertical lines (1), (2) and (3) in Fig. 4). With decreasing latitude, gonad development showed a tendency to start earlier in the year and the same was observed for spawning periods, which increased in length towards the south to ~7 mo, from March to September, in the Guadalquivir estuary (vertical line (8) in Fig. 4). Spawning period duration showed linear relationships, both with latitude and temperature (Fig. 5), increasing along a north–south gradient, to-
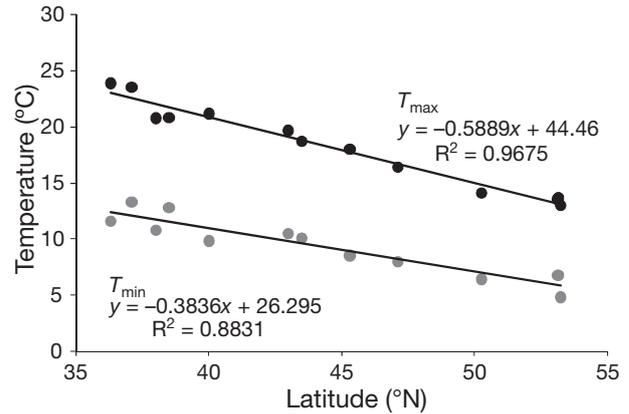

Fig. 3. Regression equations and R^2 values relating latitude to monthly average maximum (T_{max}) and minimum (T_{min}) temperatures
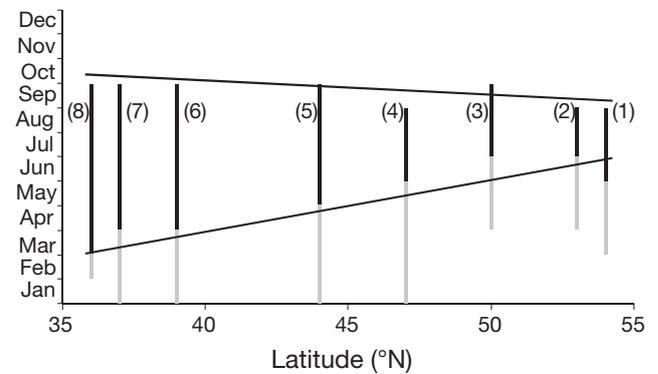

Fig. 4. *Scrobicularia plana*. Spawning (black vertical lines) and gonad development (grey vertical lines) periods at different latitudes: (1) Mweeloon Bay, (2) Conway Bay, (3) Tamar estuaries, (4) Bourgneuf Bay, (5) Bidasoa estuary, (6) Tagus estuary, (7) Mira estuary, (8) Guadalkivir estuary. Horizontal lines are a graphic representation of the enlargement of the spawning periods from higher latitudes towards lower latitudes

wards warmer climates. Benthic recruitment periods were also shorter in northern populations, and increased as we looked south, where populations showed 1 large or even 2 separate shorter recruitment periods, resulting in 1 or 2 cohorts yr^{-1} (Table 2).

High variability of mean abundance values was observed for the studied *Scrobicularia plana* populations along the Western European and Mediterranean coasts (Fig. 6A). Northern populations (e.g. Wadden Sea, Ireland, UK and the French side of the English Channel) registered low abundance values, often <250 ind. m^{-2}. With decreasing latitude, these values tended to increase and more abundant populations were found, particularly between 40 and 45°N (~1000 ind. m^{-2} in the Gironde estuary and Arcachon Bay, ~2500 ind. m^{-2} in the Bidasoa estuary, ~3000 ind. m^{-2} in the Prévost lagoon and ~1500 ind. m^{-2} in the Mondego estuary), while further south, the mean population abundance values decreased again. *S. plana*'s population abundance seems to follow a

Table 2. *Scrobicularia plana*. Benthic recruitment periods at different latitudes, listed from north to south

