

REPRODUCTION, POPULATION DYNAMICS, GROWTH AND PRODUCTION OF *SCROBICULARIA PLANA* DA COSTA (PELECYPODA) IN THE BIDASOA ESTUARY, SPAIN

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Key words: *Scrobicularia plana*, population dynamics, recruitment, production, Biscay Bay.

ABSTRACT

The breeding cycle, recruitment, population dynamics, growth and production of *Scrobicularia plana* were studied at one station in the Bidasoa estuary (SE of the Biscay Bay, Spain) during a period of 3 or 4 years. To complete this study, the reproduction for a period of 1 year was analysed at two other sites of the estuary. At none of the stations important differences in spawning activity were observed between the different years. The animals reproduced for the first time when they reached the age of two years. The histological data and the recruitment analysis showed only one spawning period between June and mid-September, with a peak in July-August. This breeding pattern differs from those shown by other southern European populations. The recruitment of spat (0.25-0.50 mm) occurred from June-July to October-December in different years. The population showed different annual patterns of density and population structure, depending on recruitment success. Growth was most rapid in spring and summer. The bivalves reached a mean length of 21.8 mm at the age of approximately 16 months; in the following year they grew to 30 mm. The growth during the life span fitted the theoretical growth equation of Von Bertalanffy. Annual production was in the range of 59.0-83.4 g AFDW m⁻² year⁻¹. The P/B ratios of the population varied between 0.84 and 1.48 (1.06 ± 1.36; \bar{x} ± 95% C.I.).

INTRODUCTION

This study was undertaken within the framework of the European programme COST 647 (HEIP *et al.*, 1986). The purpose of this programme was to distinguish between natural variability and man-induced changes in reproductive biology and population dynamics of the key species of the shelf waters. To achieve this, studies of geographical distribution and its control, and of the possible existence in latitudinal trends in the biological parameters of the populations over the geographical distribution of a species are necessary (LEWIS, 1986). The tellinid bivalve *Scrobicularia plana* was selected as one of the key species by the Intertidal Sediment Working Group of the COST 647 project (ESSINK *et al.*, 1991).

Scrobicularia plana (Da Costa 1778) is a euryhaline, littoral species widely distributed throughout Europe and other geographical regions (TEBBLE, 1976). The species is a selective deposit-feeder which can also feed on suspended matter at high tide (HUGHES, 1969). It can be an important link in the food chains of estuaries and coastal lagoons (HUGHES, 1970b; BACHELET, 1982; GUERLORGET and MAZOYER-MAYÈRE, 1983). In the Bidasoa estuary (Fig. 1), *S. plana* shows highest densities in the intertidal muddy and muddy-sand zones (BORJA, 1988). These zones are generally dominated by the 'Macoma-reduced community' (PETERSEN, 1913; 1918) where *S. plana*, *Hediste diversicolor* and *Hydrobia ulvae* are the principal components of the biomass (SOLA, 1994).

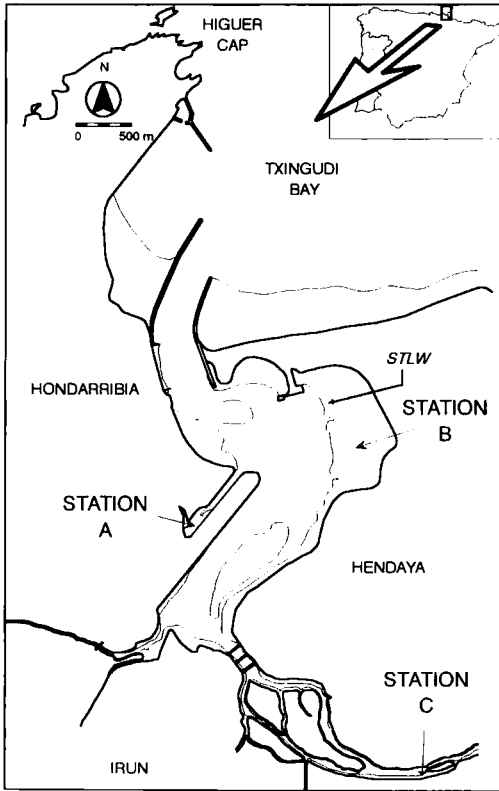


Fig. 1. Bidasoa estuary with sampling stations A-C. STLW: Spring Tide at Low Water.

The population biology of the species is well studied, particularly in northern Europe (HUGHES, 1970a; WARWICK and PRICE, 1975; WORRALL and WIDDOWS, 1983; WORRALL *et al.*, 1983; ZWARTS, 1986; 1991). Compilation of the COST 647 data by ESSINK *et al.* (1991), including studies from Germany to France over periods of 11-18 years, shows a latitudinal variation in the recruitment pattern (with one cohort per year in the northern localities and 2-3 cohorts per year in the southern localities), recruitment failures after severe winters, strong reductions in abundance mostly over winter, and decreasing density due to occasional sediment instability.

Data on invertebrate reproduction show that the spawning periods of the southern populations are longer than those of higher latitudes. These longer spawning periods seem to be linked to the North-South temperature gradient which runs along the European Atlantic coast (ORTON, 1920). Studies carried out on invertebrates (BOWMAN and LEWIS,

1986; KENDALL and LEWIS, 1986; LEWIS, 1986; BHAUD, 1972; HARVEY and VINCENT, 1989; PEÑA, 1995) showed that the northern populations are characterised by short, mid-summer breeding periods. Towards the south breeding periods are lengthened and occur later, sometimes throughout the winter, but with lowest activity or absence in mid-summer. These latitudinal and geographical differences in breeding cycles could be related to the successful settlement and survival of spat during a critical stage of their growth.

S. plana populations along the European Atlantic coast show three different patterns of reproduction, viz. one period per year, mostly in northern areas (LEBOUR, 1938; STOPFORD, 1951; HUGHES, 1971; RASMUSSEN, 1973; WARWICK and PRICE, 1975; WORRALL *et al.*, 1983), two periods per year, in the Gironde estuary, Bay of Arcachon (BACHELET, 1981) and Tagus (PAES-DA-FRANCA, 1956), and one prolonged period per year, in the Mira and Tagus estuaries (SILVA, 1991).

