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Secondary production of *Capitella* sp. (Polychaeta: Capitellidae) inhabiting different organically enriched environments*

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SUMMARY: Three populations of *Capitella* sp. submitted to three different environmental conditions were monitored during one year in Alfacs Bay (Ebro Delta, NW Mediterranean) to estimate their respective contributions to the secondary production. Yearly secondary production of *Capitella* sp. at the three sites under study were 0.83 gDW. m^{-2}. y^{-1} for the disturbed sand site, 3.74 gDW. m^{-2}. y^{-1} for the typical silt site, and 36.9 gDW. m^{-2}. y^{-1} for the disturbed silt site. The corresponding P/B ratios were of 4.09 y^{-1}, 3.66 y^{-1} and 5.71 y^{-1}, respectively. At the two silty sites, *Capitella* sp. presents: (1) a marked seasonal variability, and (2) high production rates and P/B ratios, which are two characteristics of opportunists. At the disturbed sand site its seasonal pattern is much more stable, and its production much lower (although P/B ratios are still high). The "within site" seasonal differences found between the three populations probably did not result from temporal changes in food quantity nor quality. Nevertheless, differences in protein concentrations may contribute to explain differences in maximal densities and biomasses observed among sites. Our results confirm that *Capitella* sp. shows a great plasticity relative to environment.

Key words: Density, biomass, secondary production, *Capitella* sp., Polychaeta, NW Mediterranean Sea.

RESUMEN: PRODUCCIÓN SECUNDARIA DE *CAPITELLA* SP. (POLYCHAETA, CAPITELLIDAE) EN HABITATS CON NIVELES DE ENRIQUECIMIENTO ORGÁNICO DIFERENTES. – Tres poblaciones del poliqueto *Capitella* sp. (Capitellidae), sometidas a diferentes condiciones ambientales, se han monitorizado durante un año en la Bahía de Els Alfacs (Delta del Ebro, Mediterráneo noroccidental) con el fin de estimar sus resprectivas contribuciones a la producción secundaria del sistema. La producción secundaria anual de *Capitella* sp. en las tres localidades estudiadas fue: 0.83 g Peso Seco m^{-2} año^{-1} en la zona de arenas perturvadas, 3.74 g Peso Seco m^{-2} año^{-1} en la zona de fangos típicos, y 36.9 g Peso Seco m^{-2} año^{-1} en la zona de fangos perturbados. Los cocientes P/B correspondientes fueron: 4.09 año^{-1}, 3.66 año^{-1}, y 5.71 año^{-1} respectivamente. En las dos localidades fangosas, *Capitella* sp. presenta: (1) una marcada variabilidad estacional, y (2) elevadas tasas de producción y cocientes P/B, ambas características propias de especies oportunistas. En la localidad de arenas perturbadas, el patrón estacional es mucho más estable y la producción mucho menor, si bien el cociente P/B sigue siendo elevado. Los resultados obtenidos sugieren que, probablemente, las diferencias en el tiempo para cada localidad no son el resultado de cambios temporales ni en la cantidad ni en la calidad del alimento disponible. Sin embargo, diferencias en la concentración de proteínas contribuyen a explicar las diferencias, tanto en biomasa como en densidades máximas, observadas entre localidades. Dichos resultados confirman la gran plasticidad de *Capitella* sp. como respuesta a las condiciones ambientales.

Palabras clave: Densidad, biomasa, producción secundaria, *Capitella* sp., Polychaeta, Mediterráneo noroccidental.

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INTRODUCTION

There is a general pattern of distribution of benthic macrofauna along organic and stress gradients (Pearson and Rosenberg, 1978). High density and low biodiversity assemblages are usually associated with the most organically enriched and disturbed sediments (Pearson and Rosenberg, 1978). Benthic invertebrates that typically inhabit those habitats are small, thread-like, short-lived, continuously reproducing surface deposit-feeders, which have been traditionally defined as opportunists (Grassle and Grassle, 1974).

The polychaete *Capitella capitata,* which actually consists of numerous sibling species (Grassle and Grassle, 1976), occurs in disturbed or polluted areas throughout the world. Life-histories of the members of this complex have been extensively studied (Eckelbarger and Grassle, 1983, 1987a, b; Holbrook and Grassle, 1984; Petraitis, 1985a, b; Grassle *et al.,* 1987; Marsh *et al.,* 1990). Temporal and spatial distribution patterns of *Capitella* sp. populations have been widely documented as well, because these species are among the most important deposit-feeders in organically polluted environments (Rosenberg, 1972, 1976; Grassle and Grassle, 1974; Pearson and Rosenberg, 1978; Tsutsumi, 1987, 1990). Population and individual responses to food availability have also been widely investigated under controlled laboratory conditions. The effects of food quantity and quality on individual growth have been assessed by Tenore (1977, 1981, 1983). The effects of ration and food type on reproduction have been considered by Grémare *et al.* (1988, 1989a), Qian and Chia (1991, 1992), and Grémare (1994). The effect of food quantity on the responses of experimental populations has also been assessed by Chesney and Tenore (1985), by Marsh *et al.* 1989, and by Grémare *et al.* (1989b).

Curiously, secondary production of species belonging to the *Capitella* sp. complex have been largely neglected, even though laboratory experiments revealed the high production potential of some of these sibling species (Chesney, 1985). For example, there have been only two attempts to estimate secondary production of field populations of *Capitella* sp. (Oyenekan, 1983; Sprung, 1994). This is probably because opportunists have traditionally been considered as transient components of the community, with their contribution to the energy flows being subsequently underrated (Chesney, 1985).

The aim of the present study was thus to investigate the contribution to the secondary production of several field populations of a species of the *Capitella* sp. complex submitted to different environmental conditions. The studied sites were located in Alfacs Bay, a semi-enclosed shallow water area of the north-western Mediterranean Sea. We will refer to the studied species as *Capitella* sp. due to the absence of specific analyses (electrophoresis or karyotypes) required to clarify its position within the *Capitella* complex.

STUDY AREA

Alfacs Bay is a semi-enclosed, shallow-water area located in the Ebro Delta (NE coast of the Iberian Peninsula, NW Mediterranean). It is mainly characterized by a marine hydrographical regime, but is also influenced by fresh-water inputs occurring during spring and summer (Palacín *et al.,* 1991). In the absence of strong winds, exchange between the bay and the open sea either follows a periodicity of ca 10 days or has a typical estuarine circulation with a volume exchange of 5-15 x 106 m^{-3} day^{-1} (Camp *et al.*, 1991). Based on biogeochemical parameters, Alfacs Bay has been divided into 3 zones namely, “silt”, “central”, and “sand” (Palacín *et al.,* 1991). *Capitella* sp. mainly inhabits the silty zone but can also be found living in some areas of the sandy zone.

Populations of *Capitella* sp. were monitored at two sites in the silty zone and one site in the sandy zone (Fig. 1). Some of the main characteristics of these three sites are presented in Table 1. Organic contents and Redox potentials suggested that the two silty sites were subjected to different levels of disturbance. Thus, these stations are referred to as “typical silt” and “disturbed silt”. In the sandy zone, *Capitella* sp. populations were restricted to the higher level of the beach where macrophytobenthic detritus often accumulates (Pérez, 1989; Duarte and Sand-Jensen, 1990). Thus, this station will be referred to as “disturbed sand”.

