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Population dynamics and production of *Streblospio benedicti* (Polychaeta) in a non-polluted estuary on the Basque coast (Gulf of Biscay)*

LORETO GARCÍA-ARBERAS and ANA RALLO

Dept. of Zoology, University of the Basque Country. P.O. Box 644. E-48080 Bilbap, Spain. E-mail: ggbgaarl@lg.ehu.es

SUMMARY: Population dynamics and production of a population of *Streblospio benedicti* from the Gernika estuary (Basque coast, Gulf of Biscay) were studied monthly for one year, from May 1991 to May 1992. *S. benedicti* was present in the muddy sand community of Gernika throughout the period of study except in March, when it all but disappeared. Continuous recruitment was observed throughout the year, even though it was stronger in autumn. Abundance fluctuations were principally due to the incorporation of recruits and so the highest density in Gernika was recorded in autumn, and the lowest in spring, with an annual mean of 6346 ± 4582 ind m^{-2}. The same pattern of seasonal variation was shown in biomass: the annual mean biomass of *S. benedicti* in Gernika was estimated at 0.80 ± 0.54 g dry weight m^{-2}. Secondary production was 3.57 g dry weight m^{-2} year, giving a P/B ratio of 4.46. *S. benedicti* in Gernika behaved similarly to those described for Mediterranean *Streblospio* populations as regards practically continuous recruitment, but the number of individuals and the annual average density were considerably lower on the Basque coast.

Key words: *Streblospio benedicti*, Polychaeta, population dynamics, production, estuary, Gulf of Biscay.

RESUMEN: DINÁMICA Y PRODUCCIÓN DE *Streblospio benedicti* (POLYCHAETA) EN UN ESTUARIO NO CONTAMINADO DE LA COSTA VASCA (GOLFO DE VIZCAYA). – Se ha estudiado la dinámica poblacional y estimado la producción secundaria de una población de *Streblospio benedicti* del estuario de Gernika (Costa vasca, Golfo de Vizcaya) durante un año y con carácter mensual, de Mayo de 1991 a Mayo de 1992. *S. benedicti* estaba presente en la comunidad areno fangosa a lo largo del periodo de estudio, excepto en Marzo, época en la que casi desaparecía. Se observó un reclutamiento prácticamente continuo a lo largo del año, aunque más intenso durante el otoño. Las oscilaciones en los valores de abundancia se debían principalmente a la incorporación de los reclutas, de forma que las densidades más elevadas se registraban en otoño y las más bajas en primavera, con un valor medio anual de 6346 ± 4582 ind m^{-2}. La biomasa también presentaba el mismo patrón estacional, estimándose una biomasa media anual para *S. benedicti* en Gernika de 0.80 ± 0.54 g peso seco m^{-2}. La producción secundaria se estimó en 3.57 g peso seco m^{-2} año, lo que suponía una relación P/B de 4.46. En la comunidad areno fangosa estudiada en Gernika, *S. benedicti* se comportaba de forma similar a poblaciones mediterráneas de *Streblospio* en lo referente al reclutamiento prácticamente continuo, aunque el número de individuos y la densidad media anual eran inferiores en la Costa Vasca.

Palabras clave: *Streblospio benedicti*, poliquetos, dinámica de poblaciones, producción, estuario, Golfo de Vizcaya.

INTRODUCTION

The estuary of Gernika (Basque Country, northern Iberian Peninsula) has a high botanical and faunistic diversity with a wide variety of aquatic and terrestrial habitats. It is also an important over-wintering and migratory site for birds. Due to these main reasons, it was declared a Natural Biosphere Reserve by UNESCO in 1984. With regard to the benthos, most of the studies in the Gernika estuary have been done on molluscs (Navarro *et al*., 1989; Borja, 1991; Soto *et al*., 1996), but the ecology and

distribution of other benthic taxa are poorly known. A preliminary characterisation of the intertidal soft bottom benthic communities was therefore carried out (García-Arberas and Rallo, 2000). *Streblospio benedicti* Webster, 1879 has a widespread distribution in the intertidal muddy sand areas of the Gernika estuary, where it is one of the most abundant polychaete species, mainly in fine sediments with a relatively high organic matter content.

Traditionally, *Streblospio benedicti* was considered to be the only species in this genus, with *S. shrubsolii* (Buchanan, 1890) and *S. dekhuyzeni* being treated as synonyms of *S. benedicti* (Foster, 1971; Light, 1978). Cazaux (1985) studied the reproduction and larval development of *S. shrubsolii* in the bay of Arcachon (France), and compared his results with those from similar studies on *S. benedicti* on the coasts of North America, confirming the taxonomic value of both species. According to Fonseca-Genevois and Cazaux (1987), the basic morphological characteristics to distinguish between the two species are the number of hooded hooks and the segment where they first appear (5-7 hooks from setiger 7 in *S. benedicti* and 3-5 hooks from setiger 9 in *S. shrubsolii*), and the number of capillary seta (4-5 in *S. benedicti* and 2 in *S. shrubsolii*). According to these authors we attributed the specimens studied to *S. benedicti*; *S. shrubsolii* was not found either in Gernika estuary or in other nearby estuaries such as La Arena and Plentzia (García-Arberas, 1999). However, intermediate characters were sometimes found, as also occurs with other spionids (Rice and Simon, 1980; Ramber and Schram, 1983). The two species are found on the Iberian Peninsula coast: *S. shrubsolii* in both the Atlantic (Sola, 1997; Lopes *et al.,* 2000) and the Mediterranean areas (Martin, 1991), and *S. benedicti* in the Atlantic (Aguirrezabalaga *et al.*, 1990; Junoy and Vieitez, 1992).

