



The effect of different primary producers on *Hydrobia ulvae* population dynamics: a case study in a temperate intertidal estuary

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Abstract

The effect of macroalgal blooms and the consequent disappearance of *Zostera noltii* meadows on *Hydrobia ulvae* population dynamics and production was studied in the Mondego estuary based on data obtained from January 1993 to September 1995. Sampling was carried out at a non-eutrophicated area, covered with *Z. noltii*, and also at an eutrophicated area, where seasonal *Enteromorpha* spp. blooms occur.

Stable populations represented by individuals of all age classes were found only at the *Z. noltii* meadows throughout the study period. On the contrary, at the eutrophicated area, during most of the time, solely juveniles were present, with adults appearing only during the macroalgal bloom (> 1.5 mm width).

During the algal bloom (e.g. 1993), *H. ulvae* population density was clearly higher in the eutrophicated area due to the combined effect of stronger benthic recruitments (99% of veliger larvae newly recruited) and dispersion of juveniles proceeding from the *Z. noltii* meadows to this area. On the other hand, in the absence of macroalgae (spring of 1994), 98.9% of veliger larvae was recruited in the *Z. noltii* meadows. Therefore, *H. ulvae* seems to respond rapidly to macroalgal dynamics and its presence at the eutrophicated area depends on the existence of green macroalgae.

H. ulvae presented the same benthic recruitment pattern at the two sampling areas, with new cohorts being produced in March, June, July and September. Depending on the time of the year in which the recruitment took place, cohorts showed different growth rhythms. However, after 12 months they reached a similar size.

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A three-generation life cycle involving a short-lived (16 months), fast growing spring generation, a medium growing (17–19 months) summer generation and a longer-lived (20 months) slower growing generation that overwinters is identified.

As a general trend, productivity and mean population standing biomass were higher at the *Z. noltii* meadows, during the entire study, except for a short period, during the macroalgal bloom, when production was higher at the eutrophicated area. On the contrary, P/\bar{B} ratios were higher at the eutrophicated area. According to our results, *H. ulvae* population structure and yearly productivity are clearly affected by eutrophication, namely by the dynamics of macroalgal blooms.

In the long run, we may infer that, following the disappearance of the *Z. noltii* meadows, due to eutrophication, *H. ulvae* would also tend to disappear, since reproductive adults were almost exclusively found in this area.

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1. Introduction

Over the last years, eutrophication has been recognized as a major threat to coastal marine ecosystems (Vadas and Beal, 1987; Beukema, 1991; Beukema and Cadeé, 1997; Jørgensen and Richardson, 1996; Norkko and Bonsdorff, 1996a,b; Raffaelli et al., 1998; Lillebø et al., 1999; Pardal et al., 2000; Cloern, 2001; Martins et al., 2001; Sfriso et al., 2001). The term eutrophication is commonly used to describe the process of changing the nutritional status of a given water body by increasing the nutrient resources (Jørgensen and Richardson, 1996). In particular, nutrients from agricultural run-off and domestic sewage discharges have a significant effect in semi-enclosed systems, supporting extensive growth of opportunistic algae (Hull, 1987; Raffaelli et al., 1989, 1991).

The occurrence of green macroalgal blooms, mainly of the genera *Enteromorpha*, *Chaetomorpha*, *Cladophora* and *Ulva* constitutes a common phenomenon on intertidal flats along much of the world's coastlines (Lavery et al., 1991; Hardy et al., 1993; Hodgkin and Hamilton, 1993; Everett, 1994; Norkko and Bonsdorff 1996a,b; Marques et al., 1997; Peralta et al., 1997; Raffaelli et al., 1998; Lillebø et al., 1999; Pardal et al., 2000; Martins et al., 2001).