In Alfacs Bay, the organic inputs reaching the shallow coastal shelfs (0.6 m of average depth) were due to phytoplankton, microphytobenthos, macrophytes and terrestrial runoff (Camp *et al.,* 1991). Neither phytoplankton nor microphytobenthos production showed an apparent seasonality, and yearly average values at the shelfs of the Bay were 273 mg C m^{-2} day^{-1} and 96 mg C m^{-2} day^{-1}, respectively (Delgado, 1987, 1989; Camp *et al.,* 1991). Organic

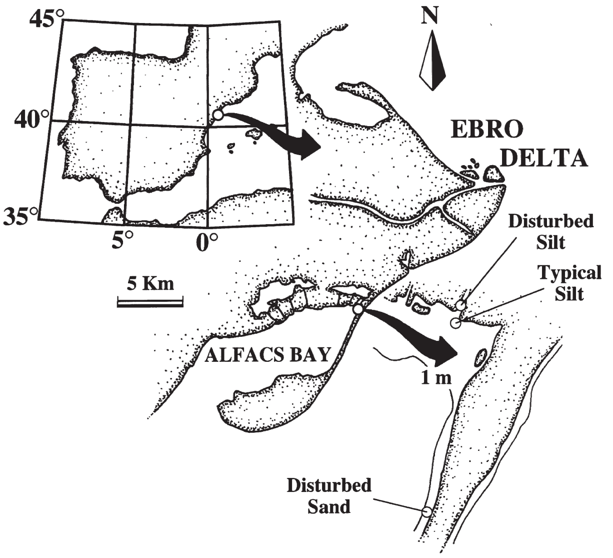

FIG. 1. – Map of the study area showing the location of the three sampling sites.

inputs coming from fresh waters were of 62 mg C m^{-2} day^{-1}, but they scarcely reached the two silty sites and never affected the sandy site (Palacín *et al.,* 1991). Among macrophytes, macroalgae growth peaked between January and July (average production of 610 mg C m^{-2} day^{-1}), while the phanerogams showed production maxima between March and October (average of 1080 mg C m^{-2} day^{-1}) (Pérez, 1989; Camp *et al.,* 1991). Thus, probably, the organic matter present at the three sampling sites derives mainly from macrophytes, specially phanerogams.

MATERIAL AND METHODS

Based on previous studies of the small scale structure of the infaunal communities of the Bay (Martin, 1992; Martin *et al*., 1993), manual cores (30 cm^2, 6.2 cm in diameter, 5 cm depth in the silty zone; 200 cm^2, 16 cm in diameter, 20 cm depth in the sandy zone) were collected monthly between August 1987 and July 1988. Four replicates were carried out at the two silty sites vs. only two replicates at the sandy site. Each sample was sieved and macroinfaunal specimens of *Capitella* sp. were collected on a 500 μm mesh. Additional replicates (same number as above) were collected and sieved through a 500 μm mesh prior to extraction using an elutriator (60 μm mesh). An aliquot fraction (1/10 of the sample) was then examined under a stereo microscope to estimate the temporary meiofaunal fraction. All samples were preserved in buffered 10% formaldehyde-seawater before analysis.

TABLE 1. – Main characteristics (mean ± standard deviation) of the three studied sites during summer. The surface Redox potentials are taken from Mallo *et al.* (1993) and Palacín *et al.* (1991).

ABIOTIC PARAMETERS	Disturbed Sand	Typical Silt	Disturbed Silt
WATER COLUMN DEPTH (m)	0.3	0.5	0.2
SILT CONTENT (DW %)	0.06±0.00	16.5±2.1	91.5±10.7
SURFACE REDOX POTENTIAL (mV)	-8.3±6.9	-103.0±26.2	-207.6±28.5

The width of the 4th thoracic setiger was used to infer worm biomass. Setiger measurements were carried out by using a stereo microscope coupled with a camera lucida and a digitizing tablet (Genitizer GT-1212B) linked to a computer. Selected entire individuals from representative size categories were measured, dried 24h at 110°C and then weighed to the nearest 0.001 mg. The regression linking setiger width (SW in mm) and dry weight (DW in μg) was as follows:

$$DW = 0.517\ SW^{2.031}\ (r^2 = 0.867\ ;\ p < 0.001\ ;\ n = 25)$$

We attempted to discriminate the overlapping Gaussian components of the size histograms (size class intervals of 0.08 mm) by the Bhattacharya (1967) method using "The Complete ELEFAN" software (copyright © ICLARM, 1989). The recognition of cohorts in the three populations under study was impossible, and methods involving the separation of cohorts to estimate the secondary production could not be applied. Thus, secondary production was estimated using the Hynes' average cohort method (Hynes and Coleman, 1968; Hamilton, 1969; Benke, 1979). It should be pointed out that this method has already been applied to a laboratory population of *Capitella* sp. I by Grémare *et al.* (1989). During the present study, we have used the formula given by Cornet (1986) and by Sardá and Martin (1993):

$$P = \left[\sum_{j=1}^{i} i\,(N_j - N_{j+1})(w_j * w_{j+1})^{0.5}\right] * 12/CPI$$

were N_j and N_{j+1} are average number of individuals of class j and j+1, (w_j * w_{j+1} $)^{0.5}$ is the geometric mean of DW of two successive size classes, i is the number of size classes and CPI is the cohort production interval. CPI for the three studied populations was assumed to be unity since the production period was exactly one year.

Protein content of the sediment were estimated on the basis of the organic matter content of the sediment (as differences between 105°C, 24 h dried and 450°C, 1 h burned sediment), by means of the monthly protein-organic matter ratios provided by Mallo *et al.* (1993).

Statistical analyses were performed on log-transformed data using the SYSTAT software (copyright (c) SYSTAT Inc., 1990). Two-way ANOVAs were used to assess the effect of sites and sampling dates on the monitored parameters. Student-Newmann-Keuls multiple comparisons test was used to assess differences between groups.

RESULTS

Protein content of sediments

Changes in protein content of the sediment (% based on DW) at the three studied sites are presented in Fig. 2. A two-way ANOVA showed that protein content were: (1) significantly affected by site (p=0.001), and (2) not significantly affected by sampling date (p=0.123). There was no significant interaction between these two factors (p=0.855). At the disturbed silt site, protein content ranged from 6.19 (July) to 14.80% (February). At the typical silt site, protein content ranged from 1.02 (April) to 2.89% (September). At the disturbed sand site, protein content ranged from 0.07 (April) to 0.38% (February). Thus, the spatial variability of protein content confirmed the marked environmental differences of the three sites under study.