On the coasts of Europe these two species of *Streblospio* occupy similar ecological niches and show similar environmental adaptations (Sardà and Martin, 1993). *Streblospio* is a surface deposit feeders that lives in the intertidal and subtidal areas of estuarine and coastal lagunar habitats, showing preference for muddy bottoms, sometimes with high organic matter contents (Bellan, 1964; Levin, 1984; Junoy and Vieitez, 1990; Larsen and Doggett, 1991; Maze *et al.,* 1993), where it builds fine tubes which break up easily in sieving operations (Bachelet, 1984). In fact, *Streblospio* is considered as an opportunist living in organically enriched sediments

(Grassle and Grassle, 1974; Pearson and Rosenberg, 1978), and is one of the first organisms colonising defaunated sediments (Levin *et al.*, 1996).

There are numerous studies on the reproduction and larval development of *Streblospio* (Levin, 1984; Cazaux, 1985; Levin and Creed, 1986; Fonseca-Genevois and Cazaux, 1987; Chu and Levin, 1989) and their influence on the demography of the species (Levin and Hugget, 1990; Lardicci *et al.*, 1997). Other aspects of *Streblospio* biology have also been studied, such as feeding behaviour (Dauer, 1984) and biotic interactions (Whitlatch and Zajac, 1985; McCann and Levin, 1989; Zobrist and Coull, 1994; Posey *et al.*, 1995). However there are fewer studies on the dynamics and secondary production of *Streblospio*. Demographic and production data are known for populations of *S. benedicti* on the east coast of North America (Levin and Huggett, 1990; Sardà *et al.*, 1992; Sardà and Martin, 1993). In the Iberian Peninsula, the dynamics and production of several populations of *S. shrubsolii* have been studied on the Catalonian coast (Martin, 1991; Dueso and Sardà, unpublished data), but there are no previous data about production rates of *S. benedicti*. In this work, data about demography and secondary production of a population of *S. benedicti* from a muddy sand flat in the Cantabrian Sea are presented.

MATERIALS AND METHODS

Study site and field sampling

The estuary of Gernika, in the Biosphere Reserve of Urdaibai, is located near Bilbao in the Basque Country (northern Iberian Peninsula) (Fig. 1). The estuary is 12 km in length, with a maximum width of 1 km and a mean depth of 3.5 m (Orive *et al.*, 1984); almost 70% of it is intertidal domain. The estuary is considered as non-polluted. Some minor industrial and fishing activities take place in the estuary, though most of the human activities in the area are related to agriculture, forestry, and tourism. Only discrete events of increased metal bioavailability have been recorded (Soto *et al.*, 1996). In the middle part of the estuary, there is a small muddy sand flat near San Antonio Beach, in Sukarrieta, where a *Cerastoderma edule-Scrobicularia plana* community was described in a previous study (García-Arberas and Rallo, 2000). This area was sampled monthly from May 1991 to May 1992; three
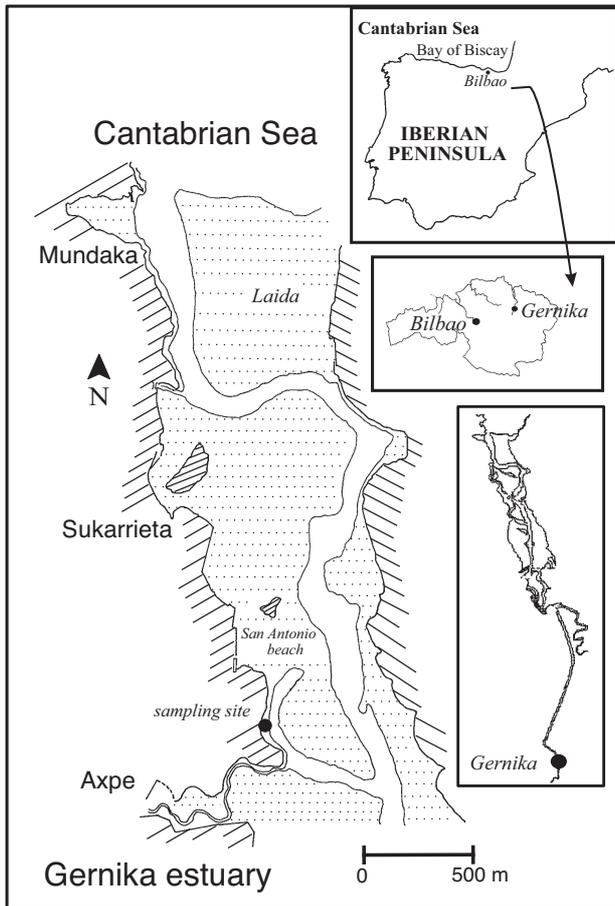
FIG. 1. – Map of the Gernika estuary in the province of Biscay (Basque Country, Bay of Biscay), and location of the study area. Intertidal flats are drown in dotted lines.

core samples were collected randomly using a 12 cm diameter plastic tube (0.011 m²), and an additional core sample was obtained for sediment characterisation. Sediment analysis, using standard methods, included percentage content of granulometrical fractions and organic matter content (Method of Walkley and Black, 1934). Air and sediment temperatures (5 and 20 cm depth) were also measured.