The Mondego estuary represents a small estuarine system that is presently under severe environmental stress, namely an ongoing eutrophication process. Seasonal intertidal macroalgal blooms (mainly of *Enteromorpha* spp.) have been observed in the two last decades (Marques et al., 1993a, 1997; Flindt et al., 1997; Pardal, 1998; Pardal et al., 2000; Lillebø et al., 1999; Martins et al., 2001), probably due to nutrient enrichment of the estuary, which supports several industrial activities and aquacultures, besides receiving nutrients from 15 000 ha of cultivated land (mainly rice fields) located upstream (Lopes et al., 2000). According to previous studies (Flindt et al., 1997; Pardal, 1998), the annual nitrogen loading to the south arm was estimated at 134 tons year⁻¹ of which 14 tons remain in the system, while 120 tons are exported to the ocean. Concerning phosphorus, the loading was estimated to – 14 tons (1 ton is imported and 15 tons are exported), which means that 14 tons were produced in the system, resulting from remineralisation processes.

Macroalgal blooms occur preferentially in the inner areas of the south arm from late winter to early summer, when algae often collapse (Marques et al., 1993a, 1997; Flindt et al., 1997; Pardal, 1998; Lillebø et al., 1999; Martins et al., 2001). The blooms may have significant effects on the microbiology and chemistry of the underlying sediments (Hull, 1987; Cloern, 2001), on the physical environment at the sediment–water interface, on plant communities (Flindt et al., 1997; Cloern, 2001), on benthic invertebrates (Hull, 1987; Pardal, 1998; Pardal et al., 2000; Lillebø et al., 1999; Norkko et al., 2000) and on other animals that may utilize the resource provided by the plants (Raffaelli et al., 1998).

As a consequence of this eutrophication process, *Zostera noltii* meadows, which constitute the richest habitat regarding productivity and biodiversity (Marques et al., 1993a, 1997; Pardal, 1998), have been suffering a drastic decline in the south arm of the estuary, presumably outcompeted by *Enteromorpha* (Raffaelli et al., 1991, 1998; Hodgkin and Hamilton, 1993; Marques et al., 1997; Pardal, 1998; Pardal et al., 2000; Cloern, 2001).

The prosobranch *Hydrobia ulvae* is a widely distributed inhabitant of intertidal areas of lagoons and estuaries along the Atlantic coasts, from Norway to Senegal, including the Mediterranean (Graham, 1988). Several studies conducted in the Mondego estuary benthic communities (Marques et al., 1997; Pardal, 1998; Pardal et al., 2000; Lillebø et al., 1999) showed that *H. ulvae* was the most abundant species in the *Z. noltii* meadows. The snail can form dense populations, constituting an important link in the estuarine food web (Newell, 1979). Thus, populations of *H. ulvae* are of great importance in the dynamics of the ecosystems in which they are found.

Considering these facts, the major objectives of this study were: (a) to assess the impact of macroalgal blooms on *H. ulvae* population structure, dynamics and productivity based on data from 32 months; (b) to elucidate the impact of a possible disappearance of *Z. noltii* meadows on *H. ulvae* population; (c) to clarify estimations of *H. ulvae* life span based on the identification and tracking of several different cohorts; (d) to understand how the species does respond in terms of adaptative strategy to the shift in primary producers (*Z. noltii* being replaced by green macroalgae) induced by eutrophication.

2. Materials and methods

2.1. Study site

The Mondego estuary, located on the Atlantic coast of Portugal (40°08N, 8°50W) is about 7 km long and 2–3 km wide, with an area of approximately 1072 ha of wetland habitats (Lopes et al., 2000). It comprises two different arms, northern and southern, separated by an alluvium-formed island (Murraceira Island) (Fig. 1). The northern arm is deeper (4–8 m during high tide, tidal range about 1–3 m) and constitutes the principal navigation channel and the location of the Figueira da Foz harbour. The southern arm is shallower (2–4 m during high tide, tidal range 1–3 m) and is almost silted up in the upper zones, which causes the freshwater to flow mainly by the northern arm. Circulation in the southern arm is mostly dependent on the tides and on the freshwater input from the Pranto River, a small tributary (Marques et al., 1993b, 1997; Flindt et al., 1997; Lillebø et al., 1999; Pardal et al., 2000). The discharge from this tributary is controlled by a sluice (Flindt