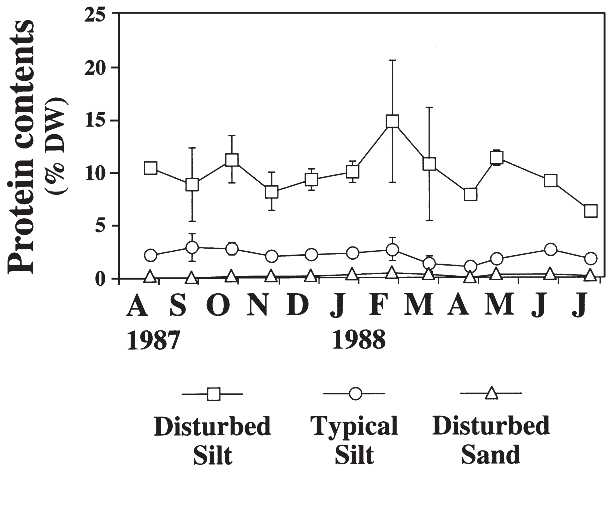

FIG. 2. – Changes in sediment protein contents at the three studied sites. Vertical bars represent standard deviations.

Size structure

Temporal changes in the structure of the studied populations are presented in Fig. 3. Both small and large worms were found simultaneously in most samples. Thus, at the three studied sites, *Capitella* sp. showed a polymodal distribution throughout most of the year. Such a distribution is characteristic of species with several reproductive periods (or continuous reproduction) per year. Moreover, it should be pointed out that small worms seemed to constitute the most important component of the populations. Over the winter months (November to February), an age class of smallest individuals (i.e., probably recruits) was present in all three studied sites without a regular advancement in size each month.

Biomass and abundance

At the disturbed silt site, biomass of *Capitella* sp. per unit of surface area ranged from 0 (June) to 16.069 gDW. m^{-2} (January) (Fig. 4A). At the typical silt site, biomass ranged from 0.109 (May) to 2.593 gDW. m^{-2} (February). At the disturbed sand site, biomasses ranged from 0.033 (October) to 0.346 gDW. m^{-2} (January). Biomass of *Capitella* sp. was significantly affected by site and sampling date (p=0.001 in both cases; with a significant interaction between these two factors, p=0.001). Multiple comparison tests showed that biomass did not significantly differ among sites during the warmest period (i.e., August to October and March to July) (p>0.05). On the contrary, during the coldest period (i.e., November to February), biomass was always highest at the disturbed silt site, intermediary at the typical silt site and lowest at the disturbed sand site (p<0.05).

At the disturbed silt site, densities of *Capitella* sp. ranged from 0 (June) to 172450 ind. m^{-2} (November) (Fig. 4B). At the typical silt site, densities ranged from 583 (May) to 21325 ind. m^{-2} (November). At the disturbed sand site, densities ranged from 213 (October) to 4238 ind. m^{-2} (January). Densities of *Capitella* sp. were significantly affected by site and sampling date (p=0.001 in both cases; with a significant interaction between these two factors, p=0.001). Temporal changes in density were similar to those of biomass since: (1) densities were minimal during the warmest period, and (2) highest densities were usually observed at the disturbed silt site. However, at this site, there was a time lag of about three months between biomass and density maxima (November vs. January).

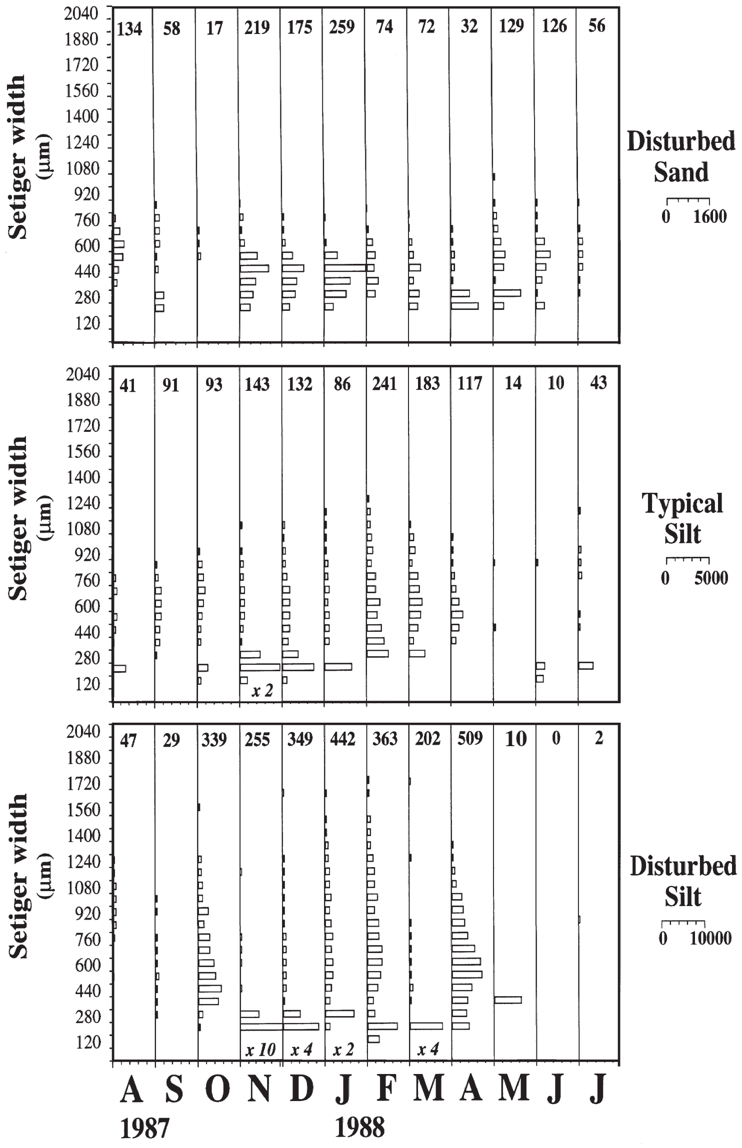

FIG. 3. – *Capitella* sp. : Monthly distribution of size-frequency histograms at the three studied sites. Note the differences in horizontal scales. x2, x4 and x10 are conversion factors for the corresponding scales. Bold numbers on the top of the graphics indicate the number of mesured specimens.

Average individual weights (Fig. 5) were significantly affected by site and sampling date (p=0.001 in both cases, with a significant interaction between these two factors, p=0.001). Multiple comparison test showed that all sites under study were significantly different from each other ($p<0.05$). There was no clear temporal pattern at the disturbed sand site. At the two silt sites, seasonality was characterized by significantly low average individual weights in November ($p<0.05$) followed by a progressive increase during winter. Thus, average individual weights reached the maximum from March to May at the typical site and in January at the disturbed site. This pattern reflects the existence of a period clearly dominated by small individuals entering the population (i.e., prevailing recruitment) followed by a period characterized by an increase in individual biomass (i.e., prevailing growth). The high average individual weights observed in August and July at the disturbed silt site ($p<0.05$) were related to the presence of a few, large worms in the population. Minimal (0.040 μgDW. ind.$^{-1}$ in November) and maximal (0.450 μgDW. ind.$^{-1}$ in August) individual weights were observed at the disturbed silt site. At the typical silt and the sandy sites, the range of variation was much narrower (i.e., from 0.040 to 0.171 μgDW. ind.$^{-1}$).