In muddy sand sediments, most species and individuals are concentrated in the upper 10 cm (Dauer *et al.*, 1987). *Streblospio benedicti* usually occupies the upper 4 cm of the sediment (Ambrose, 1984), and only 1% of adults and recruits were found below 4 cm (McCann and Levin, 1989). A preliminary survey was made in March 1992 in order to find a suitable sampling depth; finally the first 7 cm of the sediment were selected. The sediment enclosed in the cores was immediately extracted in the laboratory; the first 7 cm were separated and placed in a magnesium chloride solution as anaesthetic, and then fixed in a 4% formalin-sea water solution. Each

sample was washed through a series of screens (0.5, 0.250 and 0.1 mm), and all the sediment retained in the 0.5 mm mesh screen was examined under a stereo microscope. Aliquot fractions of the other sub samples were examined to evaluate the presence of the smaller size classes of *S. benedicti* (two aliquots by mesh screen, each aliquot of 1/32 of the sample). In order to evaluate possible seasonal changes in *S. benedicti* vertical distribution, the deeper section from one of the cores (fraction 7-10 cm) was also analysed.

In addition to *S. benedicti*, individuals from other taxa were sorted and identified to species level when possible. Several data matrix were obtained (biotic and abiotic data) and univariate and multivariate analysis were employed. Methodology is discussed in more detail in García-Arberas (1999).

Population data

The polychaete body usually appears broken due to sampling and sieving operations, so the use of partial size measurements instead of total length or the number of segments is highly extended in studies of population dynamics and in order to estimate biomass and production (Möller, 1985; Ambrogi, 1990; Sardà and Martin, 1993; Mendez *et al.,* 1997). The width of the fifth thoracic setiger is usually the maximal thoracic width of *Streblospio* and other spionid species and is generally used as a size estimate (Tamai, 1982; Yokohama, 1990; Sardá *et al.,* 1995). Setiger measurements were made through a stereo microscope using a camera lucida and a digitising tablet (Genius Tablet GT-1212B) connected to a computer. Size frequency histograms were drawn up and Bhattacharya´s method (1967) was employed to identify different cohorts using ELEFAN software (Gayanilo *et al.,* 1995). Size in *S. benedicti* was found to be a good indicator of the maturity of larval stages (Levin, 1984): in studies of dispersal and recolonisation of defaunated sediments, the width of the 5th setiger of the new colonists (mainly larvae and juveniles) ranged from 60 to 240 µm. To evaluate the recruitment of *S. benedicti* in Gernika, we considered the presence of individuals in meiofauna samples and also the number of individuals from the smaller size classes of macrofauna (up to 240 µm width of the 5th setiger).

To convert size measurements of all specimens to biomass, the relationship between thoracic width and dry weight was established. Selected individuals belonging to all size classes were measured,

then dried for 24 h at 110ºC and weighed. The regression line obtained between dry weight (DW, mg) and the width of the fifth setiger (TW, mm) was DW = 4.817 * $TW^{2.674}$ (r^2 = 0.63; p= 0.000; n = 34). Differences over time in density and biomass data were analysed using one-way ANOVA. Secondary production was estimated using the Average Cohort method (Hynes and Coleman, 1968), which is especially recommended when cohorts cannot be well identified; calculations are based on biomass differences between the different size classes during the whole period under study. We followed the formula given by Cornet (1986): P = $[\Sigma i(N_j - N_{j+1})(W_j * W_{j+1})^{0.5}]12/CPI$, where CPI is the cohort production interval, i.e. the life-time of the cohort expressed in months. Calculations are explained in detail in the table of results.

RESULTS

Environmental data

The study site was characterised by muddy sand sediments; the average (± S.D.) percentage of the finer granulometric fractions (silt+clay, ϕ < 0.02 mm) over the year was 37.2 ± 4% and the mean organic matter content of the sediment was 2.6 ± 0.4%. Air and surface sediment temperature showed the same oscillations during the study period (Fig. 2), and a mean annual value near 15ºC. As expected, temperature fluctuations were higher in the air not only as regards ranges, but also temperature oscillations between successive months were lower in the sediment (2.6 ± 1.4ºC on average) than in the air (4.3 ± 2.4ºC).

