POPULATIONS OF *STREBLOSPIO* (POLYCHAETA: SPIONIDAE) IN TEMPERATE ZONES: DEMOGRAPHY AND PRODUCTION

RAFAEL SARDÁ AND DANIEL MARTÍN

Centro de Estudios Avanzados de Blanes, (CSIC), Camí de Sta Barbara s/n, 17300 Blanes (Girona), Spain

The life cycle, seasonal dynamics and production of two populations of *Streblospio* species (Annelida: Polychaeta), *S. benedicti* Webster, 1879, from muddy sediments of the Great Sippewissett Salt Marsh (southern New England, USA), and *S. shrubsolii* (Buchanan, 1890), from muddy areas of the Alfacs Bay (north-eastern Spain), were studied from November 1986 to September 1988. Both species have life-cycles shorter than one year. The American population showed a unimodal distribution most of the year while in the European population polymodal distributions were common. Average density of *S. benedicti* over the two-year period ranged from 24,086 to 677 individuals m^{-2} (annual average 4,554). The observed numbers of *S. shrubsolii* ranged from 65,668 to 2,579 individuals m^{-2} (average 35,311). The biomass of the American population ranged from 2.1 to 0.04 g dry weight m^{-2} (average 0.5). The values obtained for the European population ranged from 5.9 to 0.1 g dry weight m^{-2} (average 4.1). Secondary production was higher in the European population (15.65 g dry weight $\text{m}^{-2} \text{y}^{-1}$) than in the American population (3.0 g dry weight $\text{m}^{-2} \text{y}^{-1}$). Production to mean biomass ratios were 4.4 y^{-1} for *S. shrubsolii* and 5.4 y^{-1} for *S. benedicti*. Population densities are compared with previously published data for other *Streblospio* populations.

INTRODUCTION

The spionid species of the genus *Streblospio* Webster, 1879 are small (<2 cm long), tube-dwelling polychaetes inhabiting the upper 2-3 cm of muddy sediments in enclosed estuarine zones and brackish waters. *Streblospio* are suspension and surface-deposit feeders (Dauer, 1984), and are well-known as opportunistic species that colonize organically-enriched sediments (Grassle & Grassle, 1974; Pearson & Rosenberg, 1978).

The two species of *Streblospio*, *S. benedicti* Webster, 1879 and *S. shrubsolii* (Buchanan, 1890), are both widely distributed. *Streblospio benedicti* mainly inhabits estuarine areas of North America (see Levin, 1984b), Venezuela (Carlton, 1979) and Northern Europe (da Fonsêca-Genevois & Cazaux, 1987). Reports of *S. benedicti* in Mediterranean waters (Bellan, 1964) should be questioned, as it had probably been confused with *S. shrubsolii* (da Fonsêca-Genevois & Cazaux, 1987). *Streblospio shrubsolii* has been reported in enclosed, brackish, European zones (see Bachelet, 1987; Koukouras & Russo, 1991).

Populations of *S. benedicti* and *S. shrubsolii* live in similar ecological niches in highly-disturbed, deposit-feeding communities and exhibit similar adaptations to the environment. Although both species have isolated distributions, da Fonsêca-Genevois & Cazaux

(1987) showed how *S. benedicti* replaced *S. shrubsolii* in the Loire Estuary (France). Other polychaetes (*Capitella capitata*, *Nereis diversicolor*, and *Polydora ligni* or *P. ciliata*), amphipods (*Corophium* sp., *Leptocheirus* sp.), oligochaetes (*Paranais* sp., *Limnodrilus* sp., *Peloscolex* sp., *Monopylephorus* sp.), molluscs (*Hydrobia* sp.), and occasionally, large nematodes (*Methoncholaimus* sp.) may also be abundant in these macroinfaunal communities. Seasonal patterns of abundance in *S. benedicti* are rather well-documented as the species is one of the most important organisms in deposit-feeding assemblages in North America (Watling, 1975; Whitlatch, 1977; Rhoads *et al.*, 1978; Zajac & Whitlatch, 1982; Levin, 1984a). Although *S. shrubsolii* plays a similar role, its seasonal cycle has seldom been studied (Bachelet, 1984; Parisi *et al.*, 1985).