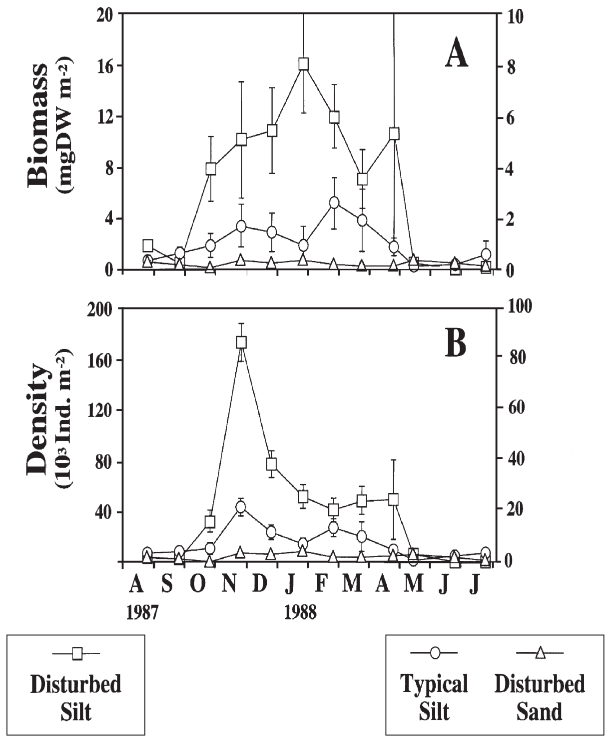

FIG. 4. – *Capitella* sp. : A.- Changes in biomass per surface area at the three studied sites. B.- Changes in density per surface area at the three studied sites. Vertical bars are standard deviations. Note the differences in vertical scales.

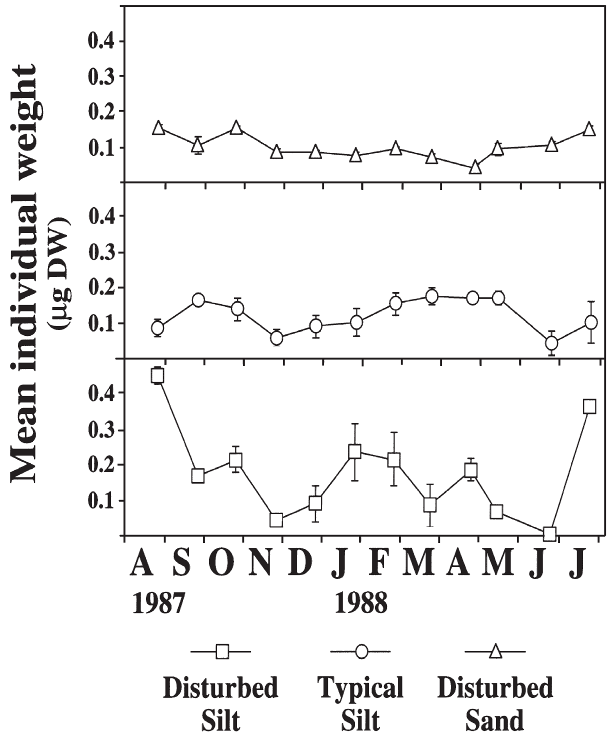

FIG. 5. – *Capitella* sp.: Changes in mean individual weights at the three studied sites. Vertical bars represent standard deviations.

Secondary production

Yearly secondary production of the three *Capitella* sp. populations under study, as estimated by the Hynes method, were: 0.83 gDW. m^{-2} y^{-1} for the disturbed sand site, 3.74 gDW. m^{-2} y^{-1} for the typical silt site, and 36.9 gDW. m^{-2} y^{-1} for the disturbed silt site. The corresponding P/B ratios were of 4.09 y^{-1}, 3.66 y^{-1} and 5.71 y^{-1}, respectively.

DISCUSSION

Methodological considerations

One of the major problems with ecological studies carried out on field populations of *Capitella* sp. is linked with the definition of the species. The limitations of the current study were: (1) the fact that there was only one species under study, and (2) the exact identification of this species. The observations carried out during the present study (e.g., presence of brooding tubes at the three studied sites, same morphology of males modified setae) seem to support the fact that the same *Capitella* species was present at the three sites. Although differences among sites (especially in individual size) thus probably resulted from organic matter availability (Tsutsumi *et al.*, 1990; Qian and Chia, 1992), we decided to use the Hynes method (which was originally developed to assess production of whole communities) to estimate the secondary production of the studied populations. However, the possibility to check for the existence of different sibling species in Alfacs Bay remains open.

Like most opportunistic invertebrates, *Capitella* sp. exhibits continuous reproduction. This particular life-history trait complicates the identification of cohorts using techniques based on size analysis. The observations carried out on *Capitella* sp. by Tsutsumi (1987) in an organic polluted cove, and by Qian and Chia (1994) in an intertidal mud-flat reveals the existence of recruitment peaks similar to those found during the present study. Additional evidence has been provided in experimental populations of *Capitella* sp.I (Chesney and Tenore, 1985; Grémare *et al.*, 1989b). Such a synchronization may either result from an external zeitgeber (such as the lunar cycle according to Tsutsumi, 1987) or from food availability (Grémare *et al.*, 1989b). The existence of a certain level of synchronization in the reproduction of opportunistic invertebrates explains why approaches based on the analysis of size frequency histograms have often been used to assess the dynamics of such populations (Warren, 1976; Carrasco and Arcos, 1980; Oyenekan, 1983; Tsutsumi, 1987; Sardá and Martin, 1993). Nevertheless, during the present study, such apparent synchronization was not sufficient to allow for the identification and the study of cohorts of the *Capitella* sp. populations in Alfacs Bay. This finding led us to use a method not based on cohort recognition (i.e., the Hynes method) to estimate secondary production.

Another characteristic of opportunistic invertebrates is their ability to show high growth rates (Tenore, 1983; Tenore and Chesney, 1985; Marsh and Tenore, 1990). This particular trait may be of importance when determining sampling periodicity, since this parameter has a direct effect on the confidence interval of production estimates (Morin *et al.*, 1987). During the present study, samples were taken monthly. The same periodicity has already been used by Warren (1976), Tsutsumi and Kikuchi (1984) and by Qian and Chia (1994) to assess dynamics of field populations of *Capitella* sp. It is superior to the periodicity (bimonthly sampling) used by either Oyenekan (1983) or Sprung (1994) to determine the only available production estimates of field populations of *Capitella* sp. before the present study. The existing literature concerning the generation time of *Capitella* sp. mention values ranging from 1.5 (Tsutsumi, 1987, from 12.9 to 24.9°C) to 3.5 months (Qian and Chia, 1994, <16°C) depending on temperature. At the three sites, worm biomass was maximal between October and April. Field temperatures during this period are always less than 20°C (Sardá and Martin, 1993). Moreover, species of the *Capitella* complex are generally polytelic, which implies that their life spans are longer than only one generation time. We thus assume that the sampling interval used during the present study is (1) much shorter than the duration of one life cycle of *Capitella* sp. in Alfacs Bay, and (2) longer enough to assume that most individuals grew from a given size class to the immediately superior from month to month.