S. plana has a long planktonic stage. At 18°C the veliger larvae take one month to reach the settling pediveliger stage, and several further weeks to complete metamorphosis to become siphoned juveniles (FRENKIEL and MOUÉZA, 1979).

The Bidasoa estuary is located between the northern and southern populations of *S. plana* along the Atlantic coasts, and is an important geographical location to examine the existence and nature of latitudinal trends in the biology of the species. The aim of this study was to determine the biological characteristics (breeding cycle, recruitment, population dynamics, growth and production) of the Bidasoa estuary population and compare them with those from other geographical regions.

MATERIALS AND METHODS

The Bidasoa estuary is situated in the SE of the Bay of Biscay (43° 20'-23' N; 1° 44.5'-48' W). It covers an area of 2.8 km², of which approximately 50% is intertidal. The estuary receives untreated sewage of approximately 70,000 inhabitants (approximately 15,000 more in summer) of the Spanish communities of Hondarribia and Irún. Hendaya (France), with approximately 15,000 inhabitants, purifies its sewage before discharging it into the estuary. The area is slightly industrialised (SOLA, 1994).

Sampling was carried out at 3 intertidal stations (Fig. 1). At station A studies on reproduction, po-

pulation dynamics, growth and production, and at stations B and C only studies on reproduction were performed. Station A was situated on a platform of homogeneous sediments, with a predominance of fine sediments (percentage of particles smaller than 63 μm always higher than 73%) and high levels of organic matter (10.5% in the top layer of 2 cm; 9% at a depth of 20 cm). The station was situated approximately 1.5 m above the maximum low water level. The surface temperature of the water, taken in the afternoon, varied between 10-12°C in winter and 23-26°C in summer. Station B was located in the largest intertidal area in the estuary. The sediment, sandy mud, was covered by the same plant species as at station A. Station C, with muddy sand deposits, formed the upper limit of the distribution of *S. plana* with the largest specimens in the estuary.

Sampling

At station A, sampling consisted of monthly (from February 2, 1987 to December 29, 1989) and half-yearly (June and December of 1990 and 1991) collections of 0.5 m² (1987-1988) or 0.3 m² (other years) of sediment using a box of 0.1 m² which was pushed into the sediment to a depth of 25-30 cm. At this depth the sediment is more compact and no live specimens were observed. The sediment was sieved through a 1 mm mesh and the layers of 0-5 cm and 5-30 cm sediment were sieved separately. The bulk residue was preserved in 10% formaldehyde in sea water.

The settlement study was based on monthly collections (exceptionally fortnightly) of 3-5 samples of superficial sediment (to 2 cm depth) from November 2, 1988 to December 20, 1990 at Station A, using a core of 10 cm². The samples were washed through a 200 μm mesh. The maximum shell length of each specimen was measured to the nearest 0.1 mm using a dissecting microscope with an ocular micrometer.

The reproductive cycle was studied by monthly histological analysis of 10-12 adult specimens on each sampling date. The specimens were collected monthly (exceptionally every 15 days: see Figs. 2 and 3) at Station A between November, 1987 and October, 1990, and at Stations B and C between September, 1989 and October, 1990.

Gonad condition index

At the start of the study (1987-1988), gonadal tissue was fixed in 10% formaldehyde. Later, giving better results, the tissues were fixed for 24 hours in Bouin's fluid and stored in 70% ethanol. Before

Table 1. Scheme of classification of stages of gonad condition.

Stage	Index value	Characteristic features
0	0.00	Resting or spent gonad empty follicles, no gametes present
1	0.25	Developing stages onset of gametogenesis; islands of germinal tissue appear in the matrix of dense connective tissue; no ova or spermatozoa are present at this stage
2	0.50	marked increase of the gonadal tissue; developing gametes appear; no ripe gametes detectable
3	0.75	gonad with maximum proliferation and preponderance of ripe gametes within the follicles
4	1.00	gonad full of ripe ova or spermatozoa
-3	0.75	Spawning stages after spawning reduction in the number of gametes; ova are rounded rather than polygonal
-2	0.50	further reduction of genital tissue
-1	0.25	only a few residual gametes; cytolysis may be in progress

embedding in paraffin wax they were dehydrated with ethanol, and 5-15 μm transverse sections were made at several levels along the dorsal-ventral axis of the gonads; they stained in haematoxylin-eosin.

The gonad condition was classified according to onset and duration of the reproductive cycle. The histological sections were arbitrarily classified, based on their degree of development and density of gametes, into eight stages of gonad condition, with an index ranging from 0 to 1. These stages are described in Table 1. The degree of gonadal development of the population was estimated by calculating a mean Gonad Condition Index (GCI) for each sample by multiplying the number of individuals in each stage by its index value and dividing the sum of these products by the total number of individuals in the sample (SEED, 1975; SEED and BROWN, 1977).

Age classes

The group of specimens which had not passed its first winter (December 31) has been taken as age class 0; class 1 is the group which had passed only one winter, but not a second; etc. The classes 0, 1 and 2 could be distinguished easily by eye. Distinction of older classes, however, was more difficult due to weakly developed growth rings or extra (disturbance) rings in these latitudes.