Streblospio benedicti shows both planktotrophic and lecithotrophic development (Levin, 1984b; Rice, 1991). Although less well-known, planktotrophic (Wolff, 1973; Manoleli, 1980) and lecithotrophic (Cazaux, 1985) larvae have also been reported for *S. shrubsolii*. Reproductive and developmental biology of the *Streblospio* species (Dean, 1965; Collier & Jones, 1967; Campbell, 1957; Eckelbarger, 1980; Levin, 1984b; Cazaux, 1985; Levin & Creed, 1986; da Fonsêca-Genevois & Cazaux, 1987) as well as the demographic consequences of developmental mode (Levin *et al.*, 1987; Levin & Huggett, 1991) have been studied in different populations. Although some other aspects of the biology of *Streblospio* species have been documented, *e.g.* feeding behaviour (Dauer *et al.*, 1982; Frithsen & Doering, 1986), and biotic interactions (Virnstein, 1977; Wiltse *et al.*, 1984; Watzin, 1983; Levin, 1981; McCann & Levin, 1989; Bell, 1980), population dynamics and secondary production rates in the field remain unknown in *Streblospio* species.

The dynamics of a *S. benedicti* population in the Great Sippewissett Salt Marsh (southern New England, USA), and a *S. shrubsolii* population in Alfacs Bay, a western Mediterranean, semi-enclosed, shallow-water bay (north-eastern Spain) were investigated during 1986-1988. In this paper we analyse life cycles, population sizes, biomass, growth, and production of the two populations, and we compare the present data with other available data on *Streblospio* species from different geographical areas.

MATERIAL AND METHODS

Study areas

The Great Sippewissett Salt Marsh is located on the western shore of Cape Cod (Massachusetts, USA). Sea-water from Buzzards Bay flows into the marsh through a single entrance, reaching the study area twice daily (Valiela & Teal, 1979). Different substrate types can be found in the marsh, the sandy sediments of the main channels changing to silty muds in the more landward, low energy areas (Sardá *et al.*, in preparation).

The Alfacs Bay (Ebro Delta, Spain), located on the north-east coast of the Iberian Peninsula is a semi-enclosed, shallow-water area which is characterized by a marine hydrographic regime, but which is also highly influenced by continental fresh-water inputs during the spring-summer period (Palacín *et al.*, 1991). The studied area included the muddy zone along the northern shore of the bay. Its sediment was characterized by

high organic matter content, high percentage of silt, and a very low redox potential (Palacín *et al.*, 1991). There were scattered shoots of marine seagrasses, *Ruppia cirrhosa* (Petagna) Grande, and *Cymodocea nodosa* (Ucria) Acherson, in the area (Pérez & Camp, 1986).

Sampling techniques

Muddy creeks at Great Sippewissett were sampled monthly from November 1986 to October 1988. Four core samples (33.2 cm², 15 cm depth) were obtained from two muddy control creeks (Sardá *et al.*, 1992). Samples were sieved through a 500-µm screen and preserved in buffered formalin-sea-water containing Rose Bengal stain. The sediment passing through the sieve was saved and an aliquot fraction (one-tenth of the sample) was examined under a stereo microscope to quantify the smaller size-fraction of the macroinfauna (temporary meiofauna).

Muddy sediments from Alfacs Bay were collected monthly from August 1987 to July 1988. Four core samples (30 cm², 5 cm depth) were obtained. All samples were sieved through a 500-µm screen. An additional core was collected and filtered by density through a 60-µm sieve using an elutriator (Boisseau, 1957). An aliquot fraction (one-tenth of the sample) was examined under a stereo microscope to count the smaller size classes of macroinfauna (temporary meiofauna). Specimens were preserved in buffered 10% formalin-sea-water.

