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Streblospio shrubsolii (Polychaeta : Spionidae): temporal fluctuations in size and reproductive activity.

Claudio LARDICCI*, Giulia CECCHERELLI & Francesca ROSSI
Dipartimento di Scienze dell'Uomo e dell'Ambiente, Università degli Studi di Pisa,
Via Volta 6, Pisa I-56126
Fax: 39 50 49694
**e-mail: lardic@discat.unipi.it*

Abstract: Temporal fluctuations in size and reproductive activity of a *Streblospio shrubsolii* population were studied in a small brackish basin, to evaluate how these features influenced population dynamics and determine the persistence of this species in such an unstable environment. In the three study years, *S. shrubsolii* exhibited continuous reproduction from March to November but with two seasonal peaks in late spring and autumn. Larvae were lecithotrophic and developed between the female body and the tube wall. Individual fecundity showed significant differences between seasons, with trends coinciding with variations in mean female size. Changes in population size structure gave evidence that density fluctuations resulted mainly from recruitment during spring-early summer, or autumn. Potential larval production patterns peaked 1 or 2 months prior to periods of maximal abundance, and exhibited a progressive increase especially during the autumn of the study periods. Different life-history traits and different levels in reproductive activity were observed both on the temporal (study population) and spatial scale (other populations described) in *S. shrubsolii*. It is suggested that *S. shrubsolii* life-history flexibility may represent a successful way to maximize fitness in a fluctuating environment

Résumé : Streblospio shrubsolii, *(Polychaeta : spionidae), fluctuations temporelles de la taille et de l'activité reproductrice d'une population.*
Les fluctuations temporelles de la taille et de l'activité reproductrice d'une population de *Streblospio shrubsolii* ont été étudiées dans un petit bassin saumâtre pour élucider comment ces caractères influencent la dynamique de la population et déterminent la persistance de l'espèce dans ce milieu instable. *S. shrubsolii* a montré une reproduction continue de mars à novembre, avec deux maximums saisonniers à la fin du printemps et en automne au cours des trois années étudiées. Les larves sont de type lécithotrophe et sont incubées dans le tube de la femelle. La fécondité individuelle a montré des différences saisonnières significatives liées à la taille moyenne des femelles. Les variations de la structure en taille de la population confirment que les fluctuations de la densité sont liées principalement au recrutement qui a lieu au printemps-début de l'été et en automne. La production larvaire atteint son maximum principalement deux mois avant l'abondance maximale et montre une augmentation progressive surtout en automne. Pour *S. shrubsolii* les différentes caractéristiques du cycle vital et les différents niveaux d'activité reproductrice ont été observés sur une échelle temporelle (la population étudiée à l'Île d'Elbe) et sur une échelle spatiale (les populations étudiées ailleurs). Il semble qu'un cycle vital flexible soit, chez cette espèce, un important moyen pour optimiser la survie dans les milieux variables.

Keywords : *Streblospio shrubsolii*, population ecology, life-cycle, reproductive activity, Island of Elba, Western Mediterranean

Introduction

Streblospio shrubsolii (Buchanam, 1890) is distributed along European temperate Atlantic (Marchand & Elie, 1983,

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1983, Bachelet 1984, Cazaux, 1985) and Mediterranean coasts (Bellan, 1964, Lardicci, 1987, Koukouras & Russo, 1991, Sardà & Martin, 1993). *S. shrubsolii* is a small (<2 cm long), tube-building, sediment-living annelid, found in high densities in intertidal flats and brackish waters characterized by high levels of organic matter in their sediments. It is highly tolerant of physico-chemical parameter fluctuations (particularly salinity).

S. shrubsolii is the dominant species of many benthic communities, and has been widely reported to increase in abundance following natural or organic enrichment-related disturbances (predation, anoxic crisis, H_2S production) in brackish and estuarine areas (Cazaux, 1985, Castelli & Prevedelli, 1993, Sardà & Martin, 1993). However, its seasonal dynamics and life-cycle have seldom been studied (Cazaux, 1985, Sardà & Martin, 1993). Conversely, seasonal patterns of abundance, life-history, demography, larval development and feeding behavior in different populations of *Streblospio benedictii* Webster, 1879 are well documented (Levin, 1984a, Levin *et al.*, 1987). *S. benedictii* also seems to contribute in deposit feeding assemblages of North America (Sardà & Martin, 1993).