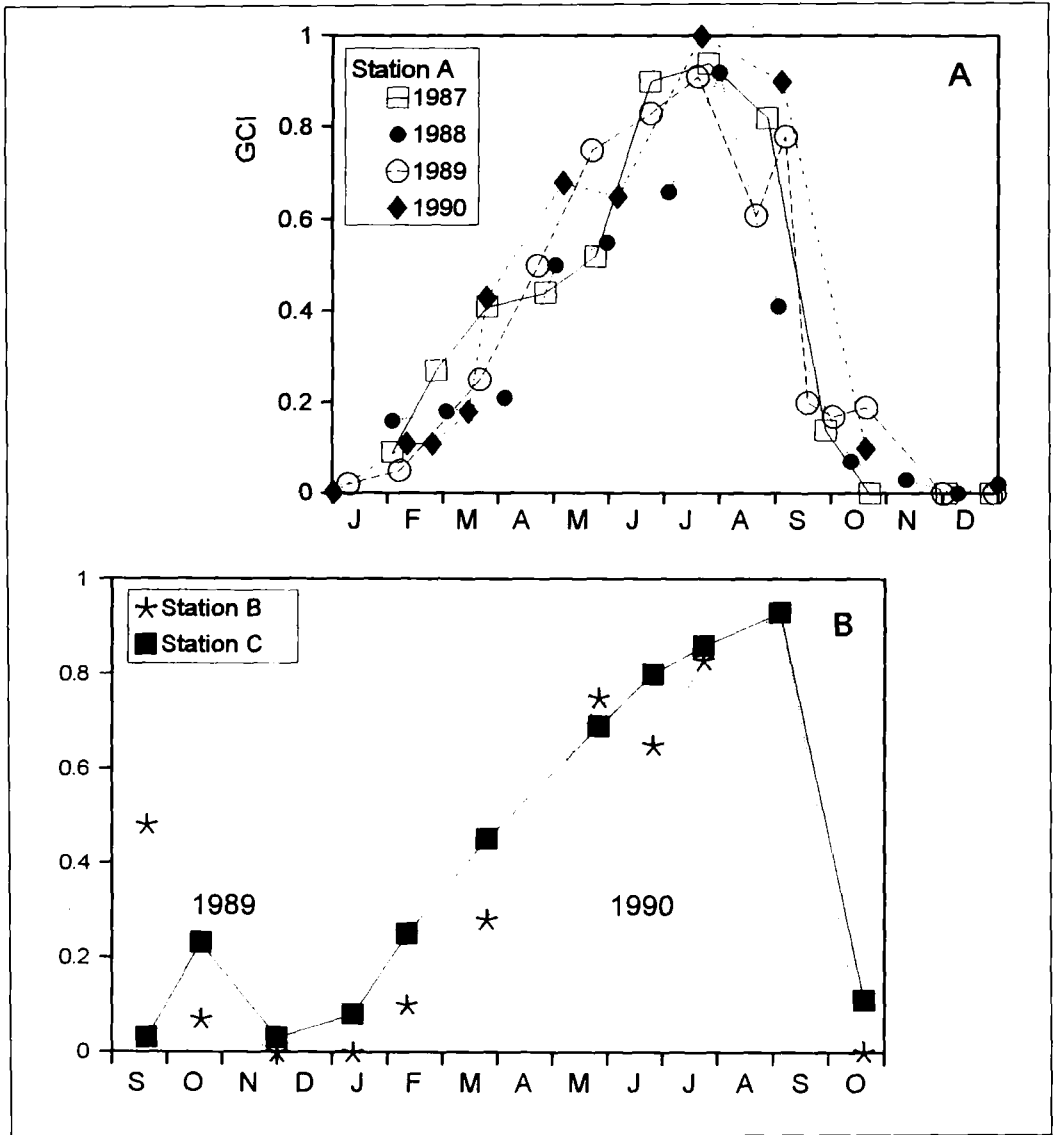


Fig. 2. Seasonal variation of gonad condition index (GCI) of *Scrobicularia plana* at station A from 1987 to 1990 (A), and at stations B and C from September, 1989 to October, 1990 (B).

Production

Production was calculated by regression analysis of the logarithm of Ash Free Dry Weight (AFDW) and shell length. AFDW was determined as weight loss after two hours of incineration at 550°C of formalin-preserved (for several months) specimens, dried at 100°C for 24 hours and after decalcification in a 10% solution of HCl (RUMÖHR *et al*, 1987). The regressions were calculated se-

parately for each of the monthly samples in 1989 and applied in the production calculations to each of the monthly samples for the whole study period 1987-1989. The production was estimated according to the method II described by CRISP (1971), modified by SIEGISMUND (1982).