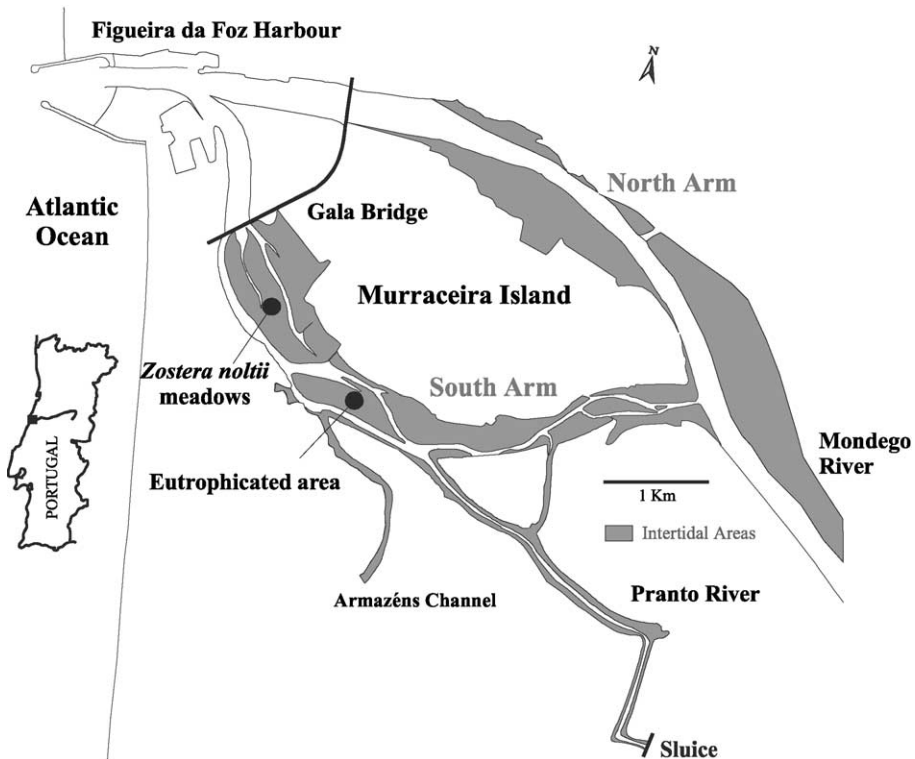


Fig. 1. Location of the sampling areas in the south arm of the Mondego estuary.

et al., 1997; Pardal, 1998; Pardal et al., 2000) and is regulated according to the water needs in rice fields from the Mondego Valley (Martins et al., 2001).

As a response to excessive nutrient (nitrogen and phosphorus) release into the estuary (Lillebø, 2000; Lillebø et al., 1999; Pardal et al., 2000; Martins et al., 2001), massive macroalgal blooms of *Enteromorpha* spp. have been regularly observed in the southern arm during the two last decades (Lillebø et al., 1999; Pardal et al., 2000; Martins et al., 2001).

Two study areas were established in the southern arm of the estuary: (a) *Z. noltii* beds are located downstream on a mud-flat covered by *Z. noltii* (Pardal et al., 2000; Martins et al., 2001). The mean organic-matter content is $6.8\% \pm 0.99$ (\pm SD). This area is characterised by higher salinity values ($20\text{--}30 \text{ g l}^{-1}$), lower total inorganic nitrogen (TIN) concentrations ($15\text{--}30 \mu\text{mol N l}^{-1}$) and higher water-flow velocity ($1.2\text{--}1.4 \text{ m s}^{-1}$); (b) Eutrophicated area is placed upstream in the inner areas of the estuary on a sandy mud flat, characterised by the absence of rooted macrophytes and covered seasonally by green macroalgae, especially *Enteromorpha* sp. (Pardal et al., 2000; Martins et al., 2001). The mean organic-matter content is $3.7\% \pm 1.0$ (\pm SD). In contrast to the *Z. noltii* beds, this area is characterised by lower salinity values ($15\text{--}25 \text{ g l}^{-1}$), higher TIN concentrations ($30\text{--}50 \mu\text{mol N l}^{-1}$) and lower water-flow velocity ($0.8\text{--}1.2 \text{ m s}^{-1}$).

2.2. Field programme

The *H. ulvae* population was monitored in the Mondego estuary for 32 months, from January 1993 to September 1995, at the two sampling stations (Fig. 1).