A detailed field study on the population ecology of *S. shrubsolii* was performed in a small brackish basin in the Western Mediterranean (Island of Elba) for roughly three years. The aims of this study were to analyse the reproductive strategies of the population observed and any temporal variations in population characteristics and reproductive activity, as well as to determine how these life-history traits could influence the population dynamics and the persistence of the species in an unstable environment.

Material and Methods

Study site and field sampling

The study area (Salina) is situated in Portoferraio Bay, on the north coast of the Island of Elba (Western Mediterranean). It is an intertidal basin of 50 cm average depth with a surface area of 6400 m^2, surrounded by a series of barriers which permit water exchange only at high tide (30 cm mean tidal range). A small drainage channel is the major input of fresh water. The silty-sand sediments of the Salina are moderately polluted by heavy metals such as Pb, Fe, Zn and Cr. This area is characterized by large fluctuations in environmental factors, due to irregular fresh and sea water supply, and to seasonal balance between evaporation and rainfall. Oxygen, temperature, and salinity were measured on the bottom every month during ebb and rising tide (10 replicates in all) on each sampling date using a multiparametric probe (Idronaut Mod. 501).

The *S. shrubsolii* population was sampled every month from July 1990 to February 1993. On each sampling date, four core samples were taken randomly in a 20x20 m area, using a 6 cm diameter plastic tube (surface area of 28.26 cm^2) inserted to a depth of 15 cm. For each sample the fauna was anaesthetized during 15 minutes in a magnesium chloride solution (8%), then fixed in 4% formalin-sea water solution *in situ*. Samples were sieved through a 150 µm mesh in the laboratory and all *S. shrubsolii* specimens were then collected and counted.

Population data

The size of individuals was based on the number of setigers. For fragmented worms (60%) the number of setigers (S) was estimated using the equation: $S = 95{,}1075\ W + 6{,}5346$ ($R^2 = 0.814$, $p < 0.000001$, $N = 433$) where W was the width of the 5th setiger in mm.

Individuals were grouped into 6 size-classes including worms with 19-31 setigers (J_1), 32-43 (J_2), 44-49 (A_1), 50-55 (A_2), 56-61(A_3) and >61(A_4) setigers. The juvenile and adult classes were distinguished on the basis of the first reproduction size (see Results). Size-classes within juveniles and adults were chosen arbitrarily because no quantitative data on the *S. shrubsolii* growth rate were available in the literature. We assumed a greater growth in juvenile stages in comparison with adults, as already observed under laboratory conditions (Lardicci, unpublished) and in a Spanish population of this species (Sardà & Martin, 1993).

Female worms were distinguished by the presence of oocytes within paired ovaries in anterior setigers or by the presence of larvae between the female body and the tube wall. Oocyte sizes (mean diameter of 10 oocytes) were measured (maximum diameter) through the transparent body wall of the females using a microscope with an ocular micrometer. Fluctuations in reproductive activity were studied by the observation of mean oocyte diameter for each female collected every month. The first gametogenic setigers and the total number of oocyte-containing setigers were also counted. Collected larvae were classified according to the developmental phases described by Cazaux (1985). Fecundity was measured only in females with intact gametogenic setigers (90% of total females). Because two day larvae, as defined by Cazaux (1985), appeared to adhere tightly to the female body surface, mean number of such larvae per setiger was calculated from 30 females observed under a microscope. Potential individual fecundity was estimated by multiplying this mean number by the total number of gametogenic setigers for each female. Fecundity was also estimated on this basis for females who had ripe oocytes in the ovary and presumably would release them during the period between sampling dates. We considered ripe oocytes to be those with a well developed yellow-orange yolk and with a maximum diameter between 200-300 µm.

Abundance data were transformed $(x + 1)^{0.5}$ and analysed using one-way ANOVA. Cochran's test was also performed to check for homogeneity of variances. Temporal fluctuations in oocyte sizes, female sizes and fecundity were analysed by Kruskal Wallis non-parametric tests. Female sizes and fecundity data were combined into seasonal groups (spring: March, April, May; summer: June, July, August; autumn: September, October, November; winter: December, January, February). The relationships between larval production and population abundance were analysed by a Cross correlation analysis. All analyses were carried out using Statistica 5.0.

