LIFE HISTORY AND PRODUCTION OF *CAPITELLA CAPITATA* (CAPITELLIDAE: POLYCHAETA) IN RÍO DE LA PLATA ESTUARY (ARGENTINA).

J. P. MARTIN[1, 2] AND R. BASTIDA[2, 3]

ABSTRACT

A benthic survey was carried out from November 1998 to December 1999 in the tidal flats of Bahía Samborombón (Río de la Plata estuary, Argentina), in order to study the population structure, reproductive aspects, growth and secondary production of *Capitella capitata* (Fabricius, 1780). Growth was analyzed using ELEFAN routine, and the secondary production was estimated by Hynes and Coleman's method (1968). *C. capitata* did not present periods of very important recruitments throughout the year; however, the abundance of smallest size classes was higher during summer and autumn. The summer cohort showed a growth rate (K) of 2.05 and a seasonal growth oscillation (C) of 0.6, pointing out that worms grew very slowly during winter months. The life span of this cohort was 13 months. The autumn cohort showed a lower growth rate (K= 1.5) and its growth was lowest during winter. The life span was 15 months for this cohort. *C. capitata* in Punta Rasa presented an extended reproductive period, with absence of activity during winter months. The type of eggs and larvae suggest that *C. capitata* has benthic larval development in the study area, destining its reproductive effort to the production of a low number of eggs, and assuring larvae survival through incubation in brooding tubes. The annual mean biomass in Punta Rasa was 0.117 g m^{-2} (AFDW), with a mean secondary production of 0.23 g m^{-2} y-1 and a P/B ratio of 1.96 y-1. The relatively low density, biomass production and P/B ratio of *C. capitata* in Punta Rasa can be considered as reference values for this species inhabiting undisturbed or moderately disturbed areas.

[1] Centro de Investigaciones de Puerto Deseado, Universidad Nacional de la Patagonia Austral, CC 238, (9050) Puerto Deseado, Argentina. e-mail: martin_jpablo@yahoo.com.ar
[2] Depto. de Ciencias Marinas, Universidad Nacional de Mar del Plata, Mar del Plata, Argentina.
[3] Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET).
Corresponding author: J. P. Martin, Centro de Investigaciones de Puerto Deseado, CC 238 (9050) Puerto Deseado, Argentina. e-mail: martin_jpablo@yahoo.com.ar

INTRODUCTION

The polychaete *Capitella capitata* (Fabricius, 1780) has received special attention from researchers, due to its high density in heavily polluted areas of the world. Thus, it was designed as an important indicator species of organic pollution by several authors (Grassle and
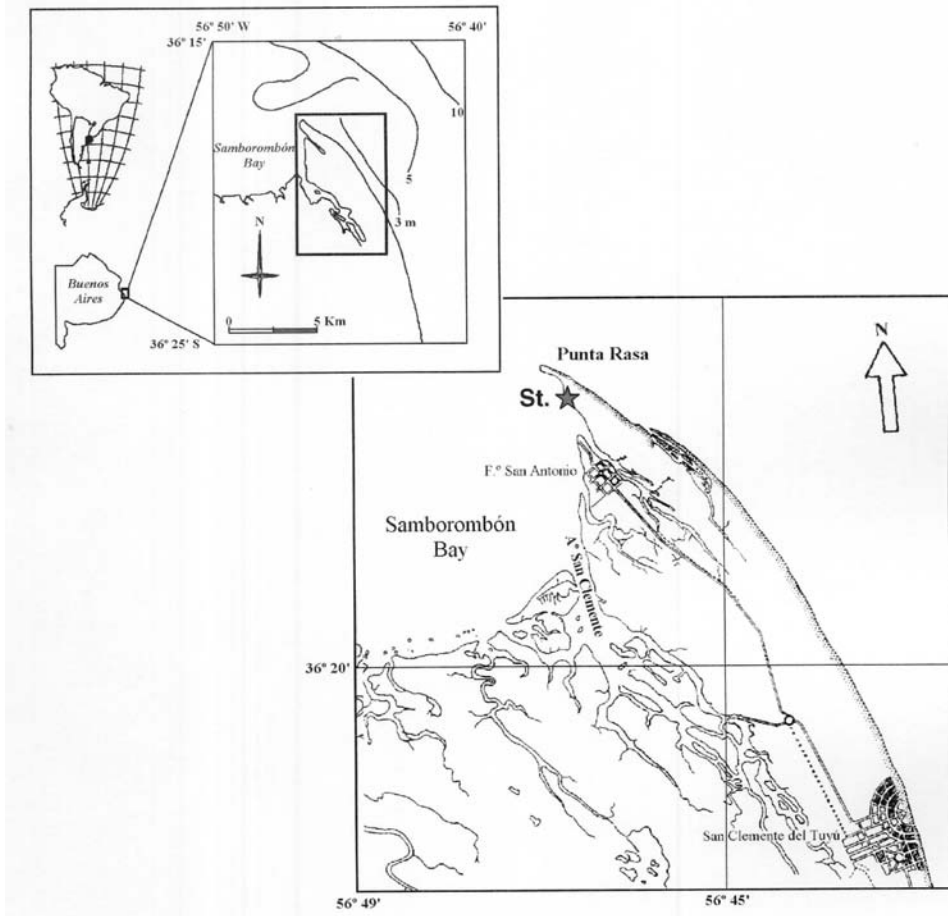
Figure 1.
Study area and sampling station (St.).

Grassle, 1974, 1976; Reish, 1974, 1978). Pearson and Rosenberg (1978) remarked the relation between the declination of benthic communities and the increase of *C. capitata* abundance in polluted areas, which is determined by the life history of this polychaete. *C. capitata* often shows high variations in its reproduction and development strategies (planktotrophic or lecithotrophic) and these could be regulated by environmental conditions (Qian and Chia, 1991a, 1991b, 1992a, 1993).

Capitella capitata is actually considered a sibling species complex, with light morphological differences among species, which can be differentiated through specific analyses (electrophoresis, karyotypes, ADN fingerprint). However, these sibling species can also show distinct patterns in its life cycle, reproduction

and development modes (Grassle and Grassle, 1974, 1976; Holbrook and Grassle, 1984). Intraspecific variations in their life histories could be the result of an evolutive response to the environmental fluctuations and can explain the success of this opportunist species to invade habitats under antropic or natural impact (Grassle and Grassle, 1974).

Population structure, growth, reproductive aspects and seasonal variation of density and biomass of *Capitella capitata* were analyzed in the present study. The main objective was to obtain information about life history and secondary production of this species, in undisturbed or moderately disturbed intertidal sandy flats of low organic matter content at Río de la Plata estuary.