Samples were collected fortnightly in the first 18 months and monthly during the rest of the study period. Each time at each sampling station, 6 to 10 cores (141 cm² each) were taken to a depth of 15 cm. Samples were washed in estuarine water through a 500-µm mesh sieve. The remainder was placed into plastic bottles and preserved in 4% buffered formalin. Later, animals were separated and kept in 70% ethanol.

At each sampling date and station, temperature, salinity, pH and dissolved oxygen were measured in situ in low water pools. Sediment samples were also collected to quantify the organic matter content.

2.3. Laboratory procedures

H. ulvae individuals were counted and two measurements were used: total shell length (TSL) and maximum width (MW). The last one was most suitable, since a great number of snails had damaged shells. In the present paper we used the conversion equation $MW = 0.4369TSL + 0.2091$, $n = 339$, $r = 0.97$ (Lillebø et al., 1999). Length–weight relationships were determined for production estimates. Since length ash free dry weight relationships did not show significant seasonal differences based on analysis of variance ($P \leq 0.05$), a data set obtained throughout the study was used to provide a single regression equation ($AFDW = 0.0564TSL^{2.2381}$, $n = 191$, $r = 0.98$) (Lillebø et al., 1999). Biomass was calculated as ash free dry weight (AFDW) (loss after 8 h of incineration at 450 °C of specimens previously dried at 60 °C for 72 h). The same procedure was used to quantify organic matter content of the sediment and AFDW of macroalgae and *Z. noltii* biomass.

2.4. Statistical analysis

Multiple regression models for *H. ulvae* were developed to relate the variation of their density/biomass with environmental (temperature, salinity and organic matter of the sediment) and biological factors (green macroalgae and macrophytes biomass). The fitted regression models were expressed as:

$$Y' = a + b_1X_1 + b_2X_2 + \dots + b_kX_k$$

where Y' are the values of a given dependent variable predicted by the equation; X_1 , X_2 , ... X_k are independent variables; the solutions are the estimate of the regression coefficients a , b_1 , b_2 , ... b_k .

The significance of fitted regressions was tested by using analysis of variance technique (F) and t -test for the regression coefficients, as described in Edwards (1984, 1985). Regressions were estimated using the MINITAB 10.1 software package. All data were previously transformed as $\ln(\text{value} + 1)$, according to Zar (1996).

2.5. Growth

Growth rates were estimated by tracking recognisable cohorts with size frequency distributions from successive sample dates. Size–frequency analysis was realized using the ANAMOD software package (Nogueira, 1992), in which the analysis consistency was tested using the χ^2 and G-tests ($P=0.05$). Since growth rates were not constant through the year, we adjusted empirical data to a model that takes into account seasonal changes (Gaschütz et al., 1980), expressed as:

$$L_t = L_\infty (1 - e^{-[kD(t-t_0)+C(kD/2\pi)\sin 2\pi(t-t_s)]})1/D$$

where L_t is the length of the organism at a given moment t ; L_∞ the maximum possible length of the organism; t_0 the instant when the organism would have a length=0; t_s the time interval between start of growth (when $t=0$) and the first growth oscillation, with growth being expressed by a sine curve with a period of 1 year; K the intrinsic growth rate; C a constant whose values can vary from 0 to 1, depending on the species; D a parameter that expresses metabolic deviations from the Von Bertalanffy rule.

2.6. Production

Annual production estimates were based upon cohort recognition. Growth increments or net production (P) were estimated as described in Dauvin (1986).

Total values of P for the population are expressed as:

$$P = \sum_{n=1}^N P_{cn}$$

P_{cn} is the growth production of cohort n . \bar{B} (annual mean population biomass) is expressed as:

$$\bar{B} = (1/T) \sum_{n=1}^N (\bar{B}_n t)$$

T is the period of study (yearly cycles); N is the number of successive cohorts in the period T ; \bar{B}_n is the mean biomass of cohort n ; t is the duration of the cohort n .

3. Results

3.1. Macrophyte and macroalgal biomass

In the *Z. noltii* beds, total biomass of this macrophyte showed a clear seasonal pattern. During spring and summer, the biomass increased substantially due to the growth of leaves, whilst in the autumn and winter, below ground biomass (rhizome and roots) reached approximately 50% of the whole biomass (Fig. 2A).