Measurement methods and production estimates

The width of the fourth thoracic setiger was used as a size estimate, to measure growth, and to identify cohorts or generations. Setiger measurements were made through a stereo microscope using a camera lucida and digitizing tablets (Houston Instruments HiPad and Genitizer GT-1212B respectively for *S. benedicti* and *S. shrubsolii*) linked to a computer. Selected individuals from representative size categories were measured, then dried (48 h at 60°C, *S. benedicti*; 24 h at 110°C, *S. shrubsolii*) and weighed. For both species, a setiger width (SW) *vs* dry weight (DW) regression was calculated and used to convert the routine setiger measurements to biomass.

Growth was analysed using different subroutines with the ELEPHAN software. The analysis of the different cohorts was done using the Bhattacharya (1967) method.

To evaluate the contribution of the two species of *Streblospio* to the secondary production in their habitats, estimates for production were calculated by two methods. In the American population of *S. benedicti*, secondary production was estimated by summing increases in biomass from one sampling date to the next for the identified individual cohorts, following the Crisp (1971) method.

In the European population of *S. shrubsolii*, the recognition of different cohorts was impossible and methods involving the separation of cohorts could not be applied. To estimate secondary production we used the Hynes method (Hynes & Coleman, 1968; Hamilton, 1969; Benke, 1979) following the formula given by Cornet (1986).

$$P = \left[\sum_{i=1}^i (\bar{N}_j - \bar{N}_{j+1}) (\bar{w}_j * \bar{w}_{j+1})^{0.5} \right] * \frac{12}{CPI} \quad (1)$$

where $\bar{N}_j$ and $\bar{N}_{j+1}$ are average number of individuals of class j and $j+1$, $\bar{w}_j * \bar{w}_{j+1}$ is the geometric mean of ash-free dry weight of two successive size classes, i is the number of size classes and CPI is the cohort production interval. The average cohort method applied to the American population of *S. benedicti* yielded similar values to those obtained by cohort identification.

Reproductive biology

The reproductive biology of *Streblospio* species has been investigated based on observations of the collected animals. *Streblospio* species have their larval development in the middle portion of the body. Males and females could be distinguished only when the worms contained eggs or larvae, the sperm of males and the eggs of females could be seen only when the worms were gravid (Dean, 1965; Cazaux, 1985). The first and the total number of segments containing gametes were counted monthly in both populations; this measure was independent of the presence of brood pouches in the posterior part of the reproductive zone.

RESULTS

Demography and life-cycles

The populations of *Streblospio benedicti* in Great Sippewissett Salt Marsh and *S. shrubsolei* in the Alfacs Bay have life-cycles shorter than a year. Size-frequencies of the American population show a unimodal distribution through most of the year, characteristic of a species with clear seasonal recruitment (Figure 1A). There are several generations of *S. benedicti* only during May, June and July (Figure 1A). In the European population, polymodal distributions were more frequent, which is characteristic of species with several annual recruitments and rapid growth (Figure 1B).

In the Great Sippewissett Marsh, the new year-class of *S. benedicti* enters the benthic community in late spring (Figure 1A). Individuals recruited in spring grow quickly. The second, low recruitment occurred in early summer. The main spawning peak in spring and the smaller one in early summer give rise to two periods of juvenile recruitment in the population. These periods of recruitment yield a bimodal size-class distribution in the early autumn (Figure 1A). During late autumn, winter and early spring, *i.e.* during periods of no recruitment, a relatively stable unimodal population is maintained.

During the severe winter of 1986-87, a thick layer of ice covered channels and creeks in Great Sippewissett Salt Marsh during January and February (Figure 2A). Although a remarkable accumulation of *Streblospio* was observed in March, after the thaw, the *Streblospio* population diminished steadily during the winter months. Beukema (1985) found an off-shore migration of some species, including polychaetes, in severe winters in the Wadden Sea. In spite of the cold weather, perhaps movements of frozen sediment

Figure 1. Size frequency histograms of setiger width (in μm) expressed as individuals m^{-2} of (A) *Streptosio benedicti* and (B) *Streptosio shrubsolii*, populations from November 1986 to August 1988. Curved lines are normalized expected frequencies.

during thaw can concentrate individuals of *S. benedicti* in the most favourable local habitats. The lower densities found in February and April of 1987 could be explained by this kind of small movement in the high salt marsh area. Although the 1987-88 winter was milder and the number of individuals was considerably lower than in the previous year, the same small movements seemed to occur and *Streptosio* accumulations were detected in January and February (Figure 2).