MATERIALS AND METHODS

Study area

Río de la Plata estuary and its oceanic front form a wide and complex ecosystem of great ecological significance, probably one of the main natural phenomena that regulate, together with the Malvinas-Falklands and Brazil currents, the general dynamics and biological production of the Argentine Biogeographical Province (Ieno and Bastida, 1998). The present study was conducted in SE Bahía Samborombón, in the estuarine zone located between Punta Rasa and San Clemente creek (Fig. 1). Punta Rasa, a NW-oriented sandy bar, defines the southern tip of Bahía Samborombón, and its internal margin is dominated by intertidal flats. Due to the low water energy of this area and the great extension of a very low slope beach (< 0.4%), an important fine sand sedimentation takes place (Martin *et al*., 2004).

The tidal amplitude is less than 2 m, with spring tides between 0.37 and 1.46 m and ebb tides between 0.58 and 1.25 m. Surface water temperature ranges from 9 to 25° C, while the salinity ranges between 0.5 and 25 ‰, depending on the tidal level and the influence of both marine and freshwater. The studied zone can be classified as a typical mixohaline (oligohaline to polyhaline) environment (Martin *et al*., 2004).

A low diversity polychaete assemblage was identified in intertidal flats of Punta Rasa, related with low organic matter content and fine sand as the main sediment fraction (0.6 to 2.9% of organic matter and up to 89% of fine sand). This assemblage has *Laeonereis culveri* as dominant species and *Capitella capitata* as subdominant species, being secondary species *Heteromastus similis, Neanthes succinea, Polydora cornuta* and *Scolecolepides sp.* (Martin *et al*., 2004).

Sample collection and analysis

Specimens of *Capitella capitata* were monthly collected in the intertidal region of Punta Rasa (36º 20' S; 56º 45' W) (fig. 1), between November 1998 and December 1999. Three replicates were obtained in each of two different intertidal levels during the ebb tide (six monthly samples) using a manual core sampler (12 cm in diameter and 30 cm depth). The
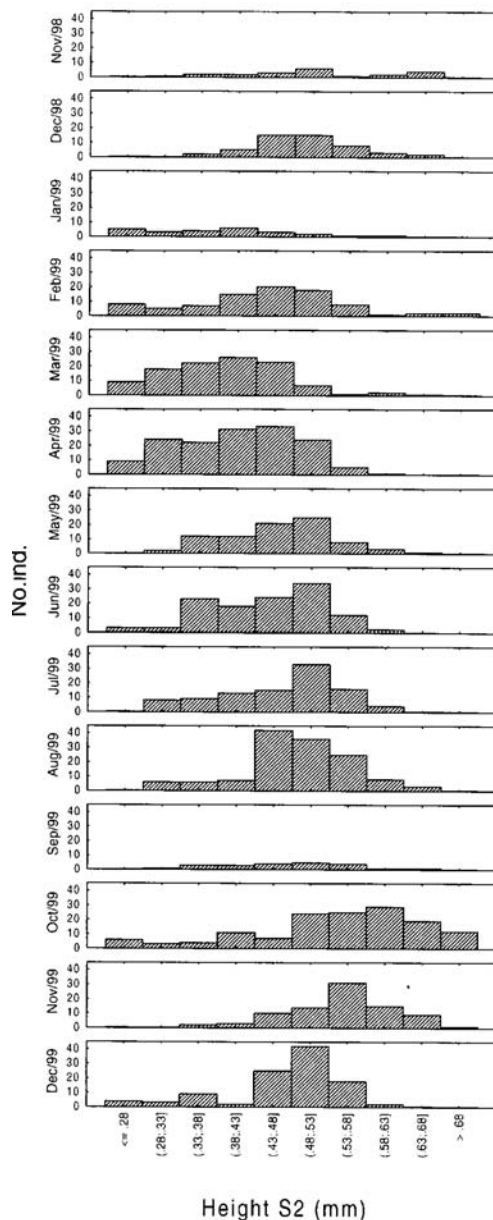

Figure 2.
Population structure of Capitella capitata in intertidal flats of Punta Rasa, measured by means of the second setiger height.

organisms were sorted from the sediments using a 0.1 and 0.5 mm mesh size sieves under a stereo microscope. All samples were preserved in buffered 10% formaldehyde-seawater before analysis. The
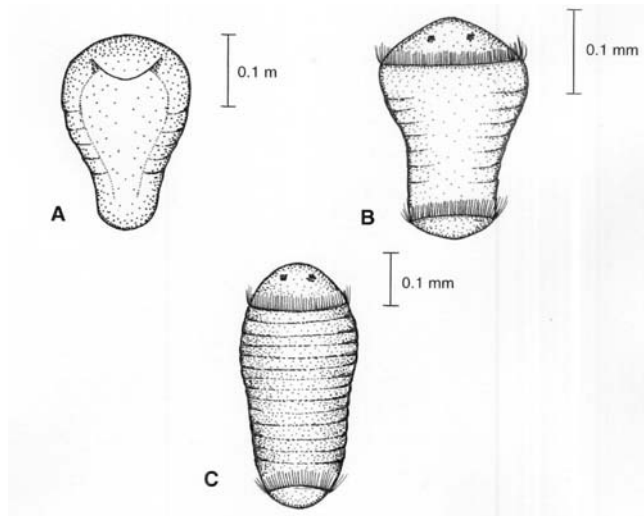
Figure 3.
Larvae stages founded inside brooding tubes. A, early stage with incipient segmentation; B, trochophore; C, metatrochophore.

specimens were identified and counted in order to determine their abundance and density. The population analysed in the present study showed a high homogeneity in the morphological characteristics of the individuals, identified as members of *C. capitata* species. However, specific analyses are required to clarify its position within the *C. capitata* complex.

Body measurements of *Capitella capitata* specimens were carried out using a stereomicroscope to the nearest 0.01 mm. The height of the second setiger (HS2) was measured in all individuals, and the total length was measured in those specimens with unbroken bodies. The height of second setiger was also used to infer worm biomass. A subsample (n= 309) of completed individuals from different size categories and different seasons were measured and afterwards dried in a stove at 70 ºC until a constant dry weight (DW) was obtained to the nearest 0.01 mg. Ash free dry weight (AFDW) was obtained incinerating individuals at 580 ºC in a muffle furnace for two hours.