Availability of organic matter

Opportunistic species such as *Capitella* sp., have been often associated with areas enriched in organic matter (Grassle and Grassle, 1974; Pearson and Rosenberg, 1978). The effect of food availability on the population dynamics of benthic deposit-feeders may be either related with quantity or quality of available food (Phillips, 1984; Grémare *et al.*, 1988; Marsh and Tenore, 1990; Grémare, 1994). In Alfacs Bay, sediment protein concentrations significantly differed among sites, but did not vary seasonally within sites. Thus, at each site, the seasonal pattern of *Capitella* sp. biomass probably did not result from a food quantity effect. At the studied sites, organic matter mainly derives from decaying vegetation. About 80% of the average mg of carbon produced per m^{-2} per day comes from macrophytes. The degradation of this type of material is rather long (Buchbaum *et al.*, 1991), with 65% of the initial biomass still remaining after 100 days in Alfacs Bay (Pérez, 1989). The maximum amount of dead leaves (30 g C m^{-2}) decomposing at a rate of 0.1 g C m^{-2} day^{-1} occurs in autumn (Pérez, 1989). Phytoplankton dynamics in the Bay typically lack marked seasonality, and maximum production tends to occur near the openings of the outlet channels from where currents usually run out of the shelfs (and even out of the Bay) (Delgado, 1987, 1989; Camp *et al.*, 1991). Thus, an effect of food quality on biomass seasonal pattern (i.e., due to the sedimentation of phytoplanktonic blooms such as in Marsh and Tenore, 1990) is also unlikely to occur. However, the coincidence of maximum accumulation rates of decaying vegetation starting at the beginning of autumn (Pérez, 1989) and the increasing total biomass linked to very low mean individual weights (i.e., peak of small worms entering the populations) in November could be interpreted tentatively as the origin of the apparent synchronization observed in Alfacs Bay.

Nevertheless, differences in protein concentration among sites may contribute to explain the observed pattern in maximal biomass. Food availability controls *Capitella* sp. population biomass in laboratory cultures (Tenore and Chesney, 1985; Grémare *et al.*, 1988, 1989a; Qian and Chia, 1992). In optimal conditions, *Capitella* sp. grows faster and produces more offspring because its generation time is shorter and its fecundity is higher (Grémare *et al.*, 1988; Qian and Chia, 1992). During the present study, the highest biomass occurred at the disturbed silt site which also had the highest sediment protein content. This was probably due to differences in food availability. Moreover, *Capitella* sp. can maintain its populations by producing a few offspring of good quality when confronted with limited food resources (Qian and Chia, 1993). Thus, the lower (but less fluctuating) biomass featured by *Capitella* sp. at the disturbed sand site could be related to limited food supply (protein contents always lower than 1%).

TABLE 2. – Annual secondary production (P: in gAFDW. m^{-2}. y^{-1}), annual mean biomass (B: gAFDW. m^{-2}) and annual production/biomass ratio (P/B: in y^{-1}) of some representative polychaetes (wet weight data excluded). Our original data on secondary production (gDW. m^{-2}. $year^{-1}$) have been converted into gAFDW. m^{-2} $year^{-1}$ assuming a 74.19% organic matter content for *Capitella* sp. in Alfacs Bay (own personal measurements).

Species	Locality	P	B	P/B	Authority
Amage adspersa	Ria Formosa	0.028	0.012	2.333	Sprung 1994
Ampharete acutifrons	Cornwall	2.320	0.426	5.450	Warwick and Price 1975
Arenicola marina	Grevelingen estuary	3.790	3.325	1.140	Wolf and de Wolf 1977
“ “	Grevelingen estuary	6.260	8.694	0.720	“
“ “	Grevelingen estuary	3.320	3.354	0.990	“
Capitella sp.	Alfacs Bay (disturbed sand)	0.610	0.150	4.087	Present study
“	Alfacs Bay (typical silt)	2.775	0.757	3.656	“
“	Alfacs Bay (disturbed silt)	27.377	4.822	5.710	“
“	Ria Formosa	0.010	0.004	2.318	Sprung 1994
“	Ria Formosa	0.272	0.166	1.636	“
“	Southampton Water	0.382	0.033	11.600	Oyenekan 1983
“	Southampton Water	1.162	0.356	3.260	“
Capitella sp. I	Laboratory (control)	39.300	8.020	4.900	Chesney 1985
“	Laboratory (0% predation)	53.800	6.987	7.700	“
“	Laboratory (12% predation)	70.500	5.779	12.200	“
“	Laboratory (15% predation)	83.500	4.718	17.700	“
“	Laboratory (23% predation)	86.800	4.429	19.600	“
“	Laboratory (min.)	0.070	0.412	0.170	Grémare *et al*. 1989b
“	Laboratory (max.)	1.050	2.692	0.390	“
Caulleriella caputesocis	Southampton Water	0.010	0.012	0.833	Oyenekan 1987
“	Southampton Water	0.940	0.272	3.456	“
“	Southampton Water	5.900	1.031	5.723	“
Chaetozone setosa	Northumberland	0.050	0.039	1.280	Buchanan and Warwick 1974
Cirriformia tentaculata	Ria Formosa	2.505	0.836	2.996	Sprung 1994
“	Ria Formosa	0.481	0.198	2.433	“
Diopatra neapolitana	Ria Formosa	1.886	0.289	6.521	“
Eone normanni	Ria Formosa	2.173	0.914	2.377	“
Euclymene oerstedi	Ria Formosa	0.0009	0.0004	2.250	“
Glycera alba	Camarthen Bay	0.261	0.269	0.970	Warwick *et al*., 1978
Glycera convoluta	Ria Formosa	0.971	0.282	3.447	Sprung 1994
“	Ria Formosa	1.096	0.353	3.104	“
Glycera rouxii	Northumberland coast	0.192	0.519	0.370	Buchanan and Warwick 1974
Goniada norvergica	Ria Formosa	0.0006	0.0003	2.000	Sprung 1994
Hediste diversicolor	Ria Formosa	19.221	3.652	5.263	“
“	Ria Formosa	31.705	9.680	3.275	“
Heteromastus filiformis	Northumberland coast	0.300	0.297	1.010	Buchanan and Warwick 1974
“	Ria Formosa	0.018	0.008	2.321	Sprung 1994
“	Ria Formosa	4.044	1.646	2.457	“
“	Ria Formosa	0.007	0.003	2.152	“
Hyalinoecia fauveli	Ria Formosa	0.349	0.144	2.420	“
Keffersteinia cirrata	Ria Formosa	0.008	0.003	2.625	“
Lumbrineris fragilis	Northumberland coast	0.078	0.058	1.340	Buchanan and Warwick 1974
Magelona mirabilis	Camarthen Bay	0.685	0.623	1.100	Warwick *et al*., 1978
Melinna palmata	Ria Formosa	0.012	0.004	2.810	Sprung 1994
“	Ria Formosa	6.207	2.656	2.337	“
Microspio mecznikovianus	Ria Formosa	0.002	0.001	2.833	“
Neanthes caudata	Ria Formosa	0.045	0.023	1.927	“
Nephtys hombergii	Southampton Water	0.092	0.051	1.804	Oyenekan, 1986
“	Southampton Water	2.456	1.506	1.631	“
“	Southampton Water	4.322	1.496	2.889	“
“	Lynher estuary	7.335	3.861	1.900	Warwick and Price, 1975
“	Swansea Bay	0.368	0.460	0.800	Warwick and George, 1980
“	Lynher estuary	2.840	3.506	0.810	Price and Warwick, 1980
“	Lynher estuary	6.000	4.225	1.420	“
“	Ria Formosa	1.422	0.309	4.601	Sprung, 1994
“	Ria Formosa	0.277	0.166	1.666	“
Nerine cirratulus	Ria Formosa	0.0003	0.0001	3.000	“
Notomastus latericeus	Acquatina lagoon	2.231	1.080	2.066	Giangrande and Fraschetti, 1993
“	Acquatina lagoon	1.077	1.090	0.988	“
“	Ria Formosa	0.564	0.255	2.209	Sprung, 1994
“	Ria Formosa	0.002	0.001	2.375	“
Owenia fusiformis	Ria Formosa	0.178	0.073	2.423	“
“	Ria Formosa	0.013	0.006	2.393	“
Paraonis lyra	Ria Formosa	0.018	0.007	2.521	“
Paraprionospio pinnata	Concepción Bay	4.526	1.886	2.400	Carrasco and Arcos, 1980
Polycirrus sp.	Ria Formosa	0.039	0.016	2.475	Sprung, 1994
Polydora ciliata	Ria Formosa	0.001	0.000	2.500	“
“	Ria Formosa	0.0006	0.0003	2.000	“
“	Ria Formosa	0.003	0.001	2.357	“