The densities of *S. benedicti* decreased sharply in July and August (Figures 1A & 2) both in 1987 and 1988. During the course of a cage enclosure experiment Wiltse *et al.* (1984) found that the high reproductive rate of *S. benedicti* enabled the species to remain common during spring and summer in sediments protected against epibenthic predation, but densities were drastically reduced in control sediments. Predation by fish and crabs depleted the *S. benedicti* populations in these muddy creeks during the summer.

The life cycle of the *S. shrubsolii* population in Alfacs Bay differed from that of *S. benedicti* in Great Sippewissett Marsh. The densities were higher and recruitment occurred throughout the entire year, although it was reduced during the winter months (Figures 1B & 2). Recruitment increased during April and May and continued throughout summer and autumn. The previous adult population was rapidly depleted during late spring and early summer, but the recruits grew quickly, reaching maturity in less than two months, and maintained a stable population throughout winter, which was to

Figure 2. (A) Air temperatures (in °C) for both areas for Great Sippewissett and Alfacas Bay. Density and biomass data for (B) *Streblospio benedicti* (Great Sippewissett) and (C) *Streblospio shrubsolii* (Alfacas Bay) during the sampling period.

be the origin of the next new period of recruitment. Although summer decreases have been observed in other salt marshes of the western Mediterranean, we are unsure of the cause of this sharp decrease in the Ebro population but suspect predation.

Reproductive biology and growth

The reproductive biology of the two populations of *Streblospio* is shown in Figure 3. Both populations behaved differently and will be described separately.

At Great Sippewissett Salt Marsh, *S. benedicti* proceeded through the autumn with no visible gonads (Figure 3). During the winter months some tiny white points were observed inside a few animals. The first organisms containing visible gonads were detected at the beginning of spring. Gametogenic segments swelled out and from April dorsal brood pouches were observed. During April, May and June, organisms had, on average, the greatest number (21-25) of gametogenic segments (Figure 3). Spawning occurred between May and August and was recognized in the animals by the presence of open dorsal brood pouches. Reproductive adults from June to August had fewer gametogenic segments than those in spring, between 12 and 19 segments. The organisms maturing during the summer did not contain developed gonads until next winter.

In the Ebro Delta the population of *S. shrubsolii* behaved differently. Although almost

Figure 3. Percentage of organisms showing reproductive activity and number of gametogenic segments through the year for (A) Great Sippewissett and (B) Alfacs Bay populations of *Streblospio*.

no reproductive activity was observed in October and November, it was possible to observe organisms with developed gonads during the rest of the year. The presence of juveniles throughout the year can be related to the low percentages of organisms showing reproductive activity (Figure 3). The maximum number of gametogenic segments detected in the *Streblospio* population was found between January and March, between 18 and 20 segments, but a high number was also observed in summer (18 gametogenic segments in August).

Although *S. shrubsolei* has more segments than *S. benedicti* (67 ± 6 and 52 ± 5 , respectively for entire large organisms of both species), the number of gametogenic segments is quite similar, 20 ± 2 for *S. shrubsolei* against 23 ± 2 for *S. benedicti*. The first gametogenic segment in *S. shrubsolei* ranged from the 24th to the 27th segment while in *S. benedicti* it ranged from the 10th to the 11th segment.

Streblospio species are characterized by their fast growth (Figure 4). Growth in the American population was very rapid during the first two months, with the adults reaching widths of around 550 μm . Following this period, growth slows down as individuals become reproductively active. Growth could not be correctly followed in the Mediterranean population as it was very rapid initially and the young worms soon became mixed with the existing population. Maximum adult sizes measured during the study reached values around 700 μm for *S. benedicti* and 550 μm for *S. shrubsolei*.