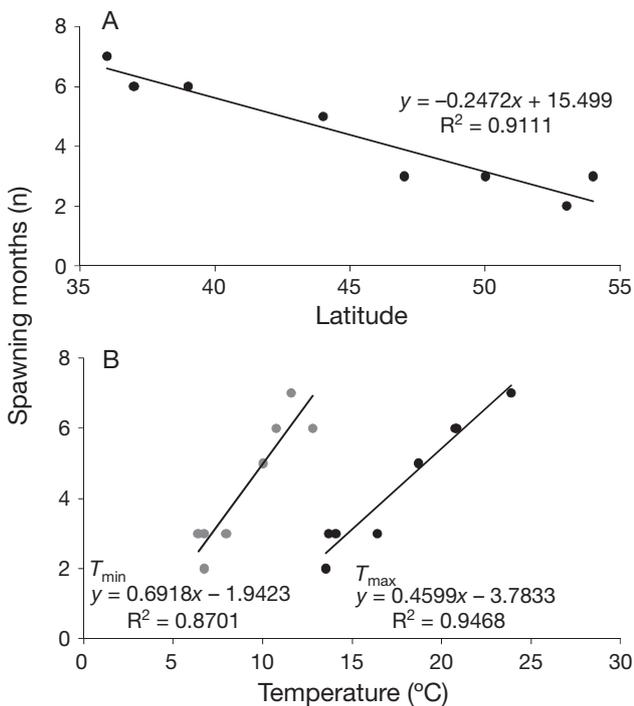| Location	Latitude	Cohorts	Recruitment period	Months
Dee estuary	53° 19' N	1	Summer	2
Gironde estuary	45° 30' N	2	Spring Summer	5
Arcachon Bay	44° 50' N	2	Spring Summer	4
Bidasoa estuary	43° 50' N	1	Summer	4
Prévost lagoon	43° 00' N	1	Autumn	3
Mondego estuary	40° 07' N	2	Spring Summer	5
Tagus estuary	38° 50' N	2	Spring Summer	4
Mira estuary	37° 43' N	2	Spring Summer	4
Ichkeul lagoon	37° 10' N	2	Spring Autumn	4

Fig. 5. *Scrobicularia plana*. Regression equations and R^2 values relating the duration of the spawning period to (A) latitude and (B) monthly average maximum (T_{max}) and minimum (T_{min}) temperatures
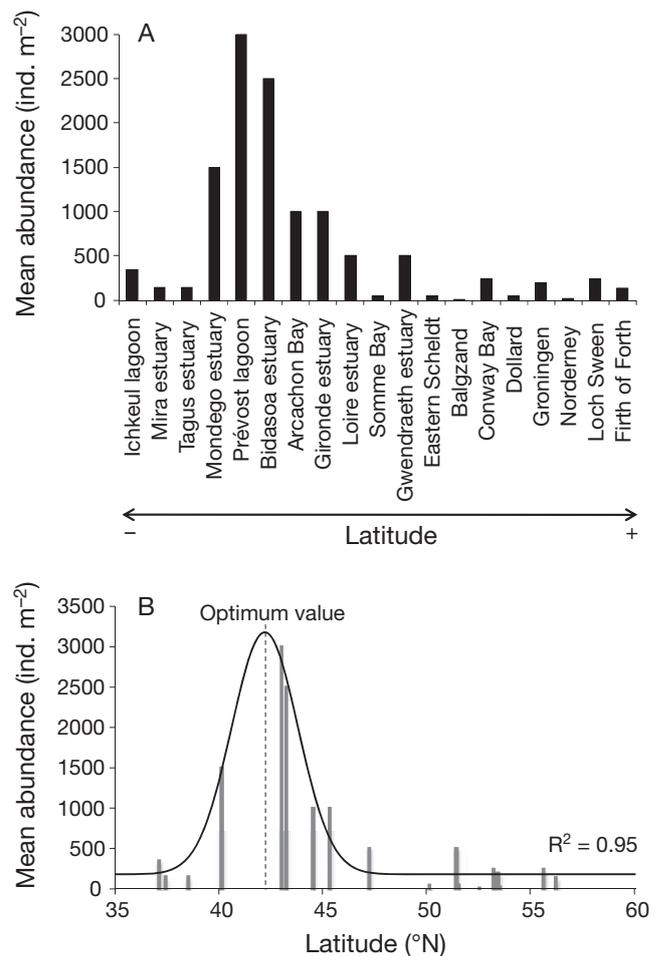

Fig. 6. *Scrobicularia plana*. (A) Mean population abundance and (B) the estimated Gaussian distribution along a latitudinal gradient

Gaussian distribution along latitude (Fig. 6B) according to the equation:

$$y = 181.95 + 3002.24^{\left(-0.5\left[\frac{(x-42.18)}{1.6^2}\right]\right)} \qquad (3)$$

in which y is abundance, and x is latitude. Abundance shows maximum values near 42°N and decreases both towards north and south.