TABLE 2. – (Cont.)

Species	Locality	P	B	P/B	Authority
Prionospio caspersi	Po River delta	8.060	1.970	4.091	Ambrogi, 1990
Pseudomalacoceros tridentata	Ria Formosa	0.004	0.002	2.333	Sprung, 1994
“	Ria Formosa	0.008	0.0002	2.371	“
Scolelepis cantabra	Ria Formosa	0.0004	0.0002	2.000	“
Scolelepis gaucha	Patos Lagoon	0.500	0.727	10.763	Santos, 1994
“	Patos Lagoon	1.850	0.143	12.960	“
“	Patos Lagoon	0.150	0.044	3.390	“
“	Patos Lagoon	2.825	0.783	3.608	“
Scoloplos armiger	Ria Formosa	0.058	0.028	2.056	Sprung, 1994
Spio filicornis	Ria Formosa	0.00012	0.0005	2.400	“
Spiophanes kroyeri	Northumberlan coast	0.196	0.140	1.400	Buchanan and Warwick, 1974
Terebella lapidaria	Ria Formosa	0.519	0.188	2.758	Sprung, 1994

Secondary production

Production was minimal at the disturbed sand site, intermediary at the typical silt site and maximal at the disturbed silt site (Table 2). The same pattern was true for annual mean biomass and P/B ratio. Differences in P/B ratios show that the increase in production was not only due to biomass. Opportunists such as *Capitella* sp. are known to react quickly to changes in food availability, both in terms of growth (biomass increase) (Tenore, 1981, 1983; Marsh *et al*., 1989), and reproductive output (Grémare *et al*., 1988, 1989a, b). Moreover, due to their particular physiology, these organisms are highly dependent on food availability (Tsutsumi, 1987). For example, Grémare *et al*. (1989a) showed that the reproductive output of *Capitella* sp. I was much higher than those of more stable polychaetes when food was abundant but rather comparable when food ran low. Since often no sound information is available on food availability, comparing production of field populations of opportunists might be difficult because what causes differences in production would not be easily determinable. With this in mind, we have nevertheless attempted to compare our values of production and P/B ratio with those of the existing literature.

The first step was to compare our results to other data concerning field and laboratory populations of *Capitella* sp. (Table 2). The production observed at the two silty sites is much higher, whereas the production at the sandy site is similar to one of the values reported by Oyenekan (1983). The observed pattern was rather different for P/B ratios which were maximal for the disturbed silt site and intermediate for the typical silt and disturbed sand sites (Table 2). The P/B ratios recorded at the 3 studied sites are of the same order as those reported by Chesney (1985) for experimental populations of *Capitella* sp. I submitted to different levels of predation (Table 2). They are much higher than those reported by Grémare *et al*. (1989b) for another experimental population of *Capitella* sp.I (Table 2).

Differences in both production (from 1 to 8680) and P/B ratio (from 1 to 115) are too large to merely result from differences in food availability. Such discrepancies are probably related to methodological problems. Indeed, several approaches have been used to assess the production of *Capitella* sp, namely: (1) maximum sustainable yield (MSY, Chesney, 1985), (2) indirect estimation based on the relationship between R/B ratio and growth (Chesney, 1985), (3) increment summation techniques either based on cohort analysis (Oyenekan, 1983) or on size class (Grémare *et al*., 1989b), (4) Hynes method (present study), and (5) indirect estimations based on a theoretical P/B ratio derived from average individual weight (Sprung, 1994). So far, Chesney (1985) has been the only one who compared two different methods. He concluded that both MSY and estimations based on growth rates provided similar results. Our data are very similar to his (Table 2). We thus believe that the Hynes method can also provide sound estimations of *Capitella* sp. production. The lower P/B ratios reported by Sprung (1994) probably reflects the limitation of the empirical approach used to derive production estimates from average individual dry weights. The low P/B ratios reported by Grémare *et al*. (1989b) are more difficult to explain. In any case, it seems necessary to try to standardise techniques designed to assess secondary production of opportunists in the near future.

The second step was to compare our results with available data concerning other polychaetes (Table 2). Except for that of *Hediste diversicolor* (Sprung, 1994), the production recorded at the disturbed silt site is the highest recorded for polychaetes in natural conditions (Table 2). At the typical silt and disturbed sand sites, the recorded productions are included in the range reported for other polychaete populations. The P/B ratios at the three sites are among the highest values recorded for polychaetes. Only the P/B ratios of *Scolelepis gaucha* (Santos, 1994), *Diopatra neapolitana* (Sprung, 1994) and *Caulleriella caputesocis* (Oyenekan, 1987) are higher than that of *Capitella* sp. at the disturbed silt site (Table 2). It is not surprising to obtain high P/B ratios for opportunists since these organisms feature very high growth rates and reproductive outputs when food is abundant (Grémare *et al*., 1988, 1989a; Marsh *et al*., 1990).

In summary, at the two silty sites, *Capitella* sp. presents: (1) a marked seasonal variability, and (2) high production rates and P/B ratios, which are two characteristics of opportunists. At the disturbed sand site, however, its seasonal pattern is much more stable, and its production much lower (although P/B ratios are still high). Thus, as postulated by Qian and Chia (1994), our results confirm that *Capitella* sp. shows a great plasticity relative to environment.