Results

Environmental data

Throughout the study period, mean salinity values ranged from 38 PSU in summer to 25 PSU in winter and dissolved oxygen values exhibited high mean values (from 6 to 15 ppm) during most seasons except for late summer 1990 (3 ppm). Data on rainfall showed peaks above all in autumn and winter, while temperature ranged from 30-34 °C in summer to 12-14 °C in winter (Fig. 1). The associated macrozoobenthos consisted mainly of polychaetes such as *Capitella* cf. *capitata*, *Cirriformia tentaculata* (Montagu, 1808), *Hediste diversicolor* (O.F. Müller) and bivalves such as *Abra segmentum* (Récluz, 1843) and *Ruditapes decussatus* (Linneus, 1758) (Lardicci, 1987).

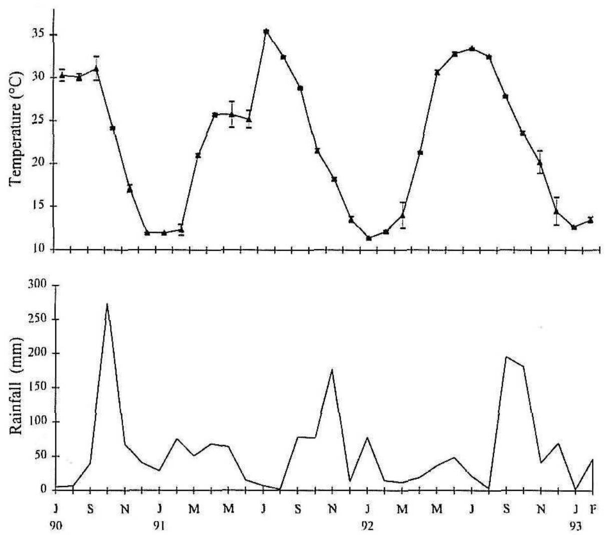

Figure 1. Fluctuations of temperature (mean value ± SE) on each sampling date and monthly rainfall values in the Bay of Portoferraio during the study period.

Figure 1. Fluctuations de la température (valeur moyenne ± SE) à chaque échantillonnage et valeurs de la pluviosité mensuelle dans la Baie de Portoferraio pendant la période de prélèvements.

Population dynamics

S. shrubsolii density exhibited significant temporal fluctuations (1-way ANOVA, $F_{31,96} = 3{,}169$ $p < 0.0001$; $C = 0.147$ $p > 0.05$) in the study period, with highest values in November 1990, January, June and November 1991, July and December 1992 and lowest values in August, September and December 1990 and September 1991. An overall general numeric increase in abundance during the last study months was also noticed (Fig. 2).

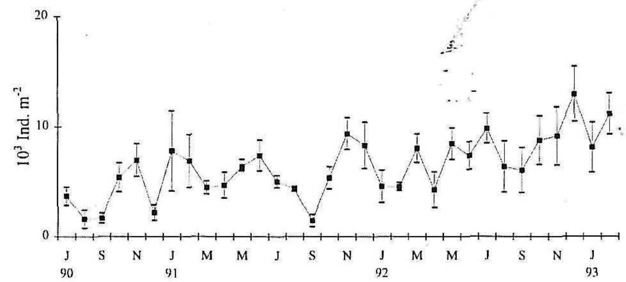

Figure 2. *Streblospio shrubsolii.* Fluctuations in population density (mean value ± SE) between July 1990 and February 1993.

Figure 2. *Streblospio shrubsolii.* Fluctuations de la densité de la population (valeur moyenne ± SE) de juillet 1990 à février 1993.

Newly recruited juveniles (19 to 31 setigers) occurred throughout virtually the entire study period, although densities were low in winter-early spring and in August 1990 and 1991. Recruitment was high in late spring-early summer especially and in late autumn of these years and the J_1 size class represented 2 to 25% of the entire population in spring-early summer and 30% to 50% in autumn. Adult size classes (> 43 setigers) comprised most of the population when recruitment was lower or extremely diminished. Similar trends were also observed in 1992 but with a higher percentage of juveniles, above all in spring and summer, in comparison with previous years (Fig. 3).

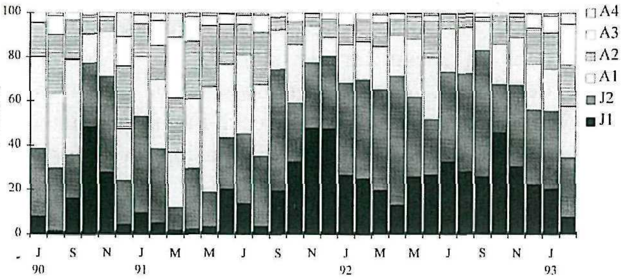

Figure 3. *Streblospio shrubsolii.* Fluctuations in population structure (size-classes) during the study period.