The identified cohorts for *S. benedicti* allowed us to recognize four periods of juvenile recruitment (Figure 4A). The spring recruitments (I, II and III) yielded an abundant fast-

Figure 4. Growth of individual year classes, expressed as thoracic setiger width, for *Streblospio benedicti*.

growth cohort which was quickly depleted, probably by predators; nevertheless, some of these worms could spawn in two or three months and gave rise to the summer recruitment (IV). The previous recruits mixed with these summer ones and both grew slowly through fall and winter until the following spring. The spring recruits were characterized by high mortality and rapid growth, and were responsible for the summer recruitment. The summer recruits had low mortality and slower growth, and were responsible for the spring recruitment the following year. *Streblospio shrubsolii* in Alfacs Bay showed a different population strategy, with constant recruitment throughout the year, lower in winter; the recruits were quickly incorporated into the population and probably spawned as soon as they reached adult size.

In the studied population of *S. benedicti* the survivorship curve was similar to the experimental curves found by Levin *et al.* (1987) for a *S. benedicti* population with lecithotrophic larvae reared under laboratory conditions (Figure 5). The field population studied here shows lecithotrophic development. Differences from the lecithotrophic

Figure 5. Survivorship of *Streblospio benedicti*. Circles represent populations reared by Levin *et al.*, (1987) under laboratory conditions at 20°C and 34‰ salinity. (○, planktotrophic strain; ●, lecithotrophic strain). ▲, field data from Great Sippewissett Salt Marsh.

population of Levin *et al.* (1987) were based on the higher mortality found in our population during the first eight weeks of life, probably caused by intense predation by fishes and crabs in the marsh (Wiltse *et al.*, 1984). No survivorship curve could be followed for *S. shrubsolii* because the worms could not be separated into cohorts or generations when they got mixed with the adult population.

Population density and biomass

The average density of *Streblospio benedicti* in the creeks of Great Sippewissett Salt Marsh over the two-year period ranged from 24,086 individuals m^{-2} in June 1987 to 677 individuals m^{-2} in November 1987 (average 4,554). The observed densities of *S. shrubsolii* in Alfacs Bay ranged from 65,668 ind m^{-2} in August 1987 to 2,579 ind m^{-2} in June 1988 (average 35,311) (Figure 2).

In Great Sippewissett Salt Marsh, peaks of abundance of the *Streblospio* population occurred as the temperature increased during late spring and early summer, and then decreased again (Figure 2). This seasonal pattern has been observed elsewhere for northern Atlantic salt marshes (Whitlatch, 1977; Wiltse *et al.*, 1984; Jackson *et al.*, 1985). Analysing data from experimental enclosures, Wiltse *et al.* (1984) showed that the summer decrease in density of benthic macroinfauna, mostly *S. benedicti* and the oligochaete *Paranais litoralis* (Müller) in our creeks, was caused by intense predation, particularly by fishes. After the summer decline, the population size remained fairly stable over the winter.

The *Streblospio* population of Alfacs Bay remained fairly stable from August to May. Although adults suffered a sharp decline during late spring and early summer, the new recruits grew quickly and the density tended to be stable during most of the year (Figure 2).

To calculate the biomass of the two species, we used the relationship of setiger width in mm (SW) *vs* dry weight in mg (DW) (Figure 6). The regressions were, for *S. benedicti*, $\text{DW} = 0.6030 * \text{SW}^{3.155}$ ($r^2 = 0.63$; $N = 28$), and for *S. shrubsolii*, $\text{DW} = 1.3581 * \text{SW}^{2.701}$ ($r^2 = 0.79$; $N = 23$).

The seasonal pattern of biomass in both populations (Figure 2) mirrors the density pattern. The biomass of the American population ranged from 2.1 g DW m^{-2} in March

Figure 6. The relationship between width (in mm) of the fourth thoracic setiger, and dry weight (in mg), for *Streblospio benedicti* (○) and *Streblospio shrubsolii* (△). (See text for regression equations.)

1987 to 0.04 g DW m⁻² in August 1988 (average 0.5). The values obtained for the Mediterranean population were significantly higher, ranging from 5.9 g DW m⁻² in January 1987 to 0.1 g DW m⁻² in July 1987 (average 4.1). Although maximum sizes observed in adults of the two populations were different (about 700 µm in *S. benedicti* and 470 µm in *S. shrubsolii*), individual biomass was similar for both species of *Streblospio* (mean individual biomass 0.20 mg for *S. benedicti* and 0.18 mg for *S. shrubsolii*).