Growth

The growth of shell length was calculated

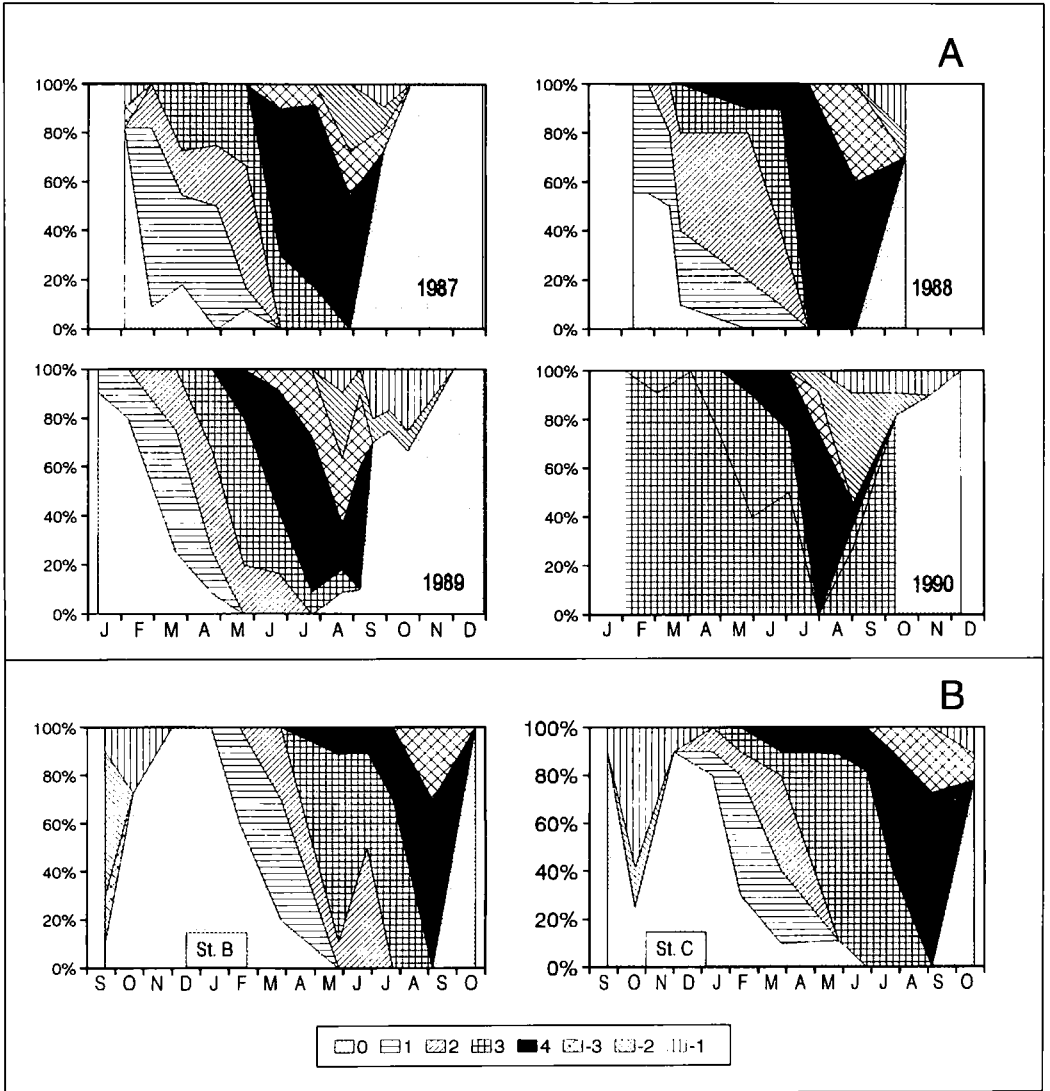


Fig. 3. Percentage of *Scrobicularia plana* at station A at different stages of gonad development from 1987 to 1990 (A), and at stations B and C from September, 1989 to October, 1990 (B) (0 = resting; 1, 2 and 3 in gonadal development; 4 = mature gonads; -3, -2, -1 with gonadal recession).

according to the VON BERTALANFFY (1938) equation:

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

where L_t = shell length at time t , L_{∞} = maximum or asymptotic length, t_0 = hypothetical age when $L_t = 0$, and K = a growth constant. K and L_{∞} were calculated with the method of LOCKWOOD (1974). The growth values used to fit the

Von Berta-lanffy equation were obtained from specimens that showed clearly defined growth rings (age classes 3, 4, 5 and 6) and from the average length in the age classes 0, 1 and 2, estimated at the end of the year. September 1 was taken as a 'mean' birth date for the different generations.

The deviation S_{log} of the empirical growth data (L_t) from those predicted by the different models cited above (L'_t) was estimated from

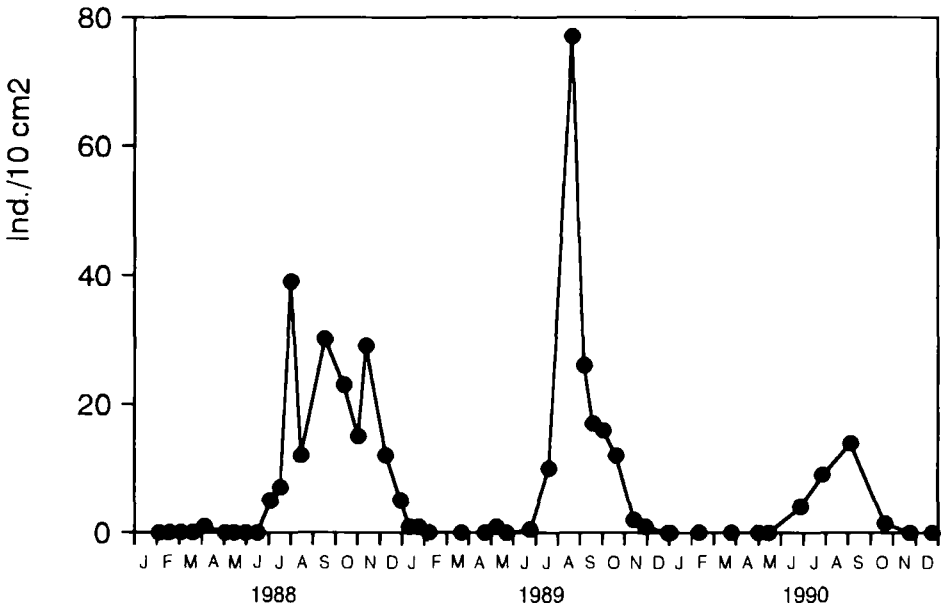


Fig. 4. Monthly abundance of *Scrobicularia plana* (length < 0.5 mm) at station A in 1988, 1989 and 1990 (sieve size = 200 μ m).

the logarithmic deviation proposed by KRÜGER (1973):

$$S_{\log} = \sqrt{\frac{\sum (\log_{10} Lt - Lt')^2}{n-3}} \quad (2)$$

where n is the number of age classes.

The level of adjustment for the observed growth values to the theoretical functions were estimated using 'the percentage mean deviation' ($S_{\%}$) expressed by the equation (KRÜGER, 1973):

$$S_{\%} = (10^{S_{\log}} \cdot 100) - 100 \quad (3)$$

RESULTS

Breeding cycle

Gonadal tissue was present throughout the visceral mass, from the hepato-pancreas to the pedal ganglion. The tissue first ripened after two years at a shell length of approximately 25 mm. Of the 338 animals collected from the three stations and examined during March-August, 170 were female and 168 male, giving a female/male ratio of 1.01.

At Station A gonadal production started in January-February (Fig. 2A). After March the GCI rapidly evolved to more mature stages. In general,

after May there were individuals with mature gonads (stage 4) and in June some had already spawned (stage -3) (Fig. 3A). The most intense reproductive activity was in June-August. In August and September the stages of gonadal regression (-3, -2 and -1) increased and individuals appeared with totally empty follicles. In October-December most individuals were in a stage of gonadal rest with empty follicles. Unlike other years, in 1987 a stage of gonadal regression was already observed in some specimens in February (there were no data from January).

This reproductive cycle at Station A was essentially the same in all four years of this study. At stations B and C a similar cycle was observed (Figs. 2B and 3B).