Analysing the estimated von Bertalanffy growth model, the resultant growth coefficient k (Fig. 7) and total length at Year 1 and Year 2 (Fig. 8A), we observed different growth patterns along latitude. The 2 analysed UK populations (Conway Bay and Gwendraeth Estuary) showed similar patterns, with constant low growth: $k = 0.194$ and 0.108, respectively, reaching ~10 mm by the first year and ~20 mm by the second. Populations in the Gulf of Biscay showed higher k values (Gironde estuary: $k = 0.625$; Arcachon Bay: $k = 0.322$; Bidasoa estuary: $k = 0.815$) and an accentuated growth especially during the first and second years, reaching ~18 mm and ~28 mm, respectively. On the Mediterranean (Prévost lagoon), growth was particularly intense, reaching 22 mm during the first year and 33 mm in the second (Fig. 8A).

For the Portuguese populations, growth was more intense during the first and second years, reaching ~22 mm, and growing ~8 mm in the following years. Growth rates seem to be somewhat intermediate between the UK and the Gulf of Biscay and Mediterranean populations, with k values between 0.2 and 0.41. When analysing the resulting growth at Year 2 along latitude, we observed a Gaussian variation, with higher values near 43°N (Fig. 8B), estimated from the application of the Gauss equation:

$$y = 19.55 + 10.13^{\left(-0.5\left[\frac{(x-43.39)}{2.83^2}\right]\right)} \qquad (4)$$

in which y is length at Year 2, and x is latitude.

Production results from different studies were highly variable, either between populations of different geographic regions and even in the same area (Table 3), although from the given results, we observed highest production (P) and P/B ratio (where B is biomass) values in areas between 40 and 45°N, particularly in the Bidasoa estuary ($P = 83.62$ g m^{-2} yr^{-1}; $P/B = 1.21$ yr^{-1}) and the Prévost lagoon ($P = 81.05$ g m^{-2} yr^{-1}; $P/B = 3.68$ yr^{-1}).

Data on reproduction patterns (number of reproduction months, or NRM), mortality (Mort) and
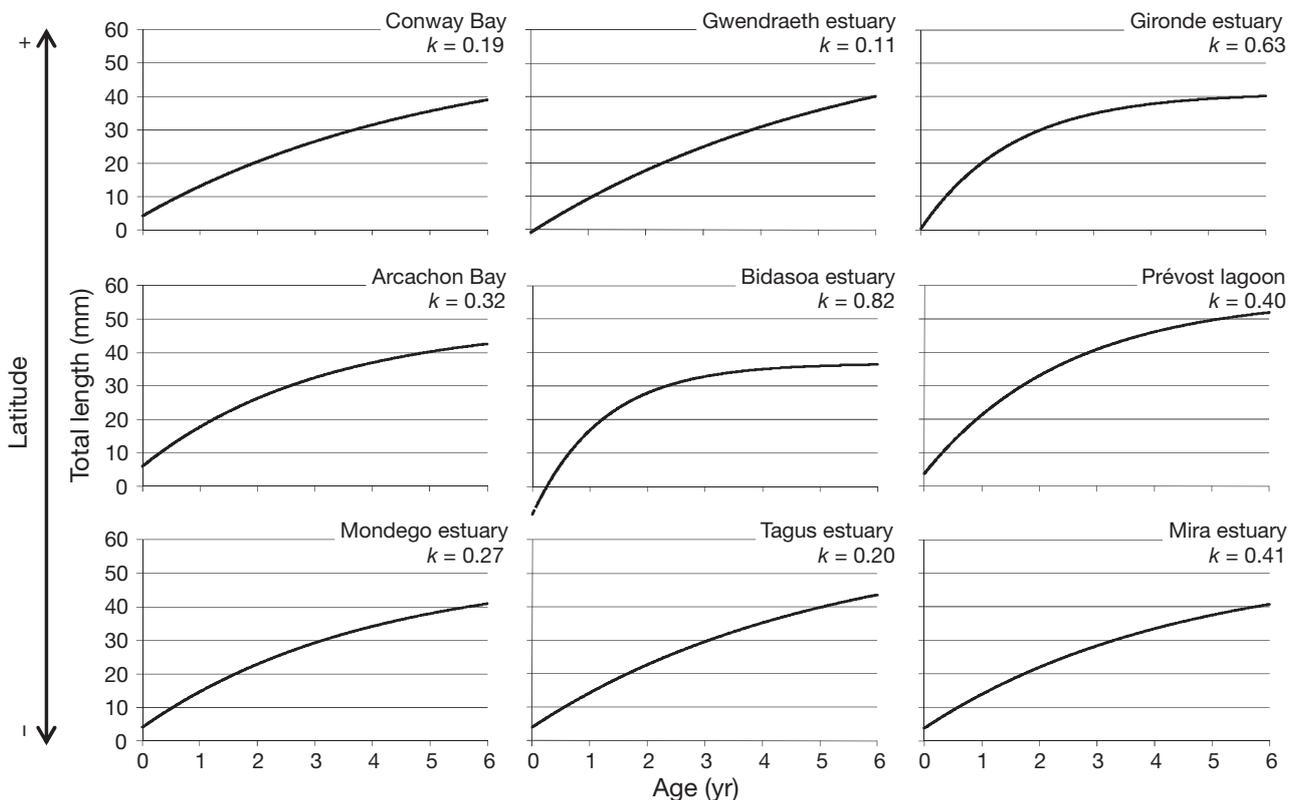