Females of *Capitella capitata* were examined under a stereomicroscope in order to observe the presence of oocytes in the coelomic cavity. The oocytes were extracted and measured under microscope. Parental brooding tubes were opened and examined under a stereomicroscope and the eggs and larvae inside were counted and measured. Ovigerous females and brooding females (with tubes bearing eggs or larvae) were counted, and their percentage in

population was calculated for all months of the study period.

Data analysis

Due to the high number of broken individuals in the samples, population structure and growth analysis were carried out using the second setiger height as an indicator of polychaete size classes. The entire specimens (n= 247) were used to make the regression analysis between the second setiger height (HS2) and the total body length (TL) of the worms. The second setiger height showed a close relationship with total body length (TL= -3.370 + 21.247 HS2; R^2= 0.854, P< 0.001), indicating that HS2 could provide a reliable measured of size classes.

The growth parameters of *Capitella capitata* were estimated using computer-based methods of length-frequency data through ELEFAN routine of the FISAT package (Pauly and Morgan, 1987; Gayanilo *et al.*, 1996), from the monthly frequency size classes distribution (from November 1998 to December 1999). A modification of the von Bertalanffy growth curve was used to consider the seasonal oscillation in the growth (Gayanilo *et al.*, 1996):

$$Lt = L_\infty \{1 - \exp[-K(t-t_0)+(KC/2\pi)\, sen(2\pi(t-t_s)) - (KC/2\pi)\, sen(2\pi(t_0-t_s))]\},$$

were Lt is the size at time t; L_∞ the asymptotic size; K the von Bertalanffy growth constant; t_0 time at

size 0; C a constant expressing the amplitude of seasonal oscillation of growth and ts the starting point of oscillation with respect to t = 0. The ts parameter is related with **WP** (Winter Point, time of the year when growth is lowest) trough the equation:

$$t_s = WP - 0.5 \text{ year.}$$

The growth parameters were estimated in two steps: 1) preliminary estimation of L_∞ by the method of Wetherall (1986) modified by Pauly (1986), and 2) utilisation of estimated L_∞ for fitting a new growth curve to the size frequency data, using the **Rn** goodness of fit index of the ELEFAN. Life span was estimated from the L_{max}, e.g. the 90% of the asymptotic length (L_∞) in the von Bertalanffy growth curve (Pagliosa and Lana, 2000).

A regression between the second setiger height (**HS2**) and the ash free dry weight (AFDW) was done in order to estimate the total biomass and its variation trough the year:

AFDW= 0.042 + exp[-9.667 + (11.647 **HS2**)] ; R^2= 0.998 (P < 0.01).

Annual secondary production was estimated following the method propose by Hynes and Coleman (1968), later corrected by other authors (Benke, 1979; Menzie, 1980). This method was used following Cornet (1986), applying the equation:

$$P = 12/CPI \left[\Sigma \, i \, (N_j - N_{j+1}) \, (M_j \, M_{j+1})^{0.5} \right] ;$$

where **CPI** is the life span in months of the cohort **I, Nj** is the individuals mean density in the size class **j**; $(M_j \, M_{j+1})^{0.5}$ is the weight geometric mean of two successive size classes and i is the number of size classes. The life span used in the formula was the one calculated for the different cohorts using the ELEFAN routine. Hynes and Coleman´s method has the advantage of not requiring the identification of different population cohorts (Benke, 1979), and previous studies showed that this method gives similar results than Crisp´s method for non-separable age classes (Martin and Bastida, 2006).

In order to compare our results with those of other similar studies, the relation between ash free dry weight (**AFDW**) and dry weight (**DW**) of worms was determined:

DW= 0.00176 + 1.3167 **AFDW**; R^2= 0.998 (P < 0.001).

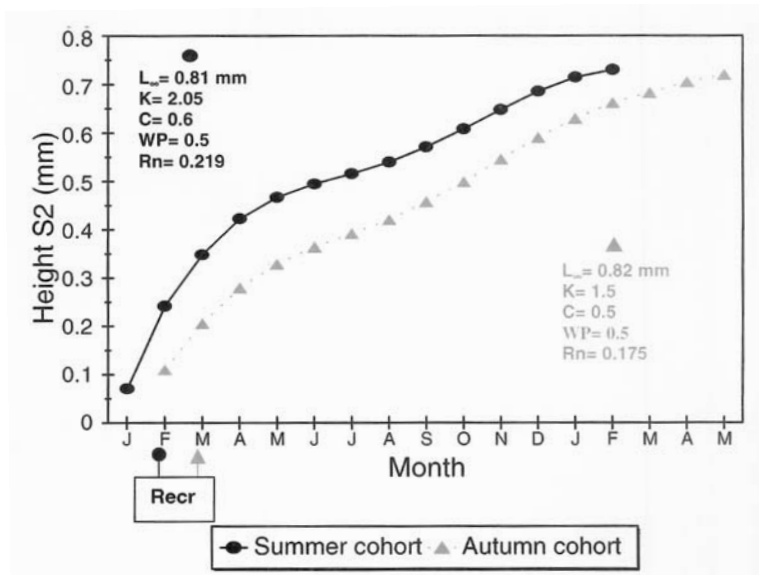All regressions were performed and tested with a standard statistical package (STATISTICA, StatSoft Inc. 1999).

Figure 4.
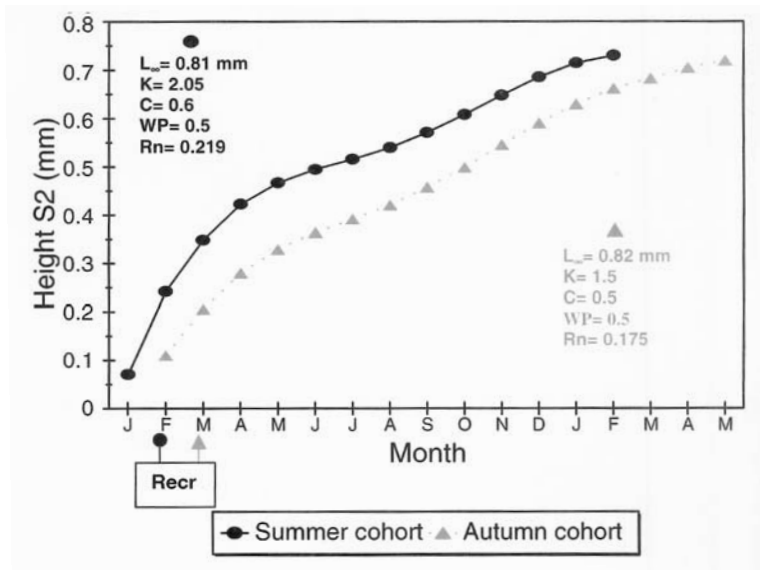*Percentage of females with mature oocytes and brooding females in adult population (HS2 > 0.5 mm).*

Figure 5.
Growth curve of Capitella capitata in Punta Rasa. L¥, asymptotic length; K, growth rate; C, seasonal growth oscillation; WP, winter point.