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REFERENCES

Ambrogi, R. – 1990. Secondary production of *Prionospio caspersi* (Annelida: Polychaeta: Spionidae). *Mar. Biol.*, 104: 437-442.

Benke, A.C. – 1979. A modification of the Hynes method for estimating secondary production with particular significance for multivoltine populations. *Limnol. Oceanogr.*, 24: 168-171.

Bhattacharya, C.G. – 1967. A simple method of resolution of a distribution into Gaussian components. *Biometrics,* 23: 115-135.

Buchanan, J.B. and R.M. Warwick. – 1974. An estimate of benthic macrofaunal production in the offshore mud of the Northumberland coast. *J. Mar. Biol. Ass. U.K.,* 54: 197-222.

Buchsbaum, R., I. Valiela, T. Swan, M. Dzierzeski and S. Allen. – 1991. Available and refractory nitrogen in detritus of coastal vascular plants and macroalgae. *Mar. Ecol. Prog. Ser.,* 72: 131-143.

Camp, J., J. Romero, M. Pérez, M. Vidal, M. Delgado and A. Martínez. – 1991. Production-consumption budget in an estuarine bay: How anoxia is prevented in a forced system. *Oecol. Aquat.,* 10: 145-152.

Carrasco, F.V. and D.R. Arcos. – 1980. Estimación de la producción secundaria de *Paraprionospio pinnata* (Spionidae: Polychaeta) frente a Bahía de Concepción, Chile. *Bolm. Inst. Oceanogr., Sao Paulo,* 29: 79-82.

Chesney Jr., E.J. – 1985. Laboratory studies of the effect of predation on production and the production: biomass ratio of the opportunistic polychaete *Capitella capitata* (Type I). *Mar. Biol.,* 87: 307-312.

Chesney Jr., E.J. and K.R. Tenore. – 1985. Oscillations of laboratory populations of the polychaete *Capitella capitata* (Type I): their cause and implications for natural populations. *Mar. Ecol. Prog. Ser.,* 20: 289-296.

Cornet, M. – 1986. Estimation de la production annuelle des populations d'*Abra alba* (Mollusque Bivalve) du plateau continental Sud-Gascogne. *Oceanol. Acta,* 9: 323-332.

Delgado, M. – 1987 Fitoplancton de las bahías del Delta del Ebro. *Inv. Pesqueras,* 51: 517-548.

Delgado, M. – 1989. Abundance and distribution of microphytobenthos in the Bays of Ebro Delta (Spain). *Est. Coast. Shelf Sci.,* 29: 183-194.

Duarte, C.M. and K. Sand-Jensen. – 1990. Seagrass colonization: patch function and patch growth in *Cymodocea nodosa. Mar. Ecol. Prog. Ser.,* 65: 193-200.

Eckelbarger, K.J. and J.P. Grassle. – 1983. Ultrastructural diferences in the eggs and ovarian follicle cells of *Capitella* (Polychaeta) sibling species. *Biol. Bull. mar. biol. Lab., Woods Hole,* 165: 379-393.

Eckelbarger, K.J. and J.P. Grassle. – 1987a. Interspecific variation in genital spine, sperm, larval morphology in six sibling species of *Capitella. Bull. Biol. Soc. Wash.,* 7: 62-76.

Eckelbarger, K.J. and J.P. Grassle. – 1987a. Spermatogenesis, sperm storage and comparative sperm morphology in nine species of *Capitella, Capitomastus* and *Capitellides* (Polychaeta: Capitellidae). *Mar. Biol.,* 95: 415-429.

Giangrande, A. and S. Fraschetti. – 1993. Life cycle, growth and secondary production in a brackish-water population of the polychaete *Notomastus latericius* (Capitellidae) in the Mediterranean Sea. P.S.Z.N. I: *Mar. Ecol.,* 14: 313-327.

Grassle, J.F. and J.P. Grassle. – 1974. Opportunistic life histories and genetic systems in marine benthic polychaetes. *J. Mar. Res.,* 32: 253-284.

Grassle, J.P., C.E. Gelfman and S.W. Mills. – 1987. Karyotypes of *Capitella* sibling species and of several species in the related genera *Capitellides* and *Capitomastus* (Polychaeta). *Bull. Biol. Soc. Wash.,* 7: 77-88.

Grassle, J.P. and J.F. Grassle. – 1976. Sibling species in the marine pollution indicator *Capitella* (Polychaeta). *Science,* 192: 567-569.

Grémare, A. – 1994. What describes fecundity of *Capitella* sp.I better: macro- or micronutrient availability? *Mar. Biol.,* 119: 367-374.

Grémare, A., A.G. Marsh and K.R. Tenore. – 1988. Short-term reproductive responses of *Capitella* sp.I (Annelida: Polychaeta) fed on different diets. *J. Exp. Mar. Biol. Ecol.,* 123: 147-162.

Grémare, A., A.G. Marsh and K.R. Tenore. – 1989a. Fecundity and energy partitioning in *Capitella capitata* type I (Annelida: Polychaeta). *Mar. Biol.,* 100: 365-371.

Grémare, A., A.G. Marsh and K.R. Tenore. – 1989b. Secondary production and reproduction of *Capitella capitata* type I (Annelida: Polychaeta) during a population cycle. *Mar. Ecol. Prog. Ser.,* 51: 99-105.

Hamilton, A.L. – 1969. On estimating annual production. *Limnol. Oceanogr.,* 14: 771-782.

Holbrook, M.J.L. and J.P. Grassle. – 1984. The effects of low density on the development of simultaneous hermaphroditism in male *Capitella* sp.I (Polychaeta). *Biol. Bull. mar. biol. Lab., Woods Hole,* 166: 103-109.

Hynes, H.B.N. and M.J. Coleman. – 1968. A simple method for assessing the annual production of stream benthos. *Limnol. Oceanogr.,* 13: 569-573.

Mallo, S., F. Vallespinós, S. Ferrer and D. Vaqué. – 1993. Microbial activities in estuarine sediments (Ebro Delta, Spain) influenced by organic matter influx. *Sci. Mar.,* 57: 31.

Marsh, A.G., A. Grémare and K.R. Tenore. – 1989. Food type and food ration effects on growth of juvenile of *Capitella* sp.I (Annelida: Polychaeta): Macro- vs. micr-nutrients. *Mar. Biol.,* 102: 519-527.

Marsh, A.G., H.R. Harvey, A. Grémare and K.R. Tenore. – 1990. Dietary effect on oocyte yolk-composition in *Capitella* sp.I (Annelida: Polychaeta): fatty acids and sterols. *Mar. Biol.,* 106: 369-374.

Marsh, A.G. and K.R. Tenore. – 1990. The role of nutrition in regulating the population dynamics of opportunistic, surface deposit feeders in a mesohaline community. *Limnol. Oceanogr.,* 35: 710-724.

Martin, D. – 1992 Macroinfauna de una bahía Mediterránea. Estudio de los niveles de organización de las poblaciones de Anélidos Poliquetos. *Col.lecció de Tesis Doctorals Microfitxades,* 1662: 1-456.