Settling

The size of the animals the time of settling varied between 0.25 and 0.3 mm. Occasionally, settled individuals of 0.15 and 0.20 mm were observed. The first always appeared in June-July (Fig. 4). The end of the settlement period, however, varied from year to year. In December, 1988 the intensity of settling decreased notably, although settling continued till January of the following year. In 1989, settling stopped towards the end of November, and in 1990 the last settling individuals were recorded in October. The maximum

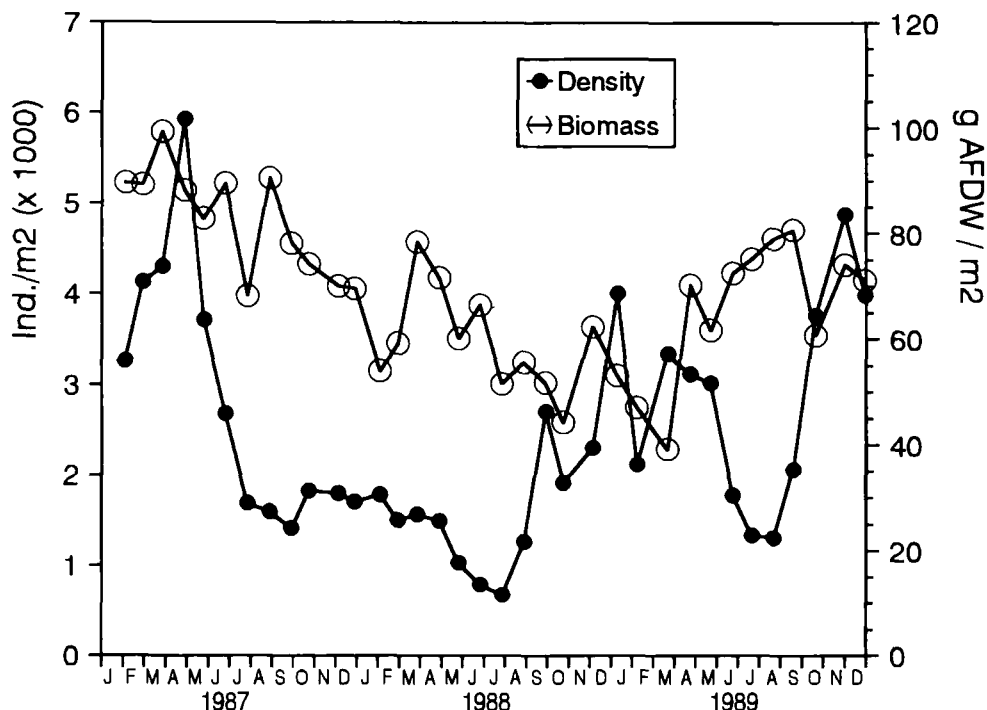


Fig. 5. Monthly estimates of density and biomass for *Scrobicularia plana* at station A during 1987 to 1989.

annual densities appeared on July 31, 1988, August 21, 1989 and September 4, 1990. Only two settling specimens were recorded outside the normal settling periods, one at April 4, 1988 and the other at May 9, 1989.

Population structure and dynamics

During 1988 and 1989, the total density of *S. plana* at station A decreased from the start of the year, reaching a minimum during summer

(Fig. 5). During autumn the density increased due to the annual recruitment, reaching a maximum in October to December. In 1987, density increased from February to the end of April, reaching the maximum density of the study period (5,892 ind m^{-2}); then it decreased until September and increased again in October to December. The minimum density observed was in July, 1988 (676 ind m^{-2}) (Table 2). The density recorded in June, 1990 was $1,093 \pm 510$ ind m^{-2} ($\bar{x} \pm 95\%$

Table 2. Minimum, maximum and annual mean density and biomass of *Scrobicularia plana* at station A during 1987 to 1989.

Density	1987		1988		1989	
	Ind. m^{-2}	Date	Ind. m^{-2}	Date	Ind. m^{-2}	Date
minimum	1,418	September 28	676	July 31	1,307	August 21
maximum	5,892	April 28	2,705	October 11	4,888	December 1
mean	2,846		1,559		2,892	
Biomass	g. m^{-2}		g. m^{-2}		g. m^{-2}	
		Date		Date		Date
minimum	68.20	July 27	44.31	November 11	39.19	March 22
maximum	99.33	March 27	78.38	April 4	80.66	September 18
mean	83.40		59.03		65.17	