In addition to *Streblospio benedicti*, the macrofauna inhabiting this zone consisted mainly of oligochaetes, the polychaetes *Hediste diversicolor* (O.F. Müller, 1776) and *Capitella capitata* (Fabricius, 1780), and the molluscs *Peringia ulvae* (Pennant, 1777) and *Scrobicularia plana* (Da Costa, 1778). Polychaetes were the main group in terms of number of species, and the two most numerically abundant taxa throughout the study period were oligochaetes and *S. benedicti*. The average Shannon diversity index (log_2) was 2.19 ± 0.48 bits, showing lower oscillations during summer and autumn and being somewhat higher in autumn. Changes in environmental and faunistic conditions in the muddy sand community are discussed in more detail in García-Arberas (1999).

Population density and biomass

Figure 2 shows the variation in mean density and biomass over the study period. *Streblospio benedicti* was present in the muddy sand community in Gernika throughout the period, from May 1991 to May 1992, except in March, when it all but disappeared. The annual mean density (± S.D.) of *S. benedicti* was 6346 ± 4582 ind m^{-2}, with a maximum density in November and a minimum in March. *S. benedicti* showed significant seasonal fluctuations (one-way ANOVA: $F_{3,32}$ = 5.74; p = 0.0029), with the highest mean density observed in autumn (September to November: 11889 ± 7922 ind m^{-2}), and the lowest in spring (March to May: 2121 ± 1706 ind m^{-2}) and summer (June to August: 3899 ± 2923 ind m^{-2}). In winter (December to February), the density remained relatively high (7475 ± 6525 ind m^{-2}), due mainly to an abundance peak observed in February. *S. benedicti* was present in the deeper sediment (fraction 7-10 cm) only in 6 samples (Fig. 2) and in a very low number of individuals (maximum density 273 ind m^{-2} in December).

The annual mean biomass (± S.D.) was 0.80 ± 0.54 g m^{-2}, with a maximum in February. Apart from March, the minimum biomass was recorded in May 1991. Seasonally, there were also significant differences in average biomass ($F_{3,32}$ = 4.09; p = 0.0145); the highest biomass was recorded in autumn (1.38 ± 1.02 g m^{-2}). Although the highest peak was obtained in February, the biomass showed wide fluctuations around that time, so the mean biomass was found to be somewhat lower in winter (0.99 ± 0.82 g m^{-2}). Over the rest of the year there was no major variation in biomass.

Temporal changes of the values of density and biomass of the population of *S. benedicti* showed the same pattern of variation throughout the year; density and biomass were positively correlated (Spearman Rank correlation coef.= 0.9231; p = 0.0014).

No significant correlations were found between *S. benedicti* density or biomass and temperature or sediment characteristics. With regard to other species presence, the only significant relationship was found between the densities of *S. benedicti* and the mollusc *Perigia ulvae* (Spearman Rank correlation coef.= 0.5750; p = 0.0464)

Demography and life-cycle

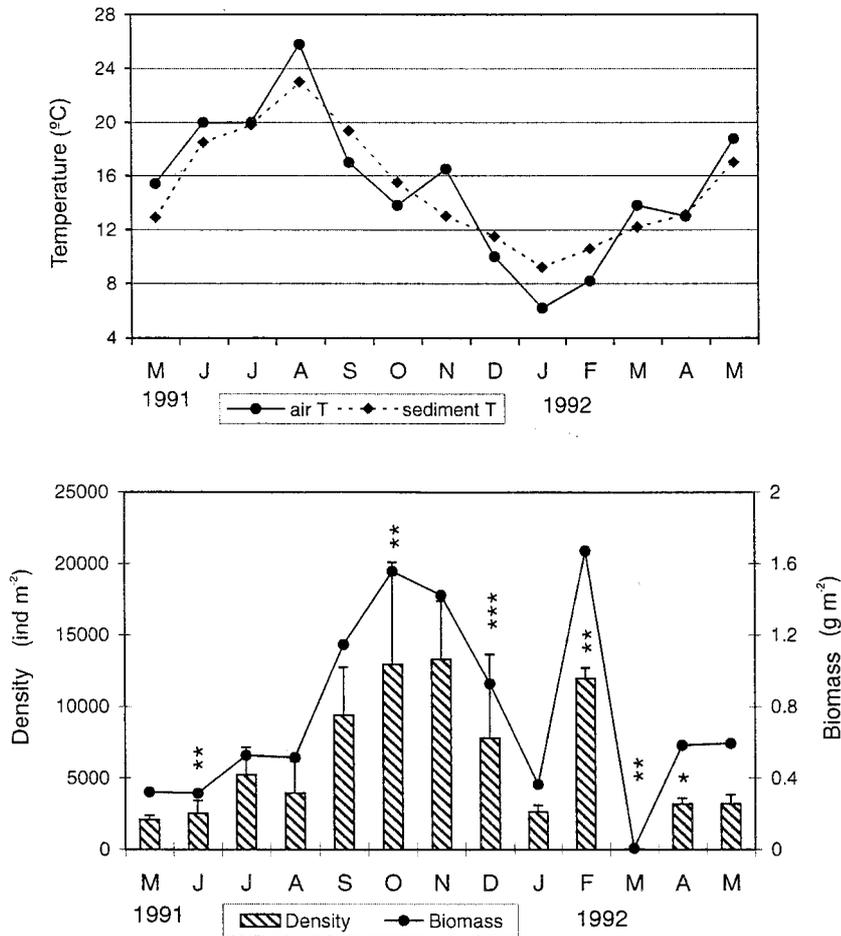Recruitment of *Streblospio benedicti* in Gernika seemed to be practically continuous as in most of