Figure 3. *Streblospio shrubsolii.* Fluctuations de la structure de la population (classes de taille) pendant la période de prélèvements.

Presence of oocytes was observed first in the J_2 size class (32-43 setigers). These females represented 9.6% of the total number but 80% of this size class had 41-43 setigers. Only in September 1992 was a noteworthy percentage of females with a size between 38 and 40 setigers found. No reproductive activity (females with visible oocytes or larvae) was observed in August 1990, in december, 1991, 1992 and in January 1991, 1992, while an increase in percentage of adult females (size > 43 setigers) was recorded in spring (March-May) and late summer-autumn (September-October) (Fig. 6). The proportion of adult females was quite low in the other months (Fig. 4). Oocytes showed significant temporal differences in size (χ^2 = 66.71 d.f. = 24 p<0.0001), with smallest diameters occurring above all in winter (Fig. 5). The first gametogenic setiger ranged from the 21th to 30th segment and the mean number of gametogenic setigers was 10.81 ± 0.15SE (n = 433). Females contained a very small number (10-38) of large ripe oocytes (230 ± 3.19SE maximum diameter, n = 115) and the mean value of larvae or oocytes per setiger of gametogenic segments was two (n = 115).

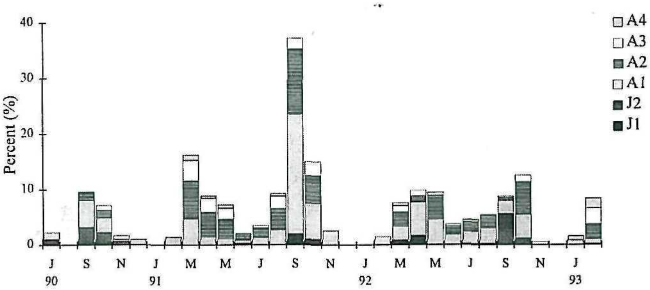

Figure 4. *Streblospio shrubsolii.* Fluctuations in the percentage of females in different size classes of the population.

Figure 4. *Streblospio shrubsolii.* Fluctuations du pourcentage des femelles dans les différentes classes de taille de la population.

Individual potential fecundity exhibited significant differences beween seasons (χ^2 = 39.81 d.f. = 8 p< 0.0001) (Fig. 7a), with highest values in spring and summer 1991, spring 1992 and winter 1993. There were also significant differences in mean female size (χ^2 = 49.67 d.f. = 8 p< 0.0001) (Fig. 7b) with a trend somewhat similar to that of fecundity. Mean female size in each month accounted for 70.3% of the variation in fecundity using an exponential model (Fig. 8).

Cross correlation analysis between potential larval production and population density showed a positive correlation (r = 0.38 p< 0.05) for a time lag of two months. Larval production showed minimum values in winter (≅ 1500, 11000 larvae.m^{-2}), maximum in spring (≅ 69600, 84000 larvae.m^{-2}) and in autumn (≅ 25000, 51600, 79000 larvae.m^{-2}) (Fig. 6).

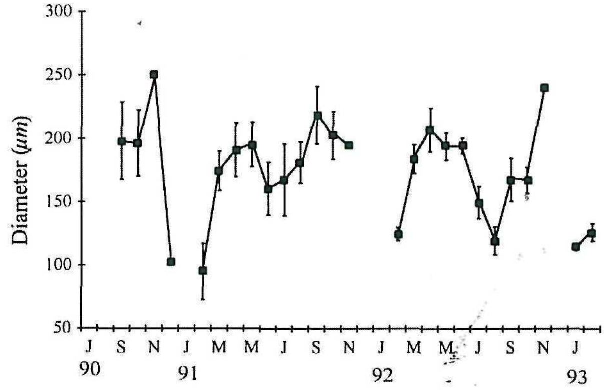

Figure 5. *Streblospio shrubsolii.* Oocyte diameters (mean values ± SE) during the study period.

Figure 5. *Streblospio shrubsolii.* Diamètres des ovocytes (valeur moyenne ± SE) pendant la période de prélèvements.