Fig. 7. *Scrobicularia plana.* Growth estimation (total length vs. age) using the von Bertalanffy equation on different populations along a latitudinal gradient. k: growth coefficient
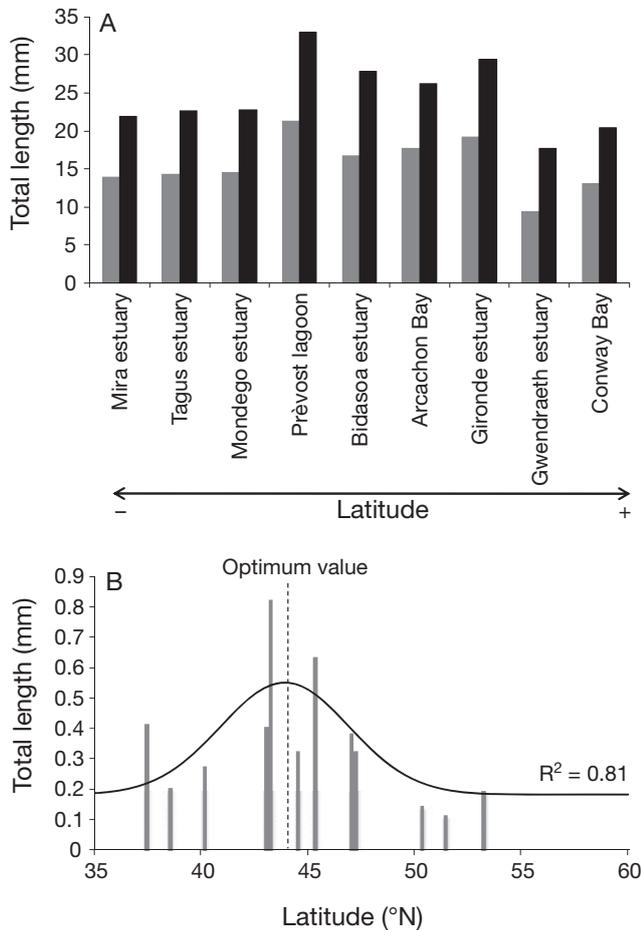
Fig. 8. *Scrobicularia plana*. (A) Total length at Year 1 (grey) and Year 2 (black) obtained from the von Bertalanffy growth estimation model applied to different populations, and (B) Gaussian distribution of total length at Year 2 along a latitudinal gradient

growth (k) were comparatively analysed using RDA, after running a DCA, in order to compare 12 *Scrobicularia plana* populations, relating them to temperature conditions, in order to outline the similarities of different geographic areas. A significant relationship between maximum temperature (T_{max}) and the biological variables was obtained ($p < 0.05$). By analysing the resulting ordination diagram (Fig. 9), similarities among populations within the same geographic area were highlighted and populations grouped according to their characteristics.