FIG. 2. – Above: variations in air temperature (continuous line) and surface sediment temperature (dotted line) during the sampling period. Below: variation over time of density (ind m^{-2}; average, in bars, and standard error) and estimated biomass (g dry weight m^{-2}; continuous line) of *Streblospio benedicti* during that period. The presence of individuals of *S. benedicti* in the deeper fraction (7-10 cm) is indicated: * =91 ind m^{-2}; ** 182 ind m^{-2}; *** 273 ind m^{-2}.

the monthly samples; juveniles were found among the meiofauna, along with specimens caught in the 0.5 mm mesh belonging to smaller size classes (Fig. 3). However, differences in recruitment intensity were observed. More recruitment took place in autumn: 51% of the smaller specimens of *S. benedicti* (5th setiger 240 μm wide or less) were collected between September and November. The number of individuals of *S. benedicti* found in the meiofauna samples was also higher during that season. In winter the number of juveniles incorporated was also large, accounting for 28.3% of the individuals up to 240 μm wide. The number of new juveniles joining the population during the summer was lower, but as is observed in the histograms they accounted for a considerable proportion of the population in that season. In spring some small specimens were collected, but they accounted for less than 4% of the total recruitment. The popula-

tion of *S. benedicti* seemed to show a bimodal distribution during most of the year, and using Bhattacharya's method on the frequency histograms two size classes were distinguished almost every month, with the exception of spring (Fig.3). Assuming age from size, the two size classes might represent adults and recently settled juveniles. In spring only one size group was found, as a low recruitment of juveniles was observed in the 0.5 mm mesh fauna samples.

It is hard to suggest growth estimates and to assess how long *S. benedicti* remains in the population, as young individuals became mixed within the existing population almost continuously throughout the year, and it was impossible to identify individuals from each input. Moreover, this species is small in size but shows rapid growth, so recently settled specimens in the macrofauna for one month could be incorporated in the adult pop-
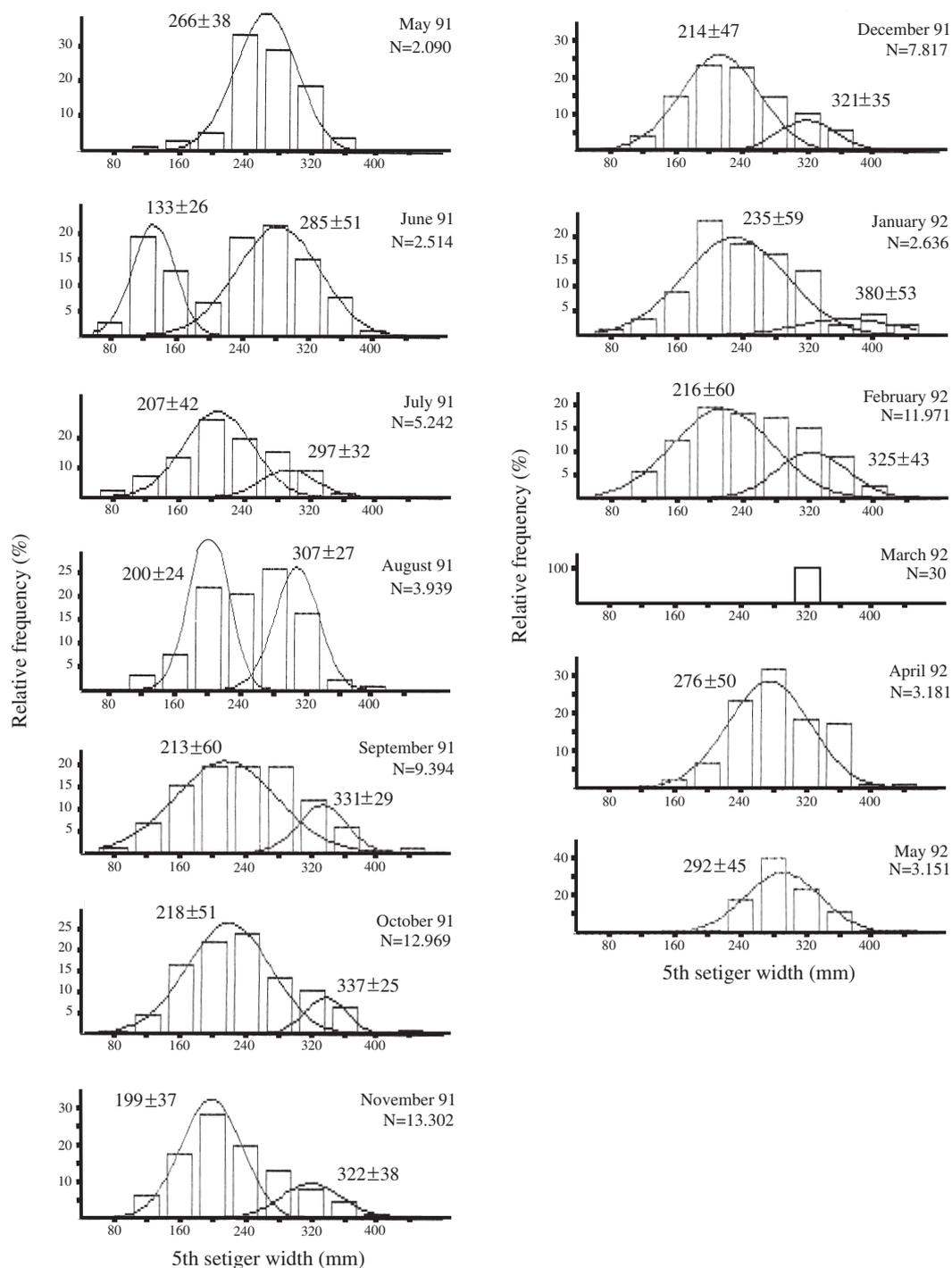
FIG. 3. – Size frequency histograms of fifth setiger width (in μm) of *Streblospio benedicti* population from May 1991 to May 1992 (relative frequency). Curved lines are normalised expected frequencies. Average setiger width (± S.D.) of the size groups determined by Bhattacharya's method are included (N = ind m^{-2}).