RESULTS

Population structure

Capitella capitata showed, in the study area, an unimodal population structure during most of the studied period, being bimodal in February, April and June 1999, and plurimodal in October and December 1999 (Fig. 2). Size frequency histograms presented main peaks in medium-small size classes (0.38 a 0.48 mm) during autumn and in medium-large ones (0.48 a 0.63 mm) during winter and spring. Nearly all size classes were present in the different seasons. There were not important recruitments process throughout the year; however, the smallest size classes were more abundant during summer, autumn and spring. In these seasons, the recruitment increased lightly between January and April 1999 and during October 1999.

Reproductive aspects

Specialized genital spines appear on the eighth and ninth thoracic segments in mature males. Females lack these specialized setae, and ovaries and oocytes are visible through the body wall of the abdominal setigers in mature specimens (from 12 or 13 setiger). Mature oocytes were yellow pale with a diameter between 220 and 250 μm.

The fertilized eggs were fixed to the inner wall of the brooding tube, surrounding the abdominal region of the female. The number of eggs by brood (n= 25 brooding tubes) ranged from 40 and 85 (mean = 53). The eggs were yellow pale and lightly oval or polyedric in shape, as a result of the contact with other eggs in the brooding tube. The diameter of its long axis ranged from 210 to 250 μm.

Larvae in different developmental stages were found inside brooding tubes (Fig. 3). The most advanced stage showed a length from 380 to 410 μm, with an evident cephalization process, a pair of eyes, complete body segmentation (12 to 13 segments), clearly visible gut and two ciliary bands (prototroc and telotroc) (Fig. 3C) . The first three segments carried capillary setae, while the following ones showed hooded hooks.

The smallest size registered for females with mature oocytes or inside brooding tubes with eggs or larvae, was 0.5 mm (HS2), with 55 setigers in average. Therefore, all female specimens with size above 0.5 mm (HS2) were considered adults with reproductive capacity. The females inside brooding tubes and that simultaneously presented mature oocytes in their celom were considered brooding females. Females with reproductive capacity in the Punta Rasa population were found during spring, summer and autumn, but these females were absent throughout winter (June to September 1999) (Fig. 4). The greatest
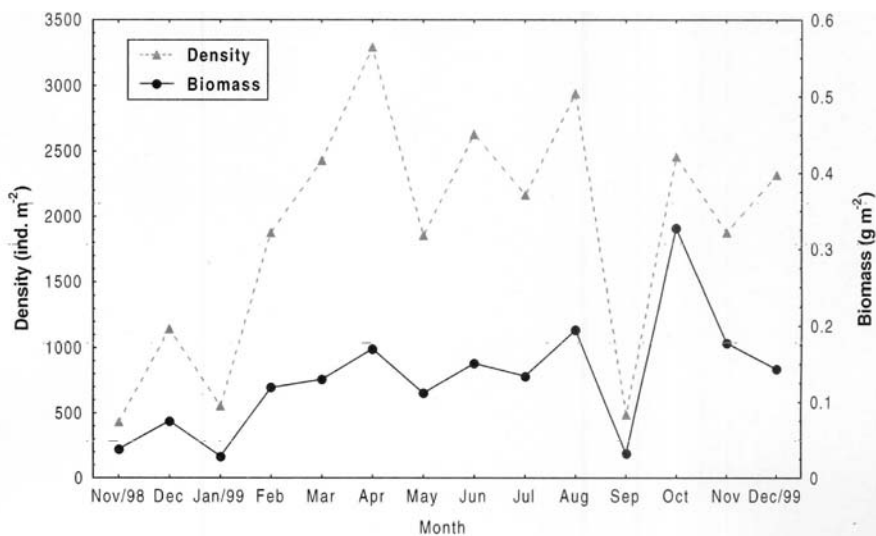
Figure 6.
Density and biomass (AFDW) of Capitella capitata in Punta Rasa.

percentage of reproductive females in the population was observed during December 1998, when more than 15 % of the individuals were brooding females (Fig. 4).

Growth and life span

ELEFAN was applied to analyze growth of individuals recruited between January and April 1999, as the recruitment was more evident during these months of the study period (Fig. 2). As a result, the growth curve of summer and autumn cohorts was obtained, showing different growth parameters.

The summer cohort, recruited along January and February, presented a growth rate (K) of 2.05 and a life span of 13 months. The seasonal growth oscillation was important (C= 0.6), pointing out that worms grew slower during the winter months (WP= 0.5) (Fig. 5). These individuals reached their early sexual maturity size (HS2= 0.5 mm) six months after recruitment (Fig. 5).

The autumn cohort, recruited during March and April, showing a growth rate (K= 1.5) lower than the summer cohort, because its growth rhythm was early attenuated during winter months (C= 0.5). As a result, the individuals reached 0.5 mm (HS2) seven months after recruitment. The estimated life span of this cohort was 15 months (Fig. 5).

Density, biomass and secondary production

The highest density of Capitella capitata in intertidal flats of Punta Rasa was registered during autumn and winter 1999, with values up to 3300 ind. m^{-2}. The lowest values were registered during summer 1998-1999 and in September 1999 with, values below to 500 ind. m^{-2} (Fig. 6).

The biomass ranged from 0.03 to 0.33 g m^{-2} (AFDW). The lowest values correspond to summer months of 1998-1999 and September 1999, and the highest ones to October 1999. The later was coincident with high densities of medium-large size individuals in the population, while the lowest values of biomass were coincident with low population density (Fig. 6).

The annual mean biomass of Capitella capitata was 0.117 g m^{-2} (AFDW), with a mean secondary production of 0.23 g m^{-2} year-1 (Table 1). The final value of annual secondary production was estimated as an average of production values of the two studied cohorts. The production/biomass ratio (P/B) was 1.96 year-1, indicating that *C. capitata* population of Punta Rasa produce almost 2 times its own biomass in one year cycle.

Table 1.
Estimated secondary production of *Capitella capitata* in November 1998- October 1999 period. N_j = mean density in the j class (ind. m^{-2}); M_j= AFDW of the j class individuals (mg); P_j = production of each length class (mg m^{-2} $year^{-1}$); CPI = life span of I cohort (month); PI = I cohort production.