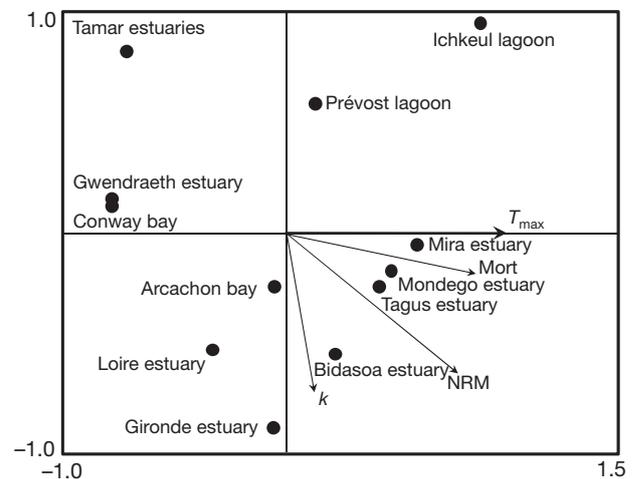The UK populations (Conway Bay, Gwendraeth Estuary and Tamar estuaries) form a group charac-

Fig. 9. *Scrobicularia plana*. Redundancy analysis showing relationship between monthly average maximum temperature (T_{max}), population dynamics (Mort: mortality; NRM: number of recruitment months) and growth (k) patterns in the 12 populations

Table 3. *Scrobicularia plana*. Mean population biomass (B), production (P) and P/B ratio for different populations along a latitudinal gradient, listed from north to south. AFDW: ash-free dry weight. na: not available

Location	Latitude	Habitat	B (g AFDW m^{-2})	P (g AFDW m^{-2} yr^{-1})	P/B ratio (yr^{-1})
Conway Bay	53° 15′ N	Seaward	46.24	13.41	0.29
		Marshward	4.37	2.97	0.68
Tamar estuaries	50° 25′ N	na	2.15	0.48	0.22
Arcachon Bay	44° 50′ N	Interior area (fine sand)	9.65	8.34	0.86
Bidasoa estuary	43° 22′ N	Estuary mouth (mud)	69.20	83.62	1.21
Prévost lagoon	43° 20′ N	Seaward (fine sand)	22.02	81.05	3.68
		Interior area (muddy sand)	1.31	6.54	4.99
		Interior area (muddy sand)	2.04	4.64	2.28
Mondego estuary	40° 07′ N	na	16.17	9.41	0.58
Tagus estuary	38° 50′ N	Interior area (marsh)	26.10	6.78	0.26
Mira estuary	37° 43′ N	Estuary mouth (sand)	4.75	1.76	0.37
		Interior area (sandy mud)	3.74	0.14	0.04
		Interior area (mud)	7.67	2.40	0.31
Ichkeul lagoon	37° 10′ N	Interior area (bare bottom)	34.27	12.17	0.36
		Channel mouth (marsh)	22.54	17.41	0.77

terised by short reproduction periods during summer, winter mortality and low k, reflecting low growth rates. The Gulf of Biscay (Gironde estuary, Arcachon Bay and Bidasoa estuary) populations are characterised by longer reproduction periods, summer mortality and high growth rates, forming another group. The Loire population is plotted near this group, resulting from similarities in the reproduction pattern, despite the existing differences in growth and mortality period. The Portuguese populations (Mondego estuary, Tagus estuary and Mira estuary) are grouped together, showing longer reproduction periods and summer mortality, while k is smaller than in the previous group. However, k values show that there are differences within this group. Finally, the Mediterranean populations (Prévost lagoon and Ichkeul lagoon) are plotted together and isolated from other groups.

DISCUSSION

Scrobicularia plana's ecological patterns are latitude-related, depending essentially on temperature, which regulates the reproductive cycle of the species and influences its survival, mortality, growth and production (Hughes 1969, 1971, Bachelet 1981, Guelorget & Mazoyer-Mayère 1983, Worrall et al. 1983, Essink et al. 1991, Sola 1997, Rodríguez-Rúa et al. 2003, Casagranda & Boudouresque 2005, Verdelhos et al. 2005, Raleigh & Keegan 2006, Mouneyrac et al. 2008). However, and despite the general latitudinal gradient, temperature is also dependent on local environmental conditions. We observed similar temperature patterns for locations at different latitudes, as in the case of the Mediterranean populations (Marseille and Tunisia).