ulation the next month (Sardà and Martin, 1993). We analysed changes in average width between size groups in successive months (the average value for each group is included in the frequency histograms): the increments in width of the juveniles in a given month and the width of adults for

the following month were similar throughout the period studied. We also analysed the temporal variation in the number of individuals of these two size classes (Fig. 4), in order to distinguish possible mortality periods. The adult population of *S. benedicti* in Gernika was found to be more or less sta-
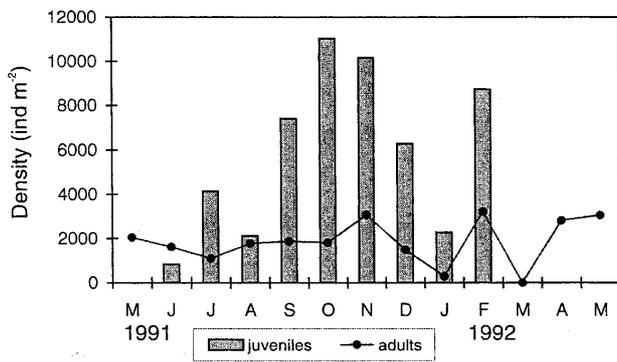
FIG. 4. – Changes in the number of individuals (ind m^{-2}) of *Streblospio benedicti* of the size classes determined by Bhattacharya's method during the sampling period; juveniles in bars and adults in continuous line.

ble throughout the period of study (around 2000 ind m^{-2} on average, March not included), but several drops in the number of individuals were observed. The highest drop was found in winter and early spring, so in March the population of *S. benedicti* disappeared from the study area, though it recovered in subsequent months.

Production

To estimate the secondary production of *Streblospio benedicti* the average cohort method was employed, following the formula used by Cornet (1986). Table 1 shows the calculations in detail. According to this method, secondary production was 3.57 g m^{-2} year. The average biomass was 0.80 g m^{-2} year, giving a P/B ratio of 4.46.

DISCUSSION

In North American and European *Streblospio* populations, density and biomass values and production rates seem to be very different. Annual mean density ranged from values close to 5000 ind m^{-2} (Whitlatch, 1981; Sardà and Martin, 1993) to 17000 ind m^{-2} (Levin, 1984), but when highest densities were compared the differences were even greater: from 13000 ind m^{-2} found in Gernika (this work) to 60000 ind m^{-2} recorded in California (Levin, 1984). The annual average biomass found in Gernika (0.80 g m^{-2}) could be considered high in comparison to that found in Massachusetts (Sardà *et al.*, 1992, 0.5 mm used); these authors found biomasses of 0.6 and 0.37 g m^{-2} in artificially fertilised areas, compared with an average of only 0.12 g m^{-2} in the control area. The P/B ratio of 4.46 obtained for *S. benedicti* in our work was within the range for species with a life cycle of one year (P/B estimated between 3.72 and 5.61), following the equation and limits of confidence calculated by Robertson (1979).

S. benedicti was found in different soft bottom communities in the estuaries of Gernika, La Arena and Plentzia (García-Arberas and Rallo, 2002a). It was considered as a relatively wide spectrum species as it was found in almost the whole range of variation of the environmental variables measured in that work, showing smaller ranges only for the coarse elements sedimentary fraction and the oxygen content of the sediment. The density of *S. benedicti* appeared to be positively correlated with the percentage of fine sand, the porosity and the humidity

TABLE 1. – Production of *Streblospio benedicti* estimated following the average cohort method, using the formula given by Cornet (1986): I = average number of individuals of class j; II = number of individuals lost from one class to the next; III = dry weight of individuals belonging to class j; IV = biomass of class j; V = geometric mean of dry weight of two successive classes; VI = biomass lost or increments between successive classes; VII = production increments. The CPI value was assumed to be 12 since the production period was exactly one year.