Height S2	N_j	M_j	N_j-N_{j+1}	$(M_j M_{j+1})^{0.5}$	P_j	Biomass
0.15-0.20	14.74	0.042				0.63
0.20-0.25	47.89	0.043	-33.16	0.043	-16.97	2.05
0.25-0.30	116.05	0.044	-68.16	0.043	-35.32	5.05
0.30-0.35	215.52	0.045	-99.47	0.044	-52.69	9.65
0.35-0.40	263.42	0.047	-47.89	0.046	-26.35	12.37
0.40-0.45	392.36	0.051	-128.95	0.049	-75.66	19.97
0.45-0.50	436.57	0.058	-44.21	0.054	-28.82	25.31
0.50-0.55	233.94	0.071	202.63	0.064	155.57	16.52
0.55-0.60	112.37	0.093	121.58	0.081	118.39	10.48
0.60-0.65	60.79	0.134	51.58	0.112	69.13	8.13
0.65-0.70	31.32	0.206	29.47	0.166	58.76	6.46
0.70-0.75	1.84	0.336	29.47	0.263	93.15	0.62
		0.336	1.84	0.336	7.43	
Σ					266.63	117.24

CP1 = 13 months P1= 12/CP1*ΣP = 246.12 mg m^{-2} y^{-1}; CP2 = 15 months P2= 12/CP2*ΣP = 213.30 mg m^{-2} y^{-1}

DISCUSSION

Life history and growth

The population structure of *Capitella capitata* observed at Punta Rasa is a common picture in species with long reproductive seasons and relatively short life span, in which the juvenile individuals - with high growth rate- reach the adult size in a few months (Grassle and Grassle, 1974; Martin and Grémare, 1997). Similar population structures have been observed in *C. capitata* from Yeal river estuary (U.K.) and from Ebro river estuary (Spain) in monthly sampled studies (Warren, 1976; Martin and Grémare, 1997).

Capitella capitata in Punta Rasa had an extended reproductive period, based in the presence of reproductive females during a great part of the year. Similar reproductive cycle characteristics have been observed in populations from other geographic areas (Grassle and Grassle, 1974, 1976; Foret, 1974; Reish, 1974; Warren, 1976; Tsutsumi and Kikuchi, 1984; Yamamoto, 1980). The absence of reproductive activity during winter months could be related with low temperatures registered in tidal flats (sometimes below 0 ºC between June and September) (Martin et al., 2004). Experimental studies have demonstrated that low temperatures can diminish sensibly reproductive activity of *C. capitata* Type I (Redman, 1985), and the extremely low temperatures registered in Punta Rasa could inhibit the reproduction of this species during the coldest season. Similar effects have been observed on several polychaete species from temperate latitudes. In Mar Chiquita lagoon (Argentina) Ficopomatus enigmaticus reproduce when water temperature is above 18º C (Obenat and Pezzani, 1994; Obenat, 2001); this species and other Serpulidae polychaete (*Hydroides norvegica, Serpula vermicularis and Eupomatus sp.*) of Mar del Plata´s harbor fouling communities (Argentina), start their

reproduction activities when water temperature reaches 16º - 17 ºC (Bastida, 1971a, 1971b), while Streblospio benedicti populations from New England (U.S.A.) ended its reproductive activity when water temperature is below 10 º C (Sardá and Martin, 1993). Laboratory experiences also confirmed that S. benedicti present its greatest reproductive activity when temperature ranged between 16 to 21 ºC (Levin and Creed, 1986).

The presence of females in process of oogenesis inside brooding tubes (with eggs or larvae) is another important characteristic to mention about *Capitella capitata* population from Punta Rasa. This fact has been also observed by Tsutsumi and Kikuchi (1984) in South Japan, and suggests that this polychaete has the capacity to reproduce many times during its life span. Warren (1976) observed similar characteristics in *C. capitata* populations from Yealm river estuary (UK) where the species also presented an extended reproductive season.

The eggs founded in brooding tubes of *Capitella capitata* from Punta Rasa are among the largest registered in capitellids. According to Reish (1977) and Pearson and Pearson (1991) the relatively large size and the low number of eggs in broods are related to lecithotrophic non-pelagic development in *Capitella*

Table 2.
Annual secondary production (P: g m-2) and annual production/biomass ratio (P/B: y-1) of Capitella capitata complex species. Production expressed as dry weight (DW) and ash free dry weight (AFDW).

Species	Locality	P		P/B	Method	Reference
		DW	AFDW			
Capitella sp.	Alfacs Bay (disturbed sand)	0.83	0.61	4.09	Hynes and Coleman	Martin and Grémare (1997)
"	Alfacs Bay (typical silt)	3.74	2.78	3.66	Hynes and Coleman	"
"	Alfacs Bay (disturbed silt)	36.90	27.38	5.71	Hynes and Coleman	"
"	Ría Formosa (Zostera bed)		0.01	2.32	Theoretical P/B	Sprung (1994)
"	Ría Formosa (mud flat)		0.27	1.64	ratio	"
capitata (Type I)	Laboratory (control)		22.10	2.70	MSYM [b]	Chesney (1985)
"	"		39.30	4.90	SGRM [c]	"
"	Laboratory (12% predation)		48.80	8.40	MSYM [b]	"
"	"		70.50	12.20	SGRM [c]	"
"	Laboratory (23 % predation)		66.80	15.10	MSYM [b]	"
"	"		86.80	19.60	SGRM [c]	"
C. capitata	Barcelona (moderately polluted fine sand)	47.55 [a]		23.80 [a]	Hynes and Coleman	Méndez (1994) Méndez et al. (1997)
"	"	47.30		23.70	Crisp	"
"	Barcelona (heavily polluted fine sand)	270.00 [a]		36.00 [a]	Hynes and Coleman	"
"	"	275.46		36.70	Crisp	"
"	Río de la Plata Estuary (sandy undisturbed flats)	0.30	0.23	1.96	Hynes and Coleman	Present study

[a] More probably values (life span between 2 and 4 months), [b] Maximum Sustainable Yield Method , [c] Specific Growth Rate Method.

sp. On the other hand, Qian and Chia (1991b, 1992b) have demonstrated that egg size can be variable, depending on environmental temperature and food availability. However, egg size is also variable within sibling species of *Capitella complex*. The characteristics of eggs and broods observed in Punta Rasa are similar to those descript by Grassle and Grassle (1976) for *Capitella sp*. Type IIIa., a species that present benthic development and whose juveniles leave the parental tube directly after metamorphosis. The big mature eggs of *Capitella sp*. Type IIIa are rich in lipids and viteline protein, and poor in glycogen, which are typical of lecithotrophic non-pelagic development species (Eckelbarger and Grassle, 1983).