Martin, D., E. Ballesteros, J.M. Gili and C. Palacín. – 1993. Small-scale structure of infaunal polychaete communities in an estuarine environment: Methodological approach. *Est. Coast. Shelf Sci.,* 36: 47-58.

Morin, A., T. Mousseau and D. Roff. – 1987. Accuracy and precision of secondary production estimates. *Limnol. Oceanogr.,* 32: 1342-1352.

Oyenekan, J.A. – 1983. Production and population dynamics of *Capitella capitata*. *Arch. Hydrobiol.,* 98: 115-126.

Oyenekan, J.A. – 1986. Population dynamics and secondary production in an estuarine population of *Nephtys hombergii* (Polychaeta: Nephtydae). *Mar. Biol.,* 93: 217-223.

Oyenekan, J.A. – 1987. Population dynamics and secondary production in an estuarine population of *Caulleriella caputesocis* (Polychaeta: Cirratulidae). *Mar. Biol.,* 95: 267-273.

Palacín, C., D. Martin and J.M. Gili. – 1991. Features of benthic infauna in a Mediterranean shallow-water bay. *Mar. Biol.,* 110: 315-321.

Pearson, T.H. and R. Rosenberg. – 1978. Macrobenthic succesion in relation to organic enrichment and polution in marine environment. *Oceanogr. Mar. Biol. Ann. Rev.,* 16: 229-311.

Pérez, M. – 1989. Fanerógamas marinas en sistemas estuáricos: Producción, factores limitantes y algunos aspectos del ciclo de nutrientes. Doctoral Thesis, Universidad de Barcelona, 200 pp.

Petraitis, P.S. – 1985a. Females inhibits males propensity to develop into simultaneous hermaphrodites in *Capitella* sp. I (Polychaeta). *Biol. Bull. mar. biol. Lab., Woods Hole,* 168: 395-402.

Petraitis, P.S. – 1985b. Digametic sex determination in the marine polychaete *Capitella capitata* (species type I). *Heredity,* 55: 151-156.

Phillips, N.W. – 1984. Role of different microbes and substrates as potential suppliers of specific essential nutrients to marine detritivores. *Bull. Mar. Sci.,* 35: 283-298.

Price, R. and R.M. Warwick. – 1980. Temporal variations in annual production and biomass in estuarine populations of two polychaetes, *Nephtys hombergii* and *Ampharete acutifrons*. *J. Mar. Biol. Ass. U.K.,* 60: 481-487.

Qian, P.Y. and F.S. Chia.- 1991. Fecundity and egg size of *Capitella* sp. were mediated by diet. *J. Exp. Mar. Biol. Ecol.,* 148: 11-25.

Qian, P.Y. and F.S. Chia. – 1992. Effects of diet type on the demographics of *Capitella* sp. (Annelida: Polychaeta): lecithotrophic development vs. planktotrophic development. *J. Exp. Mar. Biol. Ecol.,* 157: 159-179.

Qian, P.Y. and F.S. Chia. – 1993. Larval development as influenced by food limitation in two polychaetes: *Capitella* sp. and *Polydora ligni* Webster. *J. Exp. Mar. Biol. Ecol.,* 166: 93-105.

Qian, P.Y. and F.S. Chia. – 1994. *In situ* measurement of recruitment, mortality, growth, and fecundity of *Capitella* sp. (Annelida: Polychaeta). *Mar. Ecol. Prog. Ser.,* 111: 53-62.

Rosenberg, R. – 1972. Benthic faunal recovery in a Swedish fjord following the closure of a sulphite pulp mill. *Oikos,* 23: 92-108.

Rosenberg, R. – 1976. Benthic faunal dynamics during succession following pollution abatement in a Swedish estuary. *Oikos,* 27: 414-427.

Santos P.J.P. – 1994. Population dynamics and production of *Scolelepis gaucha* (Polychaeta: Spionidae) on the sandy beaches of Southern Brazil. *Mar. Ecol. Prog. Ser.,* 110: 159-165.

Sardá, R. and D. Martin. – 1993. Populations of *Streblospio* (Polychaeta, Spionidae) in temperate zones: demography and production. *J. Mar. Biol. Ass. U.K.,* 73: 769-784.

Sprung, M. – 1994. Macrobenthic secondary production in the intertidal zone of the Ria Formosa - a lagoon in the Southern Portugal. *Est. Coast. Shelf Sci.,* 38: 539-558.

Tenore, K.R. – 1977. Growth of *Capitella capitata* cultured on various levels of detritus derived from different sources. *Limnol. Oceanogr.,* 22: 936-941.

Tenore, K.R. – 1981. Organic Nitrogen and caloric content of detritus. I. Utilization by the deposit-feeding Polychaete, *Capitella capitata*. *Est. Coast. Shelf Sci.,* 12: 39-47.

Tenore, K.R. – 1983. Organic Nitrogen and caloric content of detritus. III. Effect on growth of a deposit-feeding polychaete,*Capitella capitata*. *Est. Coast. Shelf Sci.,* 17: 733-742.

Tenore, K.R. and E.J. Chesney Jr. – 1985. The effects of interaction of rate of food supply and population density on the bioenergetics of the opportunistic polychaete, *Capitella capitata* (type I). *Limnol. Oceanogr.,* 30: 1188-1195.

Tsutsumi, H. – 1987. Population dinamics of *Capitella capitata* (Polychaeta: Capitellidae) in an organically polluted cove. *Mar. Ecol. Prog. Ser.,* 36: 139-149.

Tsutsumi, H. – 1990. Population persistence of *Capitella* sp. (Polychaeta; Capitellidae) on a mud flat subject to environmental disturbance by organic enrichment. *Mar. Ecol. Prog. Ser.,* 63: 147-156.

Tsutsumi, H., S. Fukunaga, N. Fujita and M. Sumida. – 1990. Relationship between growth of *Capitella* sp. and organic enrichment of the sediment. *Mar. Ecol. Prog. Ser.,* 63: 157-162.

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

Warren, L.M. – 1976. A population study of the polychaete *Capitella capitata* at Plymouth. *Mar. Biol.,* 180: 209-216.

Warwick, R.M. and C.L. George. – 1980. Annual macrofauna production in an Abra community. In: M.B. Collins (ed.): *Problems of an industrialized embayment. A case study of Swansea Bay,* p. 517-538. Pergamon Press, Oxford.

Warwick, R.M., C.L. George and J.R. Davis. – 1978. Annual macrofauna production in a *Venus* community. *Est. Coast. Mar. Sci.,* 7: 215-241.

Warwick, R.M. and R. Price. – 1975. Macrofauna production in an estuarine mud-flat. *J. Mar. Biol. Ass. U.K.,* 55: 1-18.

Wolf, W.J. and L. de Wolf. – 1977. Biomass and production of zoobenthos in Grevelingen estuary, The Netherlands. *Est. Coast. Mar. Sci.,* 5: 1-25.

Zajac, R.N. and R.B. Whitlatch. – 1985. A hierarchical approach to modelling soft-bottom successional dynamics. In: *Proceedings of the 19th European Marine Biological Symposium,* p. 265-275. Cambridge Univ. Press, Cambridge.

Scient. ed.: T. Kikuchi