Size class (mm)	I N$_j$ (ind m^{-2})	II N$_j$-(N$_{j+1}$) (ind m^{-2})	III W$_j$ (mg)	IV N$_j$ x W$_j$ (mg m^{-2})	V Mean W (mg)	VI Biomass lost (mg m^{-2})	VII P$_j$ (mg m^{-2})
0.04	0		0.0009				
0.08	35.3	-35.3	0.0056	0.20	0.0022	-0.078	-0.86
0.12	343.3	-308.0	0.0166	5.70	0.0096	-2.957	-32.53
0.16	863.7	-520.4	0.0359	31.01	0.0244	-12.698	-139.68
0.20	1343.3	-479.6	0.0651	87.45	0.0483	-23.165	-254.81
0.24	1315.6	27.7	0.1060	139.45	0.0831	2.302	25.32
0.28	1146.3	169.3	0.1601	183.52	0.1303	22.060	242.66
0.32	785.4	360.9	0.2288	179.70	0.1914	69.076	759.84
0.36	404.0	381.4	0.3136	126.69	0.2679	102.177	1123.95
0.40	70.7	333.3	0.4156	29.38	0.3610	120.321	1323.53
0.44	37.8	32.9	0.5362	20.27	0.4721	24.415	268.56
0.48	0	37.8	0.6767		0.6024	22.771	250.48
TOTAL				803.37			3566.46
	B=0.80 g m^{-2}			P=3.57 g m^{-2}		P/B = 4.46	

and the organic matter content of the sediment, whereas significant negative correlations with the oxygen concentration and the redox values were found. In the muddy sand community studied in the present work, environmental conditions during the sampling period did not change sufficiently to find significant relationships between them and *S. benedicti* density or biomass.

Sardà and Martín (1993) analysed the importance of the temperature in *Streblospio* dynamics. Adding their results to those of earlier studies, they obtained a significant relationship between the abundance of *Streblospio* and temperature: positive with annual average temperature and negative with maximum temperature change. They also suggested that at temperate latitudes populations of *Streblospio* in warm areas were likely to be more productive than those in cold areas, while the P/B ratio would tend to be higher in the latter. However, in Gernika there was no evidence of changes in density or biomass due to temperature oscillations and our results did not fit in with the model commented above: applying the equation obtained by these authors to the temperature values registered in Gernika, the expected average densities were much higher than the actual values (at 15ºC 32000 ind m^{-2} expected versus 6346 ind m^{-2} observed). Moreover, the P/B ratio found in our work was similar to that indicated by these authors for populations in the Mediterranean (4.4), while for secondary production the value was closer to their results on the coast of North America (3.0 g m^{-2} year, calculated using Crisp's method).

In addition to the temperature regimen, the size of *Streblospio* populations can be influenced by several factors: the abundance of *S. shrubsolii* was positively correlated with the nutritive value of the sediment (Rossi, 2003), but it decreased due to macroalgal blooms (Lopes *et al.,* 2000). Baitworm and clam digging activity had a negative impact on *S. benedicti* (Brown and Wilson, 1997), but there was no evidence of changes in density of *S. shrubsolii* due to wader predation (Lopes *et al.,* 2000). However, *s*ince *Streblospio* is a small, fast-growing species with a short life cycle, recruitment is the greatest determining factor in population density and biomass variations. In a population of *S. shrubsolii* on the coast of Italy, Lardicci *et al.* (1997) found a positive correlation between potential larval production (lecithotrophic development mode) and population density with a time lag of two months. *S. benedicti* shows both lecithotrophic and plank-

totrophic development: larval length was 600 μm length when recruited into the sediment in the former (Levin and Hugget, 1990), and 900 μm in the latter (Fonseca-Genevois and Cazaux, 1987). Larval development was not studied for the Gernika population but a strong demographic similarity between planktotrophic and lecithotrophic dominated populations was found (Levin and Hugget, 1990), and according with the sizes cited above, larvae should be collected in our samples regardless of the kind of development.

The population of *S. benedicti* in Gernika showed a more or less continuous but non-uniform recruitment throughout the year. In other populations, usually in colder areas with more severe winters than those of the Basque coast*,* one or more reproduction and recruitment periods have been observed, but they were more time limited and seasonally marked (Whitlatch, 1977; Levin, 1984; Fonseca-Genevois and Cazaux, 1987; Sardà and Martín, 1993). For populations of *S. shrubsolii* studied in various areas of the Mediterranean coast, recruitment has been described as practically continuous throughout the year (Martín, 1991; Lardicci *et al.*, 1997; Dueso and Sardà, unpublished data), though in some cases it seemed to be less intense during the winter months (Martín, 1991). Therefore, in colder areas, *Streblospio* seems to recruit in one or more bursts, usually in the spring to summer or summer to autumn periods, whereas in warmer areas reproduction and recruitment go on for longer. However, those differences in recruitment were related not only to the temperature regime, as variations in photoperiod due to latitudinal location of the studied populations also regulated the reproductive activity of *S. benedicti* (Chu and Levin, 1989). In addition to temperature and photoperiod, *S. benedicti* reproduction rate and juvenile survival were affected by seasonal variation in food resources (Marsh and Tenore, 1990). No significant differences in survivorship or reproduction activity, in relation to changes in temperature or food availability, were observed between planktotrophic and lecithotrophic reproductive types (Levin and Creed, 1986).