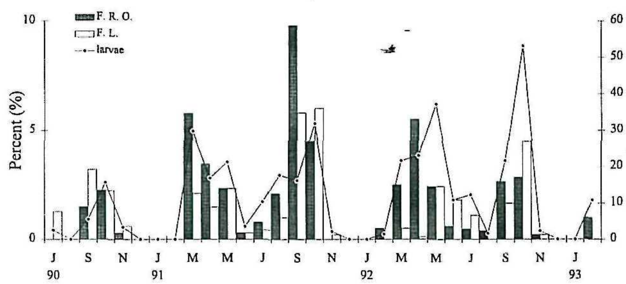

Figure 6. *Streblospio shrubsolii.* Fluctuations in the percentage of females with ripe oocytes (F.R.O.), of females with larvae (F.L.) and potential production of larvae during the study period.

Figure 6. *Streblospio shrubsolii.* Fluctuations du pourcentage de femelles avec ovocytes mûrs (F.R.O.), de femelles avec larves (F.L.) et de la production potentielle larvaire pendant la période de prélèvements.

Discussion

The *S. shrubsolii* population of the Island of Elba reproduced during a continuous period between March and November, with two annual peaks in late spring (May-June) and in autumn (15-25°C temperature range). Temperature has also been shown to influence reproduction in *Streblospio* species (Levin & Creed, 1986, Sardà & Martin, 1993). Reproductive activity disappeared or was strongly reduced at lower temperatures in winter and at higher temperatures in summer. Similar responses of reproductive activity to temperature have already been documented for *S. benedictii* which reproduces in a temperature range of 7.5-30°C, with highest reproductive level from 16 to 21°C (Levin & Creed, 1986, Fonsêca-Genevois & Cazaux, 1987) and for *S. shrubsolii* in Alfacs Bay (Ebro Delta) (Sardà &

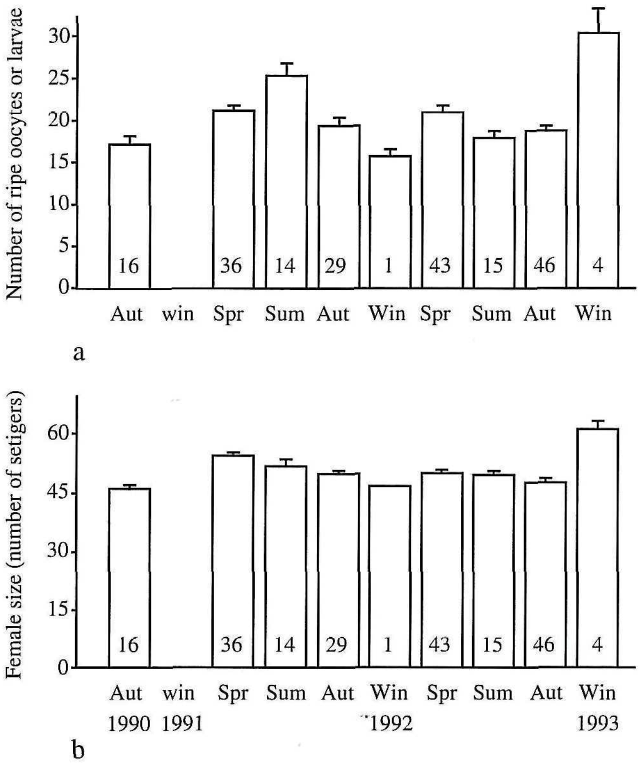

Figure 7. *Streblospio shrubsolii.* a: variations in the potential fecundity : mean value (± SE) of number of ripe oocytes or larvae by female. Numbers of females are indicated in each histogram.

b: variations in the size of females with ripe oocytes or larvae (mean value ± SE). Numbers of females are indicated in each histogram.

Figure 7. *Streblospio shrubsolii.* a: variations de la fécondité potentielle : valeur moyenne (± SE) du nombre d'ovocytes mûrs ou de larves par femelle. Les nombres de femelles sont indiqués dans chaque histogramme.

b : variations de la taille des femelles avec ovocytes mûrs ou larves (valeur moyenne ± SE). Les nombres de femelles sont indiqués dans chaque histogramme.