Eggs and broods of *Capitella capitata* observed in our study area, together with the presence of advanced larvae stages inside brooding tubes, suggest that this population has a benthic development in Punta Rasa. The advanced larval stage founded inside brooding tubes in this study was descript as metatrochophore larvae by Reish (1974) and George (1984). This larval stage was observed inside parental tubes of *C. capitata* from the littoral of Barcelona (Spain) by Méndez (1995, 2002) and also in *Capitella sp* I from Setauket Harbor (New York, US), *Capitella sp* M from shallow hydrothermal vent areas (Milos, Greece) and *Capitella* population Cm from salmon farms (Cranford, Ireland) by Méndez *et al*. (2000). These latter sibling species presented benthic development too.

The holobenthic life cycles (with absence of planktonic stages) and benthic-planktonic cycles with reduced planktonic stage (in which the dispersion of larvae is limited) allow to keep the larvae in the adult population area. These types of cycle are very common in estuarial species that inhabit areas where the water currents can drive the larvae away of the favourable habitat. This strategy is followed in spite of the reduction of dispersal area. However, the species that live in sand-muddy tidal flats have alternative mechanisms of larval dispersion, although more limited than those species with planktonic larvae. Among these, the presence of a final larvae stage with a short swimming period is the mechanism of limited dispersion used by species of Capitella, together with other strategies as displacement across the sediment and transport of juveniles associated to sediment erosion by water currents (Shull, 1997).

Several advantages have been attributed to benthic development, as for example, facilitate survival in harsh environmental conditions (Wilson, 1986; Bhaud and Duchêne, 1996); reduce the amount of adult energy assigned to reproduction (Chia, 1976); predation reduction on larvae, generally more intense in planktonic environment (Pechenik, 1979); gonad maturation in small-sized adults which are not able to generate the minimum number of planktonic larvae required to balance loss by dispersal (Strathmann, 1982), and to prevent removing juveniles from suitable habitats (Gibbs, 1968; Bhaud and Duchêne, 1996).

In the study area, *Capitella capitata* seems to orientate its reproductive strategy in the production of a low number of eggs, assuring their survival through incubation in brooding tubes. This strategy, of lower energetic cost, allows the adults to survive during the first reproductive period, and to start the gametogenesis process for a new reproductive period. In this way, disadvantages in dispersion and genetic variability associated to this reproductive strategy - as a result of a low number of larvae- can be compensated through the capacity of reproducing several times during the life span.

The measurements made on *Capitella capitata* early juvenile stages from Punta Rasa allow us to determine that these stages recruit to population with a mean size of 0.18 mm (HS2). According to laboratory measurements (Tsutsumi and Kikuchi, 1984; Qian and Chia, 1992b) this juvenile stage is reached between 10 and 15 days after parental oviposition; however this period can be very variable depending on environmental conditions (Qian and Chia, 1993).

The WP estimated from ELEFAN indicates that growth was lowest during the cold months of the year (June- August), thus the temperature could be an important factor regulating the growth rate of Capitella capitata, as well as the reproductive activity. In this way, the females recruited during February reach 0.5 mm (HS2) in July-August, however do not reproduce until the spring. On the other hand, the females recruited during March reached the early sexual maturity size seven months after recruitment, thus they reproduce firstly in spring, together with females recruited during February. This mechanism, in part regulated by environmental temperature, allows us to explain the high percentage of reproductive females present at Punta Rasa during spring.

The time required by *Capitella capitata* to reach the first reproduction in experimental cultures (at 15ºC) was estimated around two or four months by

several authors (Reish, 1974; Foret, 1974; Tsutsumi and Kikuchi, 1984; Qian and Chia, 1992b). Warren (1976) estimated the prereproductive period of *C. capitata* in about one year, based in natural populations from England. However, the long period estimated by the later author can be due to the underestimation of the growth rate.

Finally, the prereproductive time estimated in the present study is valid for individuals growing during winter, but it can be even shorter in individuals recruited during spring, as a result of temperature influence on somatic and gonadal development of this species.

The life history of *Capitella capitata* has been studied in several geographic regions by different authors (Grassle and Grassle, 1974; Reish, 1974; Foret, 1974; Warren, 1976; Yamamoto, 1980; Tsutsumi and Kikuchi, 1984; Méndez, 1995). All these studies show common pictures to Punta Rasa population, however, there are variations in the brood characteristics, in the larval development pattern (benthic or planktonic) and in the larvae morphology. These variations are comparable to reproductive differences observed among sibling species of *C. capitata* complex and differentiated through electrophoresis analysis of its enzymes. Some sibling species produce big eggs (250 to 260 mm), present broods with few eggs (less than 400) and benthic larval development (Grassle and Grassle, 1976; Méndez *et al.*, 2000; Méndez, 1995, 2002). Other sibling species present high numbers (up to 2000 by brood) of small eggs (50 to 75 mm) and larval developments with different duration of planktonic stages (Grassle and Grassle, 1976; Méndez et al., 2000). In this way, the variations registered in the life history of *C. capitata* by different authors could be due to systematic problems and not because of environmental variations between different geographical areas. Méndez et al. (2000), in a comparative analysis (under identical laboratory conditions) of reproductive mode and larval development pattern of members of the *C. capitata* complex, demonstrated that observed differences were the result of genetic differences among populations.

Density, biomass and secondary production

The population density of *Capitella capitata* in Punta Rasa was lower than in areas of high organic matter content, where can be observed the opportunistic character of this species. However, Grassle and Grassle (1974) report that, in natural and pristine estuary areas, this species can be founded in low and stable density throughout the year, and similar density values were also registered in *C. capitata* populations from sandy flats of Ebro river estuary (Spain) (Martin and Grémare, 1997). The density founded by these authors ranged from 213 to 4238 ind. m-2, with the highest values during winter and the lowest ones in summer. In these Ebro river´s flats, *C. capitata* population is restricted to the upper intertidal level, where macrophytobenthic detritus accumulates and decay (Pérez, 1989); and Martin and Grémare (1997) suggest that seasonal variations in density and biomass are more related with the quality of available food than to its quantity. A similar process, related with detritus decay period, may occur in Punta Rasa´s flats, thus explaining the observed seasonal variation pattern in density and biomass of this deposit-feeder polychaete.

Martin and Grémare (1997) also remarked that the biomass and density of *Capitella capitata* from Ebro river´s organic polluted silty flats are much higher and more variable (from 0 to 16.069g DW m-2 and from 0 to 172450 ind. m-2, respectively) than those founded in the undisturbed silty flats, denoting the bioindicator characteristic of this polychaete.