Table 1. Summary of data used in the calculation of the annual production of *Streblospio benedicti* following Crisp (1971).

Cohorts	Generation and date		$\bar{N}_j$ (ind m ⁻²)	Mean length	Mean weight	Increase in weight	$\frac{(\bar{N}_j + \bar{N}_{j+1})}{2}$	Production (g m ⁻²)
1986	IV	N	13482	0.443	0.046			
		D	13415	0.524	0.078	0.032	13449	0.433
		J	5418	0.540	0.086	0.008	9417	0.073
		F	2337	0.620	0.133	0.047	3878	0.183
		M	17184	0.621	0.134	0.001	9761	0.007
		A	1281	0.660	0.162	0.028	9233	0.262
		M	7092	0.653	0.157	-0.005	4187	-0.022
		J	5184	0.654	0.158	0.001	6138	0.005
Cohort 1986							0.940	
1987	I	M	595	0.139	0.001			
		J	5048	0.442	0.046	0.045	2822	0.126
	I+II	J	18934	0.395				
		J	3217	0.505	0.070	0.070	11076	0.772
		A	327	0.488	0.063	-0.007	1772	-0.013
	III	J	9349	0.275				
		A	727	0.367	0.025	0.025	5038	0.128
	I+II	A	1059	0.404				
		S	754	0.527	0.080	0.080	907	0.072
	+III	O	1119	0.539	0.086	0.006	937	0.006
		N	356	0.613	0.129	0.043	738	0.032
		D	1186	0.608	0.125	-0.003	771	-0.003
		O	689	0.366				
	IV	N	322	0.460	0.052	0.052	506	0.026
		D	422	0.420	0.039	-0.013	372	-0.005
	I+II	D	1607	0.558				
		J	393	0.585	0.111	0.111	1000	0.111
	+III	F	2964	0.602	0.121	0.010	1679	0.018
		M	2763	0.677	0.176	0.054	2864	0.156
	+IV	A	1105	0.705	0.200	0.024	1934	0.046
M		1685	0.648	0.153	-0.047	1395	-0.065	
	J	1294	0.703	0.198	0.045	1490	0.067	
Cohort 1987							1.475	
1988	I	M	7409	0.157				
		J	12779	0.371	0.026	0.026	10094	0.266
		J	522	0.481	0.060	0.033	6651	0.222
	II	J	3111	0.165				
		J	8158	0.360	0.024	0.024	5635	0.135
		A	240	0.320	0.017	-0.007	4199	-0.031
Cohort 1988							0.592	

$\bar{N}_j$, average numbers of individuals in month, j.

Production

The estimated production for *Streblospio benedicti* was 0.94 g m⁻² for the 1986 cohort, from November 86 to July 87, when a unimodal population was maintained. The different generations of the 1987 cohort yielded a total production of 1.48 g m⁻² for a 14-month period, and, with a mean biomass of 0.27 g m⁻², this gives a value for the production to mean biomass ratio ($P/\bar{B}$) of 5.40. The observed production of the 1988 recruiters yielded a production of 0.59 g m⁻² during the period from May to August. Details of calculations are shown in Table 1. When we applied the average cohort method to estimate the production of *S. benedicti* from November 1986 to November 1987 we obtained a value of 2.61 g m⁻², quite similar to the value obtained by separating cohorts.

The average cohort method was used to obtain the production of the European population of *S. shrubsolii*. Production estimate for this species was 15.65 g m⁻² and with a mean biomass of 3.55 g m⁻² this gives a value for the $P/\bar{B}$ ratio of 4.40. The cohort production interval was assumed to be unity since the production period was exactly one year. Details of calculations are shown in Table 2.

Although secondary production for *Streblospio* populations was considerably higher in Alfacs Bay than in the Great Sippewissett Salt Marsh (Table 1 & 2), $P/\bar{B}$ values for *Streblospio* populations obtained in Alfacs Bay were lower than in the Great Sippewissett

Table 2. Summary of data used in the calculation of the annual production of *Streblospio shrubsolii* following the formula given by Cornet (1986).