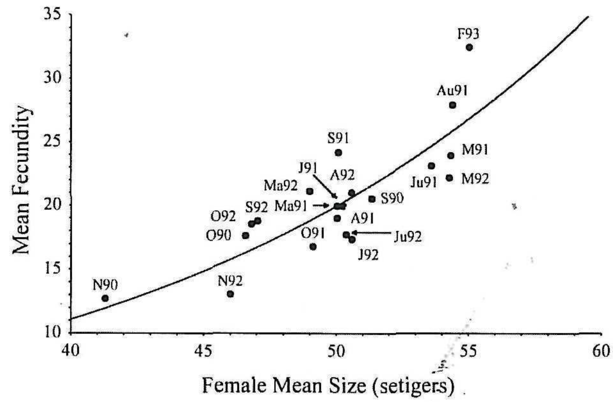

Figure 8. *Streblospio shrubsolii.* Relationship between female mean size (based on number of setigers) and mean fecundity (number of ripe oocytes or larvae per female). Exponential model is
Fecundity = $e^{[0.04 + 0.059 \text{ size (setigers)}]}$ ($R^2_{adj} = 70.28$ $p < 0.0001$).
Ma= May; Ju= July; Au= August

Figure 8. *Streblospio shrubsolii.* Relations entre la taille moyenne des femelles (évaluée d'après le nombre de segments sétigères) et la fécondité moyenne (nombre d'ovocytes mûrs ou de larves par femelle). Le modèle exponentiel est:
Fécondité = $e^{[0.04 + 0.059 \text{ size (setigers)}]}$ ($R^2_{adj} = 70.28$ $p < 0.0001$).
Ma= mai; Ju= juillet; Au= août.

Martin, 1993). Furthermore Chu & Levin (1989) have recently shown experimentally the synergistic effect of temperature and photoperiod in *S. benedictii* growth and reproduction. Synergistic interactions among environmental cues may help individuals to compensate for annual fluctuations of these parameters.

From these results Chu & Levin (1989) predicted that the *S. benedictii* reproductive season would vary with latitude since inhibition of the activity during fall and winter occurred earlier and lasted longer in the populations at higher latitudes than at lower ones. Although there are no similar experimental laboratory data for *S. shrubsolii*, field data seem to confirm this hypothesis. In cool temperate areas, with large temperature fluctuations, reproductive activity tends to be concentrated in short periods of the year, while reproduction extends throughout the year in warm temperate areas (Sardà & Martin, 1993). Reproductive activity along the French Atlantic coast was observed only in April-May or in June-July (Bachelet, 1984, Cazaux, 1985) while in the Ebro Delta along the Spanish Mediterranean coast reproductive activity was observed throughout the year, although it was lower in winter.

Reproductive activity in the *S. shrubsolii* population of Elba showed an intermediate situation with two peaks in late spring and autumn, a decrease in mid summer and a strong reduction in winter. Many macrofaunal species of this basin exhibited a similar reproductive strategy (Lardicci, 1987). Such patterns suggested that increases in reproductive activity may be linked not only to more favorable temperature and photoperiod, but also to a probable concomitant increase in the food resource, which may improve juvenile and adult survival and/or sustain the increase in larval production.

Many authors have stressed both the role of nutrition (bottom-up control) (Marsh & Tenore, 1990, Zajac, 1991b) and of predation due to fish and crabs, (top-down control) (Foreman *et al.*, 1995) in regulating the population dynamics and demography of estuarine benthic populations. Foreman *et al.* (1995) observed sharp predation effects on invertebrate abundance, above all in summer. But food resources, in particular essential nutrients, could also constitute limiting factors in the summer season (Marsh &

Tenore, 1990). Although no direct measurements of these parameters were performed during the study period, an increase in sedimentation due to a greater discharge of fresh water, or the presence of phytoplanktonic blooms (Innamorati *et al.*, 1989) was observed in spring and autumn in the Bay of Portoferraio (Elba Island). The increase in *S. shrubsolii* juvenile classes coincided with these inputs while the population decrease, at the end of summer (September), may be due to an increase in predation.

The agreement between population density and potential larval production patterns (significant correlation 2 months before the maximal abundance periods) suggests small-scale recruitment. Larval recruitment into parental populations is very common in unstable environments (Levin, 1984b, Zajac, 1991a) and has been considered as an adaptive strategy to local conditions, since the export of locally adapted individuals would not be beneficial for the population (Levin, 1984b). The females of *S. shrubsolii* produced a smaller number of oocytes in comparison with other polychaetes (Schroeder & Hermans, 1975). Larvae collected in Elba exhibited lecithotrophic developmental stages similar to those described experimentally by Cazaux (1985), in an Arcachon population, with larvae developing between the female body and the tube wall and by Levin (1984a), in a lecithotrophic population of *S. benedictii.* Brood protection in *S. shrubsolii* reduces larval mortality and removes the risk of predation. In the Arcachon population larvae did not leave the female tube until they reached 16 setigers in size. In the natural population of Elba, larvae were probably released at the same size (the smallest size collected was 19 setiger) and subsequently colonized the sediment. Abolition of the planktonic step and direct colonization of the substrate are common features of the most abundant macrofaunal species of this biotope (Lardicci, 1987), and appear to be the most favourable way of maintaining a high population density in stressed shallow-water habitats (Levin, 1984b). Our data confirm that lecithotrophic development is likely to be the most common development type of *S. shrubsolii* (Cazaux, 1985, Sardà & Martin, 1993) although planktotrophic reproductive output has also been observed for this species (Manoleli, 1980).