As local differences in recruitment were observed for *Streblospio*, peaks of abundance might occur at any time of the year in different populations, even in those which were less than 1 km apart (Martín, 1991). Biomass in Gernika followed the seasonal pattern of density (Fig. 2), as occurred in other *Streblospio* populations (Sardà and Martín, 1993; Sola, 1997), and for other small size poly-

chaetes such as *Prionospio caspersi* (Ambrogi, 1990). However, density and biomass showed a different seasonal behaviour, sometimes with opposite fluctuations, in the case of large size polychaetes with longer life cycles such as *Hediste diversicolor* (Sola, 1997; García-Arberas and Rallo, 2002b) or *Marenzelleria viridis* (Sardà *et al.,* 1995). In addition to wide seasonal variations, in which the population practically disappears some times (e.g. as occurred in March in Gernika; Fonseca-Genevois and Cazaux, 1987; Martín, 1991; Sola, 1997), inter-annual variations have also been recorded (Nichols and Thompson, 1985; Sardà and Martín, 1993), even between consecutive years.

Different growth patterns according to the cohorts have been observed for *S. benedicti* populations (Chu and Levin 1989; Levin and Huggett, 1990; Marsh and Tenore, 1990; Sardà and Martin, 1993). *S. shrubsolii* growth seems slower in winter than in summer (Martín, 1991). Continuous recruitment observed for *S. benedicti* in Gernika estuary made it difficult to analyse growth and mortality because it was impossible to identify individuals from each input. The decrease in the number of adults observed during winter and early spring could be explained by higher mortality rates during that season. Growth of *S. benedicti* in Gernika, in terms of increments in the width of the juveniles in a given month and the width of adults for the following month, was similar throughout the period studied. However, it was difficult to determine how long it took the juveniles to join the adult population so it can also be assumed that autumn and winter juveniles could grow slower than other recruits, partly explaining the drop in the number of adults observed in winter and early spring. In relation to the youngest worms, the great difference in the number of individuals between size groups gave an idea of how much mortality there must be in this size class. If we assume that adults dropped out of the population at a more or less steady rate, the most successful period for juveniles joining the adult group would be summer, particularly August and September, and to a lesser extent autumn, October and November. From November to January, mortality would be higher.

The reason for the absence of *S. benedicti* individuals in the study area in March was not clear. There were no considerable environmental changes that could explain it, but the population had recovered in the next month to a similar density to that found when the study began in the spring of 1991.

Recruitment probably occurred between samples, but the growth rate would have had to be extremely high (large sizes in spring after overwinter have been described by Chu and Levin (1989)) because the population found in April and May 1992 was mainly made up of large-size individuals. Negative interactions between tube building spionids such as *Streblospio* and free-borrowing annelids such as *Capitella capitata* or oligochaetes due to competition for space and food have been pointed out by several authors (Whitlatch and Zajac, 1985; McCann and Levin, 1989; Sardà *et al.*, 1995). In long-term field experiments, *S. benedicti* became the dominant species in non-fertilised areas, whereas oligochaetes were the dominant taxa in nutrient-enriched zones (Sardà *et al.*, 1996). However, the density of *S. benedicti* during the study period did not show a negative correlation with *C. capitata*, oligochaetes or other macrobenthic species density.

Variations in the vertical distribution of *S. benedicti* over the year have been described (Fonseca-Genevois and Cazaux, 1987), usually associated with periods of lower temperatures. However, these downward movements did not explain the disappearance of our population in March (Fig. 2); density was in fact high during the coldest months. Horizontal movements within sediment have also been described for both *Streblospio* and other depositivore species (Frid and James, 1988). In laboratory cultures *S. benedicti* frequently builds more than one tube (Mccann and Levin, 1989), and it can be highly mobile over distances of several centimetres due to feeding requirements or to avoid interspecific competition (Dauer, 1984). In populations of *S. shrubsolii* temporary defaunation has been described and might be explained in terms of migration from an unstable population to a near one less affected by environmental changes in which increased density is reported, although no recruitment was observed at the same time (Martín, 1991). Finally, although law-regulated baitworm and clam digging activity has not been analysed in this work, it could influence the dynamics of the species in the Gernika estuary, as has been found in the density of bivalves, which was lower than expected (Iglesias and Navarro, 1995).

S. benedicti from the muddy sand community studied in Gernika behaved similarly to those described for Mediterranean *Streblospio* populations as regards practically continuous recruitment, but the number of individuals and the annual average density were quite lower on the Basque coast. This

pattern has also been observed in the Gernika estuary for the polychaete *Hediste diversicolor* (García-Arberas and Rallo, 2002b).

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