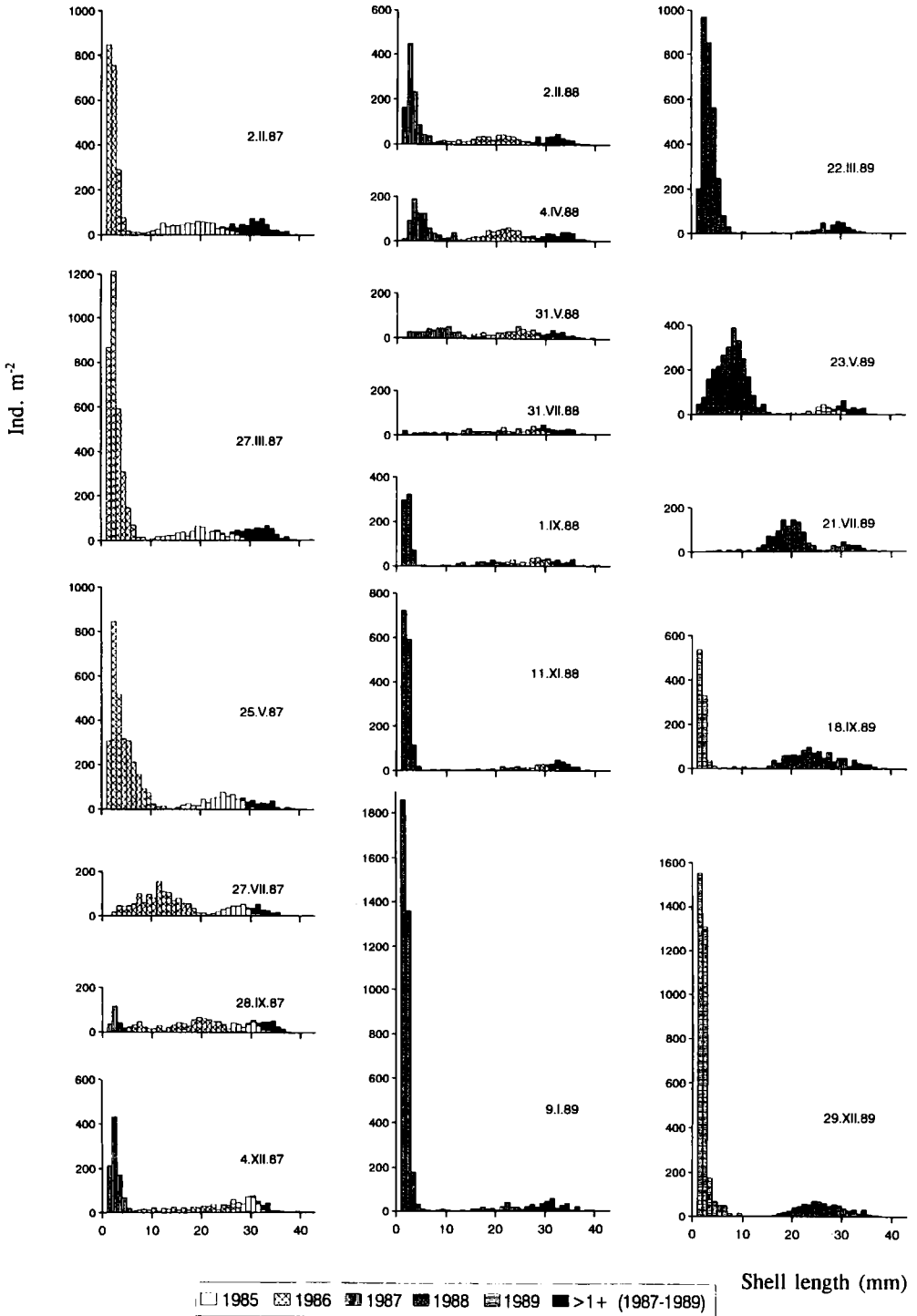


Fig. 6. Bimonthly size frequency distributions of *Scrobicularia plana* at station A. The different annual generations and the age classes older than 2 are indicated by different shading.

Table 3. Estimation of secondary production (SIEGISMUND, 1982) in $g\ m^{-2}$ AFDW decalcified for the age classes of *Scrobicularia plana* at station A during the periods February 2, 1987 to December 28, 1987, December 28, 1987 to January 9, 1989 and January 6, 1989 to December 29, 1989. \bar{B} = average biomass; P = somatic production. For age class 0 the parameters (\bar{B} , $\Delta\bar{B}$, P and P/\bar{B}) refer to the period of existence (5 months). For the other age classes and for the total population the parameters refer to annual periods.

Year	Class	\bar{B}	$\Delta\bar{B}$	P	P/\bar{B}
1987	0	0.103	0.280	0.283	2.748
	1	10.264	16.288	49.185	4.792
	2	28.513	9.529	36.856	1.293
	>2	44.582	-43.744	18.768	0.423
	total	83.402	-17.645	105.092	1.260
1988	0	0.156	0.263	0.264	1.692
	1	4.330	8.450	12.993	3.001
	2	21.824	9.506	22.635	1.037
	>2	32.799	-34.638	13.657	0.416
	total	59.025	-16.676	49.549	0.839
1989	0	0.253	0.434	0.541	2.138
	1	20.401	36.380	73.893	3.622
	2	14.976	6.093	11.849	0.791
	>2	29.689	-24.916	9.929	0.334
	total	65.172	17.990	96.212	1.476

C.I.) and in June 1991 $1,563 \pm 693\ ind\ m^{-2}$. The low densities observed in December, 1990 ($2,047 \pm 610\ ind\ m^{-2}$) and in 1991 ($1,670 \pm 796\ ind\ m^{-2}$) possibly indicate a small recruitment during these two years. The biomass varied between $39.2\ g\ AFDW\ m^{-2}$ (March, 1989) and $99.3\ g\ AFDW\ m^{-2}$ (March, 1987) (Table 2).

The frequency distributions for the first months of 1987 to 1989 (Fig. 6) show three age groups. The first and most abundant is made up of small specimens (<10 mm length); the second ranges from 10 to 30 mm, and the third ranges from 25-42 mm. In general the abundance of age class 1 during the first four months of the year increased in 1987 and decreased in 1988 and 1989. The age classes 1 and 2 showed great size increases during spring and summer. After July-August the recruitment of age class 0 began, reaching the maximum density at the end of the year. In 1988 and in 1989, recruitment of age class 0 was very high in comparison with that in 1987 (Fig. 6), causing age class 1 to be present in low numbers during most of 1988, as well as age class 2 during 1989.

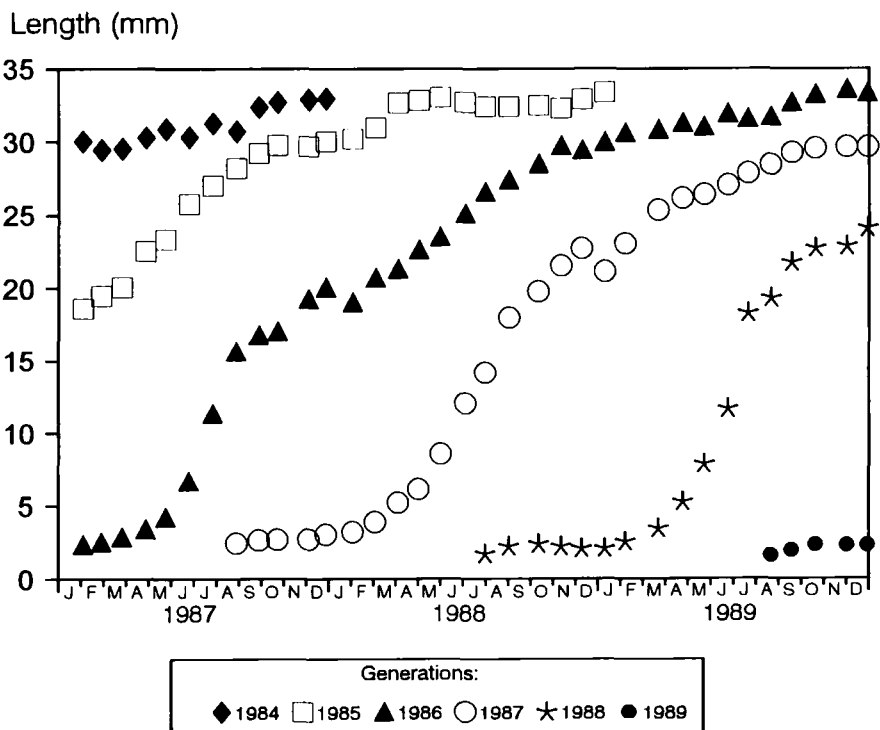


Fig. 7. Monthly variation in average length (mm) for the age classes 0, 1, 2 and 3 for *Scrobicularia plana* during 1987 to 1989 (Station A)