Three-year observation of population size-classes gave evidence of a clear seasonal trend. The smallest size-class was present in all study months, although its presences ($\geq 20\%$) was greater in spring-early summer and in autumn. This class increased until it represented $> 40\%$ of the population in October 1990, November-December 1991 and October 1992. Such a pattern was at variance with that described by Sardà & Martin (1993) for another *S. shrubsolii* population in the Ebro Delta, where juveniles were present throughout the year without appreciable fluctuations except for a small decrease in winter. However, the dominance of juvenile classes in late spring and autumn was observed in two *S. benedictii* populations of North Carolina (Levin & Hugget, 1990) and Massachusetts (Sardà & Martin, 1993). Furthermore a seasonal trend of juveniles with a late spring-early summer peak was also noticed by Whitlatch & Zajac (1982), Levin (1984b) and Marsh & Tenore (1990) in *S. benedictii* populations of many other North American sites.

Temporal fluctuations in fecundity, related to numbers of gametogenic setigers, varied with changes in female size; thus the presence of large females in August 1991 and in February 1993 coincided with a high fecundity. Temporal differences in gametogenic setiger numbers were also observed in a *S. shrubsolii* population of the Ebro Delta (Sardà & Martin, 1993), with the highest values of fertile setigers (18-20) found in January-March and August, and the lowest (8) in April-June and October. This population showed also a different location of the first gametogenic setiger (ranging between the 24th and 27th setiger) in comparison with the Elba (21th-30th) and Arcachon populations (21th-23th).

A progressive increase in potential larval production during autumn coincided with a progressive decrease in density of *Capitella* cf. *capitata*, a species with the same seasonal reproductive activity (Lardicci & Ceccherelli, 1994). The *C.* cf. *capitata* decrease in abundance was probably due to heavy autumn rainfall, during the study years, after an extended period (1987-89) of dry weather in the Bay of Portoferraio (Pinna, 1991). Actually, *C.* cf. *capitata* is less tolerant of salinity fluctuations (Bonvicini Pagliai & Cognetti, 1982) than *S. shrubsolii* and the autumn has been shown to be a critical period for *Capitella* reproduction and settlement. A negative relationship between the densities of the two groups, tube-building spionids such as *S. shrubsolii*, and free-burrowing annelids such as *C. capitata* or oligochaetes, was pointed out by several authors (McCann & Levin, 1989, Sardà *et al.*, 1995). In addition, the existence of interactions between *S. benedictii* and *C. capitata* due to competition for food and space was shown in an estuarine environment (Whitlach & Zajac, 1985). Increase in food availability could be responsible for the high individual fecundity of *S. shrubsolii*, high female size and the increase in percentage of females smaller than 43 setigers (size of first reproduction), at the end of the study period, when heavy rainfall occurred.

The population dynamics of *S. shrubsolii* on the Island of Elba thus exhibited temporal trends which could vary in magnitude on the basis of fluctuations in habitat conditions. Differences in life history traits and in reproductive activity during the study period influenced the population dynamics and demography and also induced variations in population abundance and size patterns over the short term. Such fluctuations, which were similar to those described in other spionid species such as *S. benedictii* or *Polydora lignii* (Webster, 1879) (Levin & Hugget, 1990, Zajac, 1991b) or other opportunistic species such as *Capitella capitata* (Fabricius, 1780) (Tsutsumi & Kikuchi, 1984), should therefore be considered adaptative strategies to accommodate the set of environmental characteristics. The evolution of a flexible life-history in response to temporal and spatial heterogeneity in their habitats, together with a small scale colonization ability, can be regarded as successful ways to maximize the fitness and persistence of *S. shrubsolii* in fluctuating environments.

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