Size class (mm)	$\bar{N}_j$ (ind m ⁻²)	$\bar{N}_j - \bar{N}_{j+1}$ (ind m ⁻²)	$\bar{w}_j$ (mg)	$\bar{N}_j * \bar{w}_j$ (mg m ⁻²)	Mean w (mg)	Biomass lost (mg m ⁻²)	P_j (mg m ⁻²)
0.08	0		0.0007				
0.12	4381	-4380.9	0.0027	11.84	0.0014	-5.94	-107.0
0.16	5464	-1083.3	0.0067	36.66	0.0043	-4.61	-83.04
0.20	2474	2989.8	0.0132	32.73	0.0094	28.16	506.9
0.24	2331	143.5	0.0227	53.01	0.0173	2.49	44.8
0.28	1755	575.6	0.0357	62.68	0.0285	16.40	295.3
0.32	1053	702.1	0.0526	55.35	0.0433	30.42	547.5
0.36	1642	-589.0	0.0737	121.02	0.0622	-36.66	-659.8
0.40	2739	-1096.7	0.0995	272.58	0.0856	-93.93	-1690.7
0.44	3133	-393.7	0.1304	408.53	0.1139	-44.86	-807.4
0.48	3356	-223.5	0.1667	559.60	0.1475	-32.97	-593.4
0.52	3216	140.1	0.2089	671.69	0.1866	26.14	470.6
0.56	2246	969.7	0.2571	577.55	0.2317	224.72	4044.9
0.60	1364	882.6	0.3119	425.25	0.2832	249.93	4498.8
0.64	523	841.0	0.3734	195.16	0.3412	286.99	5165.8
0.68	91	431.7	0.4421	40.19	0.4063	175.41	3157.4
0.72	46	45.4	0.5183	23.60	0.4787	21.71	390.9
0.76	8	38.0	0.6022	4.54	0.5586	21.23	382.1
0.80	0	7.5	0.6022	4.544	81.79		
Total	35821			3552			15645
						$P/\bar{B} =$	4.40

N_j , average number of individuals of class j ; ($N_j - N_{j+1}$), number of individuals lost from one class to the next; w_j , dry weight of individuals belonging to class j ; $N_j * w_j$, biomass of class j ; Mean w , geometric mean of dry weight of two successive classes.

Salt Marsh. Values of $P/\bar{B}$ for *S. benedicti* obtained in Great Sippewissett Marsh are consistent with the values (5.5) observed for *Streblospio* species in the Lynher Estuary (Warwick *et al.*, 1979).

DISCUSSION

Morphological and reproductive differences separate *Streblospio benedicti* and *S. shrubsolii* (Dean, 1965; Cazaux, 1985). Although morphological variation related to reproductive output has been observed in American populations of *S. benedicti* (Rice, 1991), it is not clear if the *S. benedicti* complex could be a group of cryptic species; however Levin (1984a) successfully interbred populations of *S. benedicti* that displayed different modes of larval development. *Streblospio benedicti* shows a wide plasticity in life history strategies (planktotrophic *vs* lecithotrophic dispersal). This reproductive variability could be responsible for its success under different natural conditions (Levin, 1984b). Although planktotrophic reproductive output has been observed for *S. shrubsolii* (Wolff, 1973; Manoleli, 1980), lecithotrophic development should be the most common developmental type in this species (Cazaux, 1985). *Streblospio shrubsolii* may also be a poecilogeneous species, as is *S. benedicti*, but it seems that it is not as powerful a competitor as *S. benedicti* in similar circumstances. This possibility has been suggested by da Fonsêca-Genevois & Cazaux (1987) to explain the replacement of *S. shrubsolii* by *S. benedicti* in the Loire Estuary. Nevertheless, it is clear that both species are adapted to occupy similar niches in estuarine and brackish waters.