The temperature increase after the cold winter months triggers gonad development (Paes-da-França 1956, Hughes 1971, Sola 1997, Guerreiro 1998, Rodríguez-Rúa et al. 2003, Raleigh & Keegan 2006, Mouneyrac et al. 2008) from a threshold value of ~8°C (Hughes 1971, Sola 1997, Raleigh & Keegan 2006) and influences its duration, lasting longer at higher latitudes and shortening towards the south.

Moreover, spawning is also dependent on temperature (Paes-da-França 1956, Hughes 1971, Sola 1997, Guerreiro 1998, Rodríguez-Rúa et al. 2003, Raleigh & Keegan 2006, Mouneyrac et al. 2008), occurring when favourable values are observed and, as a consequence, it shows a clear latitudinal trend. Usually, it occurs later in northern populations, for short periods during summer, while further south it may start ear-

lier, extending for longer time periods. In the south, spawning may show 1 or 2 main peaks, which is reflected in benthic recruitment, resulting in 1 or 2 cohorts yr^{-1} (Paes-da-França 1956, Hughes 1971, Sola 1997, Guerreiro 1998, Rodríguez-Rúa et al. 2003, Raleigh & Keegan 2006, Mouneyrac et al. 2008). Similar results have been observed for *Abra alba* (Dauvin 1986), *A. tenuis* (Dekker & Beukema 1999, Casagranda & Boudouresque 2005) and *Cerastoderma edule* (Gam et al. 2010), suggesting analogous reproduction patterns for several bivalve species.

As a general trend, the most abundant *Scrobicularia plana* populations were found between 40 and 45° N, near the middle of the geographic distribution of the species, decreasing towards the edges following a Gaussian distribution. This is probably a result of more frequent successful recruitments and lower mortality (Bachelet 1981, Guelorget & Mazoyer-Mayère 1983, Essink et al. 1991, Sola 1997, Verdelhos et al. 2005). Comparable results were registered in other bivalve species, such as *Tellina tenuis* (Dekker & Beukema 1999) and *Cerastoderma edule* (Genelt-Yanovskiy et al. 2010). These patterns suggest that a species is more abundant near the centre of its distribution range, declining towards the edges — the abundant-centre hypothesis (Sagarin et al. 2006).

The lower abundance for northern *Scrobicularia plana* populations is apparently a consequence of short successful benthic recruitments, occurring only in favourable years (Green 1957, Hughes 1970a, Essink et al. 1991), and of massive mortality episodes due to harsh environmental conditions during severe winters — extreme cold, high freshwater flows and low salinity (Hughes 1970a, Essink et al. 1991).

Further south, smaller recruitment peaks were described in the Tagus and Mira estuaries (Guerreiro 1998), leading to less abundant , albeit stable and well structured, populations. Thus, smaller populations could result in lower mortality rates when compared to larger northern populations. The Mediterranean populations (Prévost and Ichkeul lagoons) are mainly dominated by juveniles, depending on successful recruitments, which are much higher in the Prévost lagoon, leading to higher density populations (Guelorget & Mazoyer-Mayère 1983, Casagranda & Boudouresque 2005).

Several methods have been used for *Scrobicularia plana* growth estimation, and in the present study we fitted the available data to a von Bertalanffy growth model, using the same method as Bachelet (1981), in order to compare growth rates for diverse populations. However, care must be taken when analysing

and comparing different populations, since the resulting *k* value (Bachelet 1981) is merely growth coefficient and should not be regarded as a growth rate *per se* (MacDonald & Thompson 1988). In fact, the highest growth rate was observed in the Prévost lagoon (France), with individuals growing up to 33 mm in the second year, although the resulting *k* (0.404) was lower than in other populations.