Production

The annual production of the *S. plana* population at station A (Table 3) was strongly influenced by the population structure. When the age class 1 was well represented (1987 and 1989) the total annual production was considerably higher. The low recruitment in 1987 led to a much lower production in 1988. The production of age classes 2 and older diminished from 1987 to 1989 as a function of the reduction of their average biomass per m². The ratio P/\bar{B} for the whole population gave values between 0.84 (1988) and 1.48 (1989). With the exception of group 0, the values of P/\bar{B} decreased whereas its age increased (Table 3).

Growth

Age class 0 showed at station A a slight increase in length during the first months after recruitment (Fig. 7). After the first winter, growth was exponential, especially during spring and summer. It slowed down in autumn and winter. This growth pattern was roughly repeated during the following year (age class 2). Age class 3 did not show this sigmoid growth curve, but a more irregular one, possibly owing to the difficult identification of the advanced age classes 3 and older. In any case the data for the age class 3 was obtained only from specimens that showed clearly defined growth rings. The Von Bertalanffy equation resulted in:

$$L_t = 36.7522 (1 - e^{-0.8146 (t - 0.2554)}) \quad (4)$$

The points of the curve (Fig. 8) correspond to the values in Table 4. The logarithmic deviation (S_{\log}) was 0.0169 and the average percentage for the deviation ($S_{\%}$) was 3.97.

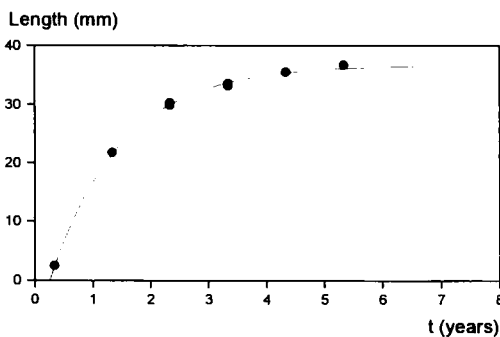


Fig. 8. Von Bertalanffy growth curve for the *Scrobicularia plana* population at station A.

Table 4. Average length (mm) of different age classes for *Scrobicularia plana* at station A. Asterisk: average of the annual averages at the end of the year; otherwise: average of the number of growth rings; n = number of samples (*) or of measurements of individuals; SD = standard deviation.

Age class	n	L	SD
0*	3	2.5	0.4
1*	3	21.8	1.7
2*	3	29.9	0.2
3*	3	33.3	0.2
2	33	30.4	1.4
3	21	33.6	0.9
4	16	35.6	0.8
5	12	36.8	0.6

DISCUSSION

Reproduction

The Bidasoa estuary population of *S. plana* showed a reproduction pattern similar to that of the northern populations (Table 5). According to HUGHES (1971) and ESSINK *et al.* (1991) the differences in the prolongation of the reproductive cycle of *S. plana* would be due to latitudinal, thermal differences along the Atlantic coast. Results obtained by BACHELET (1981) and SILVA (1991) seem to confirm this hypothesis. However, as BACHELET (1981) indicated, the late recruitment observed by GUERLORGET and MAZoyer-MAYÈRE (1983) on the French Mediterranean coast and by ELKAÏM (1976) in the Moroccan estuary of Bou-Regreg (August-September) would invalidate the relation between the spawning period and latitude (temperature).

According to SILVA (1991), the populations of *S. plana* in southern latitudes (Gironde estuary and further south) have different patterns of reproduction with the possibility of more than one annual spawning (and recruitment) period. It must be admitted that differences observed between different populations obey, in addition to latitudinal differences clearly related to temperature, to local differences related to specific characteristics of each site, such as food supply and even irregularities in temperature caused by *e.g.* upwelling. SASTRY (1970) showed that the timing of breeding of the scallop *Aequipecten irradians* is related to geographical differences in food availability and temperature. WORRAL *et al.* (1983) demonstrated that the reproduction of *S. plana* may depend on the algal spring bloom in the water column. At one site (Gannel) the population matured faster and spawned earlier than at the other two sites (Lynher

Table 5. Spawning periods of *Scrobicularia plana* in different sites of European and Moroccan coasts (** spawning period; \$\$ presence of larvae in the plankton; ++ recruitment).

Site	Months												Author
	J	F	M	A	M	J	J	A	S	O	N	D	
Isefjord (Denmark)	RASMUSSEN (1973)
Conway (Wales)	HUGHES (1971)
Plymouth (England)	LEBOUR (1938)
Liverpool (England)	STOPFORD (1951)
Lynher (England)	WARWICK and PRICE (1975)
Cornwall (England)	WORRALL <i>et al.</i> (1983)
La Gironde (France)	..	**	**	**	**	**	**	**	**	BACHELET (1981)
Arcachon (France)	**	**	**	**	BACHELET (1981)
Prévost (France)	GUELORGET and M. (1983)
Bidasoa (Spain)	This study
Tajo (Portugal)	**	**	**	**	**	**	**	PAES-DA-FRANCA (1956)
Tajo (Portugal)	**	**	**	**	**	**	SILVA (1991)
Mira (Portugal)	**	**	**	**	**	**	SILVA (1991)
Bou Regreg (Moroc.)	ELKAÏM (1976)

and E. Looe). Probably, at the first site adequate food was only available owing a shorter period than at the other localities, necessitating a more rapid gametogenesis, culminating in earlier spawning (WORRALL *et al.*, 1983).