Both *Streblospio* populations seem to be capable of reproducing within less than two months of settlement. Fecundity maxima occurred at 7, 13-14 and 23-26 weeks in lecithotrophic populations of *S. benedicti* reared under laboratory conditions (Levin *et al.*, 1987). Our field population of *S. benedicti* may follow the same pattern. The spawning period for *S. shrubsolii* is shorter in Arcachon Bay, France (Cazaux, 1985) than the spawning period of *S. benedicti* in New England, USA (Dean, 1965; Grassle & Grassle, 1974; Whitlatch, 1977; our observations). Moreover, the spawning period seems to be longer for *S. benedicti* in California (Levin, 1984a) and a constant recruitment was observed for *S. shrubsolii* in the western Mediterranean. These observations suggest that reproduction may occur throughout the year in *Streblospio* populations located in warm sites, such as California or the western Mediterranean. In cooler sites in northern regions, *Streblospio* populations exhibit, independently of taxa, short spawning periods, and recruitment is reduced drastically.

Temperature has a great influence on the reproduction of *Streblospio* species. *Streblospio benedicti* reproduces in a temperature range of 7.5-30°C, although the level of activity varies with temperature (Levin & Creed, 1986). In laboratory experiments Levin & Creed (1986) showed that the highest levels of reproductive activity were observed from 16 to 21°C. Our field observations confirm these results for *S. benedicti*; reproduction in Great Sippewissett had two peaks of activity, spring and early autumn, just when the above temperatures were recorded in the field, and reproductive activity ended when temperatures fell below 10°C. Although there is no similar experimental laboratory data for *S.*

shrubsolii, the highest recruitment peaks in Alfacs Bay were observed in months with the same range of temperature, and the lower recruitment peaks, observed in winter, were related to average monthly temperatures around 10°C. Differences in the number of recruits in spring and autumn could be due to food availability, which has been mentioned as the main factor for the explosion of the species in nature (Levin, 1986; Wiltse *et al.*, 1984; Sardá *et al.*, 1992), or to gating mechanisms (Olive, 1984). The effect of temperature on reproductive response for *S. benedicti* proposed by Levin & Creed (1986) seems to be similar in the two populations of *Streblospio* species studied in this paper, and could be a general pattern for *Streblospio* populations, independently of taxa.

Figure 7. (A) Relationship between mean annual abundance (y) and mean annual temperature (x) for different *Streblospio* populations. Line is linear regression: $y = -59.67 + 6.114x$, $r^2 = 0.76$, $P < 0.01$. (B) Relationship between mean annual abundance (y) and annual temperature fluctuation (x) for different *Streblospio* populations. Line is linear regression: $y = 71.29 - 3.190x$, $r^2 = 0.79$, $P < 0.01$. (L, Levin, 1984a; Z, Zajac & Whitlatch, 1982; F, da Fonsêca-Genevois & Cazaux, 1987; B, Bachelet, 1987; W, Watling, 1975; R, Rhoads *et al.*, 1978; A, Alfacs; and S, Sippewissett). To avoid problems of the different mesh-sizes employed by the various authors, data were normalized to individuals retained by a mesh of 500 µm according to Bachelet (1984).

Using field data of both species from various authors (Watling, 1975, in Delaware, USA; Rhoads *et al.*, 1978, in Long Island, USA; Zajac & Whitlatch, 1982, in Connecticut, USA; Bachelet, 1987, in the Gironde Estuary; Levin 1984a, in San Diego, USA; da Fonsêca-Genevois & Cazaux, 1987, in the Loire Estuary, France; our present data), we plotted mean annual abundance of *Streblospio* species against mean annual temperature and annual temperature fluctuation in these regions (Figure 7). Mean annual temperature was positively correlated with abundance ($r^2 = 0.76$, $P < 0.01$) whilst annual temperature fluctuation was negatively correlated with abundance ($r^2 = 0.80$, $P < 0.01$). The reproduc-

tive activity of *Streblospio* species extends largely throughout the year in warmer areas of temperate latitudes. In colder areas of temperate latitudes, with large temperature fluctuations, the reproductive activity tends to be concentrated in short periods of the year. The constant reproductive output observed in warm areas led to higher mean annual densities and biomass than in cold areas. *Streblospio* populations of warm temperate latitudes seem to be more productive than those inhabiting colder areas, although associated P/B ratios tended to be lower in the former than in the latter.

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