Temperature influences the start and end of the growing season, which is longer at decreasing latitudes, and consequently the annual length increments are usually smaller at higher latitudes (Beukema et al. 1985, Beukema & Desprez 1986, Dauvin 1986). However, growth in *Scrobicularia plana* appears to follow a non-linear latitudinal gradient, but has a tendency to decrease towards its northern and southern distribution limits, showing a Gaussian distribution, with higher values between 40 and 45° N. This pattern was also observed for *Tellina tenuis* (Dekker & Beukema 1999), which showed higher growth near 51° N, decreasing towards the north and south.

Production and productivity estimates of a population are good evaluation methods of the functional importance of a species in the ecosystem (Bachelet 1982, Casagranda & Boudouresque 2005). Production is dependent on habitat conditions, population structure, stability and growth rates, being also highly influenced by sampling and estimation methods (Bachelet 1982, Sola 1997, Guerreiro 1998, Casagranda & Boudouresque 2005, Verdelhos et al. 2005). Therefore, high variability is often observed between populations and even for different sampling stations of the same ecosystem (Verdelhos et al. 2005), as in other bivalve species (Dauvin 1986, Casagranda & Boudouresque 2005).

The highest production values for *Scrobicularia plana* were obtained in the Bidasoa estuary and the Prévost lagoon, which may be related to both high recruitment success and growth of the species in those locations. On the other hand, exceptionally high *P/B* ratios were observed in the Prévost lagoon, in accordance with the high growth rates and shorter lifespan found in the lagoon (Guelorget & Mazoyer-Mayère 1983). Productivity is a measurement of the biomass renewal rate of the population (Bachelet 1982) and shows high intraspecific variability, related to the species' biological cycle on different locations, and usually, *P/B* ratio values tend to decrease both towards northern or southern latitudes.

Scrobicularia plana seems to show different life strategies along its distributional range, reflected in reproduction patterns, population abundance and dynamics, growth, and production. Throughout the

distribution range, diverse populations have to face different habitats, resulting from the interaction of environmental variables, both dependent on latitudinal gradient and on local environmental conditions, that define its main characteristics (e.g. temperature and precipitation regimes, food availability, sediment) (Sola 1997).

Populations in latitudes between 40 and 45° N seem to have the highest ecological performance for this species, showing extremely successful recruitment and the highest abundance values, growth rates, production and productivity. The ecological conditions in these areas appear to be optimal for this species, with less climatic extremes of temperature and precipitation, and propitious temperature regimes for gonadal development and growth, favouring highly energetic life patterns (Clarke 2003, Sagarin et al. 2006).

In contrast, populations further north and south show 'slower' life strategies, with less successful recruitment, lower abundance, significant mortality episodes and lower growth and productivity. This is certainly a result of poorer ecological conditions in areas closer to the edges of the species' geographic distribution. In fact, animals living at the biogeographic limits of the species' distribution are assumed to live on the limits of their adaptation capacities, showing poorer ecological performance and higher sensitivity to stress, when compared to animals living at the centre of its distribution (Hummel et al. 1998, Sagarin et al. 2006, Beukema et al. 2009).

The present study is a review of published research on *Scrobicularia plana* along a latitudinal gradient, with further analysis of those studies' results. One of the main problems inherent to this type of study is the extensive bibliographic research required, in order to gather a comprehensive data set to allow a robust analysis. In this review, the main limitation was the need to use published data and results, facing the impossibility of using the raw data from the referred studies.

However, a thorough review and comparison were performed and with the analysis of *Scrobicularia plana* ecological patterns, throughout part of its distribution range, important results were achieved. Most latitudinal-gradient studies provide a powerful tool that can be used to understand temperature-dependent ecological patterns, as well as to predict adaptive tolerance and responses to climate change (Jansen et al. 2007).

Major impacts are expected on populations living on the edges of their geographic distribution, affect-

ing abundance and population dynamics and even causing shifts to distribution limits of a species (Dekker & Beukema 1999, Jansen et al. 2007, Beukema et al. 2009). Moreover, with increasing climate change, variations in temperature patterns are expected, altering both the latitudinal gradient and seasonality. This may lead to significant changes in the population dynamics throughout its geographic range, as already observed for *Mytilus* sp. and *Macoma balthica* (Jansen et al. 2007, Beukema et al. 2009). Furthermore, increased knowledge of the ecological patterns and life strategies is achieved with this kind of study, which may be useful to future approaches to *Scrobicularia plana* ecology assessment.

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