Another factor regulating *Capitella capitata* density in Punta Rasa may be the predation by fishes and benthic invertebrates. The low density registered during September 1999 was coincident with the maximum Neanthes succinea density in the intertidal flats (Martin et al., 2004). This nereidid polychaete overtakes the highest densities in the area during spring and its gut contents revealed the presence of *C. capitata* among its main prey, together with other dietary items, as well as the nereidid *Laeonereis culveri, oligochaetes, nematods and ostracods* (Martin, 2002; Martin et al., 2004). Among the fishes that feed on polychaetes in Punta Rasa intertidal flats it can be mentioned the white croaker (Micropogonias furnieri), whose gut contents revealed the presence of *C. capitata, L. culveri* and *N. succinea* among its principal prey in the region (Martin, 2002).

The secondary production and P/B ratio estimated for *Capitella capitata* from Punta Rasa were, in general, lower than those reported for this species in other areas of the world (Table 2). However, our estimations are very similar to those reported by

Sprung (1994) in Ría Formosa (Portugal) in areas with minimum disturbance by human activity.

The values of production and P/B ratio are very variable within *Capitella capitata* complex species (Table 2). Martin and Grémare (1997) remarked that important differences in production estimations are probably related to methodological problems, and it seems necessary to standardize techniques to assess secondary production of opportunist species. When it is compared the *C. capitata* production values estimated by different authors using Hynes and Coleman´s method, can also be observed important discrepancies, which may in part be due to differences in the estimated cohort life span or in the considered production interval. For example, Méndez (1994) and Méndez *et al*. (1997) considered a cohort production interval between 2 and 4 months -very much lower than the estimated in the present study- and they obtained as a result the highest values of production and P/B ratio reported for *C. capitata*. This fact shows that also techniques to estimate the life span and cohort production interval of opportunistic species must be standardized to arrive to comparable data of production and P/B ratio.

The cohort production interval of *Capitella capitata* in the present study was similar to the production interval considered by Martin and Grémare (1997) in their estimations. Thus, the P/B ratio estimated for Punta Rasa is agree with the order of magnitude obtained by Martin and Grémare (1997). These authors observed that production and P/B ratio at disturbed silty flats are higher than observed in disturbed sandy flats from Ebro river estuary (Spain) (Table 2), pointing out that size grain of the sediment may affect the production and P/B ratio of this polychaete.

The production of *Capitella capitata* is probably dependent on quality and quantity of available food, grain size of the sediment and pollution degree of the environment. In this way, the low production and P/B ratio registered in Punta Rasa may be considered as reference values for this opportunistic polychaete inhabiting moderately disturbed or undistubed sandy flats, where it can be found in low and relatively stable density throughout the year.

REFERENCES

Bastida R (1971a). Las incrustaciones biológicas en el puerto de Mar del Plata, período 1966/67. Revista del Museo Argentino de Ciencias Naurales, 3: 203-285.

Bastida R (1971b). Las incrustaciones biológicas en las costas argentinas. La fijación mensual en el puerto de Mar del Plata durante tres años consecutivos. Corrosión y Protección, 2: 1-17.

Benke AC (1979). A modification of the Hynes method for estimating secondary production with particular significance for multivoltine populations. Limnology and Oceanography, 24: 168-171.

Bhaud M, Duchêne JC (1996). Change from planktonic to benthic development: Is life cycle evolution an adaptative answer to the constraints of dispersal?. Oceanologica Acta, 19: 335-346.

Chia FS (1976). Classification and adaptative significance of developmental patterns in marine invertebrates. Thalassia jugoslavica, 10: 121-130.

Chesney Jr. EJ (1985). Laboratory studies of the effect of predation on production and the production: biomass ratio of the opportunistic polychaete *Capitella capitata* (Type I). Marine Biology, 87: 307-312.

Cornet M (1986). Estimation de la production annuelle de populations d'Abra alba (mollusque bivalve) du plateau continental Sud-Gascogne. Oceanologica Acta, 9: 323-332.

Eckelbarger KJ, Grassle JP (1983). Ultrastructural differences in the eggs and ovarian follicle cells of *Capitella (Polychaeta)* sibling species. Biological Bulletin, 165: 379-393.

Foret JP (1974). Etude des effets à long terme de quelques détergents sur la séquence du développement de la polychète sédentaire *Capitella capitata (Fabricius)*. Tethys, 6: 751-778.

Gayanilo FC, Sparre P, Pauly P (1996). FISAT, FAO-ICLARM stock assessment tools. User's manual. FAO Computerized Information Series. Fisheries, 8. Rome: FAO.

George JD (1984). The behaviour and life history of a mangrove-dwelling capitellid (Polychaeta). In: PA Hutchings, ed, Proceedings of the First International Polychaete Conference, Sydney, 323-337.

Gibbs PE (1968). Observations on the population of Scoloplos armiger at Whitstable. Journal of the Marine Biological Association of the United Kingdom, 48: 225-254.

Grassle JF, Grassle JP (1974). Opportunistic life histories and genetic systems in marine benthic polychaetes. Journal of Marine Research, 32: 255-284.

Grassle JP, Grassle JF (1976). Sibling species in the marine pollution indicator *Capitella (Polychaeta)*. Science, 192: 567-569.

Holbrook MJ, Grassle JP (1984). The effects of low density on the development of simultaneous hermaphroditism in male *Capitella* species I (Polychaeta). Biological Bulletin mar. biol. Lab. Woods Hole, 166: 103-109.

Hynes HB, Coleman MJ (1968). A simple method of assessing the annual production of stream benthos. Limnology and Oceanography, 13: 569-573.

Ieno E, Bastida R (1998). Spatial and temporal patterns in coastal macrobenthos of Bahía Samborombón, Argentina: A case study of very low diversity. Estuaries, 21: 690-699.

Levin LA, Creed EL (1986). Effect of temperature and food availability on reproductive responses of Streblospio benedicti (*Polychaeta: Spionidae*) with planktotrophic or lecithotrophic development. Marine Biology, 92: 103-113.

Martin D, Grémare A (1997). Secondary production of Capitella spp. (*Polychaeta: Capitellidae*) inhabiting different organically enriched environments. Scientia Marina, 61: 99-109.

Martin JP (2002). Aspectos biológicos y ecológicos de los poliquetos de ambientes mixohalinos de la Provincia de Buenos Aires. Universidad Nacional de Mar del Plata, Mar del Plata.