Population dynamics

Density and biomass of the population of *S. plana* in the Bidasoa estuary are high as compared with the results of other studies. For a station of fine sand located in the lagoon of Prévost (French Mediterranean) GUELORGET and MAZOYER-MAYÈRE (1983) reported the exceptional high annual average density of 4,901 ind. m⁻² and the annual average biomass of 123 g DW m⁻². Among the local factors that could influence the extraordinarily high numbers in the Bidasoa estuary we can point out (1) the stability of the sediment (SOLA, 1994), an important factor for the development of deposit-feeding populations (WOLFF, 1973; BACHELET, 1980); (2) the high organic matter content of the sediment, favouring the development of bacterial populations (DALE, 1974) that form the basis of the diet of deposit-feeders (LOPEZ and LEVINTON, 1987); (3) the low numbers of competing bivalves and predators on adult individuals (SOLA, 1994). On the other hand, the high densities and large biomasses of the Bidasoa population could also be related to the temperature regime at its southern position in the center of the geographical distribution of *S. plana*. This may result in less recruitment failures (ESSINK *et al.*, 1991), more protracted breeding periods, a faster growth, and higher densities of individuals

of smaller size and shorter life span (LEWIS, 1986; PEÑA, 1995). As migration seems to be of little importance in this species (HUGHES, 1970b), its population dynamics is principally governed by timing and degree of mortality, and by variability in recruitment.

In the Bidasoa estuary the recruitment (established by means of a 1 mm sieve) occurred throughout autumn and winter. In the Gironde estuary and Arcachon bay (France), and in the Mira estuary (Portugal), protracted recruitment periods were also found (BACHELET, 1981; SILVA, 1991), although in spring and summer. This variation in recruitment period is caused by differences in spawning period; the French and Portuguese populations showed a first spawning period in winter-early spring allowing an earlier recruitment in spring-summer. There is no evidence of primary and secondary settlement in *S. plana* such as has been described in *Macoma* species (BEUKEMA and DE VLAS, 1989; CUMMINGS *et al.*, 1993) which can get resuspended on a mucus thread if their primary settlement site is unsuitable.

The Bidasoa population, however, showed an extraordinary increase of age class 1 towards the end of the spring in 1987, which was not observed in 1988 and 1989. Such year-to-year variation is well known (THORSON, 1957). An explanation could be slow growth during the first months of 1987, by which the majority of the individuals is too small to be retained on the sieve (1 mm mesh). This might be connected with the low water temperature (SOLA, 1994) during these months; during

the period January to March of 1987 to 1989 the number of days in which the air temperature fell under 0°C was 25 in 1987, 3 in 1988 and 6 in 1989. There is also the possibility of a delay or prolongation in the reproductive period in 1986 (SOLA, 1994) which would result in a late recruitment during the first months of 1987.

Production

A latitudinal trend in secondary production can be observed for populations of *S. plana* (HUGHES, 1970a; WARWICK and PRICE, 1975; MAYÈRE 1979; BACHELET, 1982; GUELORGET and MAZOYER-MAYÈRE, 1983; SILVA, 1991). This could be related to higher growth rates in southern latitudes, as shown by BACHELET (1980) for *Macoma balthica*, and may also hold for *S. plana*. In spite of the fact that P/B is reasonably constant for a certain species (WATERS, 1977), it can vary according to the relative composition of the population in the different age classes (BURKE and MANN, 1974; GUELORGET *et al.* 1980; BACHELET, 1982) and to the number of annual generations (WATERS, 1977). As demonstrated before, the ratio P/B is higher greater in age class 1 than in 2 and older, which is the same as saying that for any given average biomass the assimilation of food by the younger generations is superior to that of adults.

Growth

In the Bidasoa estuary growth rings are produced between December and February when the water temperature is lowest (12-13°C). As the individuals get older the earlier growth rings become less visible on the outside and in many cases disturbance rings are formed. LAMMENS (1967), SALZWEDEL (1979), RAMON and RICHARDSON (1992), GASPAR *et al.* (1994) and other authors have shown that in several species of bivalves these extra rings can be produced at summer seawater temperature (24-26°C in July and August in the Bidasoa estuary). The problem of age determination is more serious in southern regions, such as the Bidasoa estuary, where winter conditions are not as marked as in northern countries and do not provoke a sufficient decrease in metabolism to form clearly visible winter rings. Moreover, the protracted recruitment period in the Bidasoa estuary complicate growth

and production analysis due to the differences between early and late settlers.

BACHELET (1981) analysed the parameters of the Von Bertalanffy growth curves in various populations of *S. plana*, which resulted in K values of 0.139 (Wales; GREEN, 1957), 0.194 (Wales; HUGHES, 1970b), 0.320-0.380 (Brittany, France; CHASSÉ, 1972), 0.070 (England; WARWICK and PRICE, 1975), 0.322 and 0.625 (resp. Arcachon Bay and Gironde estuary, France; BACHELET, 1981). BACHELET advocated further studies in other latitudes that would permit the confirmation of the existence of a latitudinal trend, with growth rates increasing southwards, as has been quoted in other bivalves (BROUSSEAU, 1979; BACHELET, 1980; 1981; IGLESIAS and NAVARRO, 1990). Our results seem to support this hypothesis as the growth rate constant K estimated for the Bidasoa estuary (0.815) is the highest mentioned in the literature. Nevertheless, the growth parameters calculated by SILVA (1991) in Portuguese estuaries of the Tagus (K = 0.2) and Mira (K = 0.229-0.494, range for three stations) would seem to invalidate the hypothesis. In any case it is reasonable to admit that environmental conditions in each biotope, such as salinity, pollution, temperature, food availability and position on the tidal area would produce breaks in the hypothetical latitudinal gradient of the growth constant K (BROUSSEAU, 1979; BACHELET 1981; SILVA 1991; HUMMEL *et al.*, 1989). So, for example, at the higher limit of the *S. plana* distribution in the Bidasoa estuary (station C, Fig. 1) *S. plana* can reach 51 mm. This suggests a growth pattern different from that observed at station A. An other possible interpretation is that *S. plana* shows maximum growth rates in intermediate latitudes as has been suggested by BEUKEMA and MEEHAN (1985) for *Macoma balthica* along European coasts. The differences in growth pattern are attributed to metabolic compensation and an extended growth period.

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