Martin JP, Bastida R (2006). Population structure, growth and production of *Laeonereis culveri* (Nereididae: Polychaeta) in tidal flats of Río de la Plata estuary, Argentina. Journal of the Marine Biological Association of the United Kingdom, 86: 235-244.

Martin JP, Bastida R, Trassens M (2004). Polychaete assemblages of intertidal mixohaline flats of Bahía Samborombón (Río de la Plata estuary-Argentina). Thalassas, 20: 39-52.

Méndez N (1994). Perturbaciones antropogénicas en el litoral: comunidad de poliquetos y dinámica de poblaciones de Capitella capitata en fondos arenosos frente a Barcelona. Universidad de Barcelona, Barcelona.

Méndez N (1995). Non-pelagic development of *Capitella capitata* (Polychaeta) in the littoral zone of Barcelona, Spain. Scientia Marina, 59: 95-101.

Méndez N (2002). Experimental evidence of polymorphism of sexual development in Capitella sp. B (*Polychaeta: Capitellidae*) from Barcelona, Spain. Scientia Marina, 66: 103-110.

Méndez N, Linke-Gamenick I, Forbes VE (2000). Variability in reproductive mode and larval development within the *Capitella capitata* species complex. Invertebrate Reproduction Development, 38: 131-142.

Méndez N, Romero J, Flos J (1997). Population dynamics and production of the polychaete *Capitella capitata* in the littoral zone of Barcelona (Spain, NW Mediterranean). Journal of Experimental Marine Biology and Ecology, 218: 263-284.

Menzie CA (1980). A note on the Hynes method of estimating secondary production. Limnology and Oceanography, 25: 770-773.

Obenat S (2001). Biología del anélido introducido Ficopomatus enigmaticus (*Polychaeta: Serpulidae*). In: O Iribarne ed, Reserva de Biosfera Mar Chiquita, características físicas, biológicas y ecológicas. Editorial Martín, Mar del Plata, 101-108

Obenat S, Pezzani S (1994). Life cycle and population structure of the polychaete *Ficopomatus enigmaticus* (Serpulidae) in Mar Chiquita coastal lagoon, Argentina. Estuaries, 17: 263-270.

Pagliosa PR, Lana PC (2000). Population dynamics and secondary production of Nereis oligohalina (Nereididae: Polychaeta) from a subtropical marsh in southeast Brazil. Bulletin of Marine Science, 67: 259-268.

Pauly D (1986). On improving operation and use of the ELEFAN programs. Part 3. Correcting length-frequency data for the effects of gear selection and/or incomplete recruitment. Fishbyte, 4: 11-13.

Pauly D, Morgan GR (1987). Length- based methods in fisheries research. ICLARM, Manila.

Pearson M, Pearson T (1991). Variation in populations of *Capitella capitata* (Fabricius, 1780) (Polychaeta) from the West coast of Scotland. Ophelia, 5: 363-370.

Pearson TH, Rosenberg R (1978). Macrobenthic succesion in relation to organic enrichment and pollution of the marine environment. Oceanography and Marine Biology Annual Review, 16: 299-311.

Pechenik JA (1979). Role of encapsulation in invertebrate life histories. The American Naturalist, 114: 859-870.

Pérez M (1989). Fanerógamas marinas en sistemas estuáricos: Producción, factores limitantes y algunos aspectos del ciclo de nutrientes. Universidad de Barcelona, Barcelona.

Qian PY, Chia FS (1991a). Effects of food concentration on larval growth and development of two polychaete worms, *Capitella capitata* (Fabricius) and Polydora ligni Webster. Bulletin of Marine Science, 48: 477-484.

Qian PY, Chia FS (1991b). Fecundity and egg size are mediated by food quality in the polychaete worm *Capitella spp.* Journal of Experimental Marine Biology and Ecology, 148: 11-25.

Qian PY, Chia FS (1992a). Effect of aging on reproduction in a marine polychaete *Capitella spp*. J. Exp. Mar. Biol. Ecol. 156: 23-38.

Qian PY, Chia FS (1992b). The "morphological females" of a marine polychaete, *Capitella spp*. are functional hermaphrodites. Invertebrate Reproduction Development, 21: 107-112.

Qian PY, Chia FS (1993). Larval development as influenced by food limitation in two polychaetes: *Capitella spp*. and Polydora ligni Webster. Journal of Experimental Marine Biology and Ecology, 166: 93-105.

Redman CM (1985). Effect of temperature and salinity on the life history of *Capitella capitata* (Type I). Abst. Int. Pt. Sci. Eng., 46: 91.

Reish DJ (1974). The establishment of laboratory colonies of polychaetous annelids. *Thalassia jugoslavica*, 10: 181-195.

Reish DJ (1977). The role of life history studies in polychaete systematics. In: DJ Reish, K Fauchald, eds, Essay on polychaetous annelids in memory of Dr. Olga Hartman, Allan Hancock Found, Los Angeles, 461-476.

Reish DJ (1978). Interlaboratory calibration experiments using the polychaetous annelid *Capitella capitata*. Marine Environmental Research, 1: 109-118.

Sardá R, Martin D (1993). Population of Streblospio (Polychaeta: Spionidae) in temperate zones: Demography and production. Journal of the Marine Biological Association of the United Kingdom, 73: 769-784.

Shull DH (1997). Mechanisms of infaunal polychaete dispersal and colonization in an intertidal sandflat. Journal of Marine Research, 55: 153-179.

Strathmann RR (1982). Selection for retention or export of larvae in estuarines. In: VS Kenedy, ed, Estuarine comparisons, Academic Press, New York, 521-536

Sprung M (1994). Macrobenthic secondary production in the intertidal zone of the Ría Formosa- a lagoon in the Southern Portugal. Estuarine, Coastal and Shelf Science, 38: 539-558.

Tsutsumi H, Kikuchi T (1984). Study of the life history of *Capitella capitata* (Polychaeta: Capitellidae) in Amakusa, South Japan including a comparison with other geographical regions. Marine Biology, 80: 315-321.

Warren LM (1976). A population study of the polychaete *Capitella capitata* at Plymouth. Marine Biology, 38: 209-216.

Wetherall JA (1986). A new method for estimating growth and mortality parameters from length- frequency data. Fishbyte, 4: 12-14.

Wilson WH (1986). Detachment of eggs masses of a polychaete: environmental risks of benthic protective development. Ecology, 67: 810-815.

Yamamoto I (1980). Ecological study on indicator species of eutrophic waters. Annual report of the study supported by the Grant from Ministry of Education of Japan 1979.