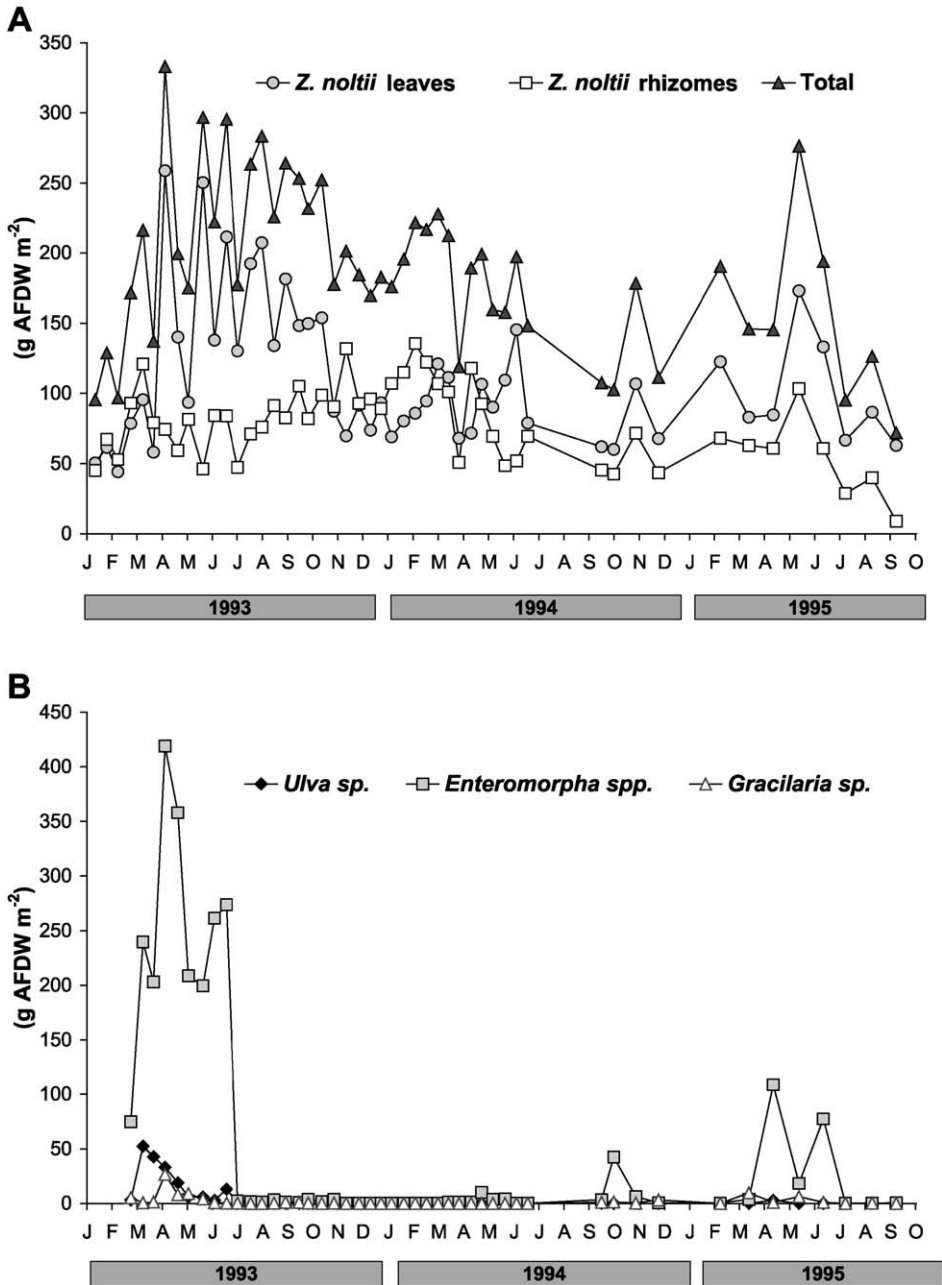


Fig. 2. Variation of plant biomass from January 1993 to September 1995. (A) *Z. noltii* meadows; (B) eutrophicated area.

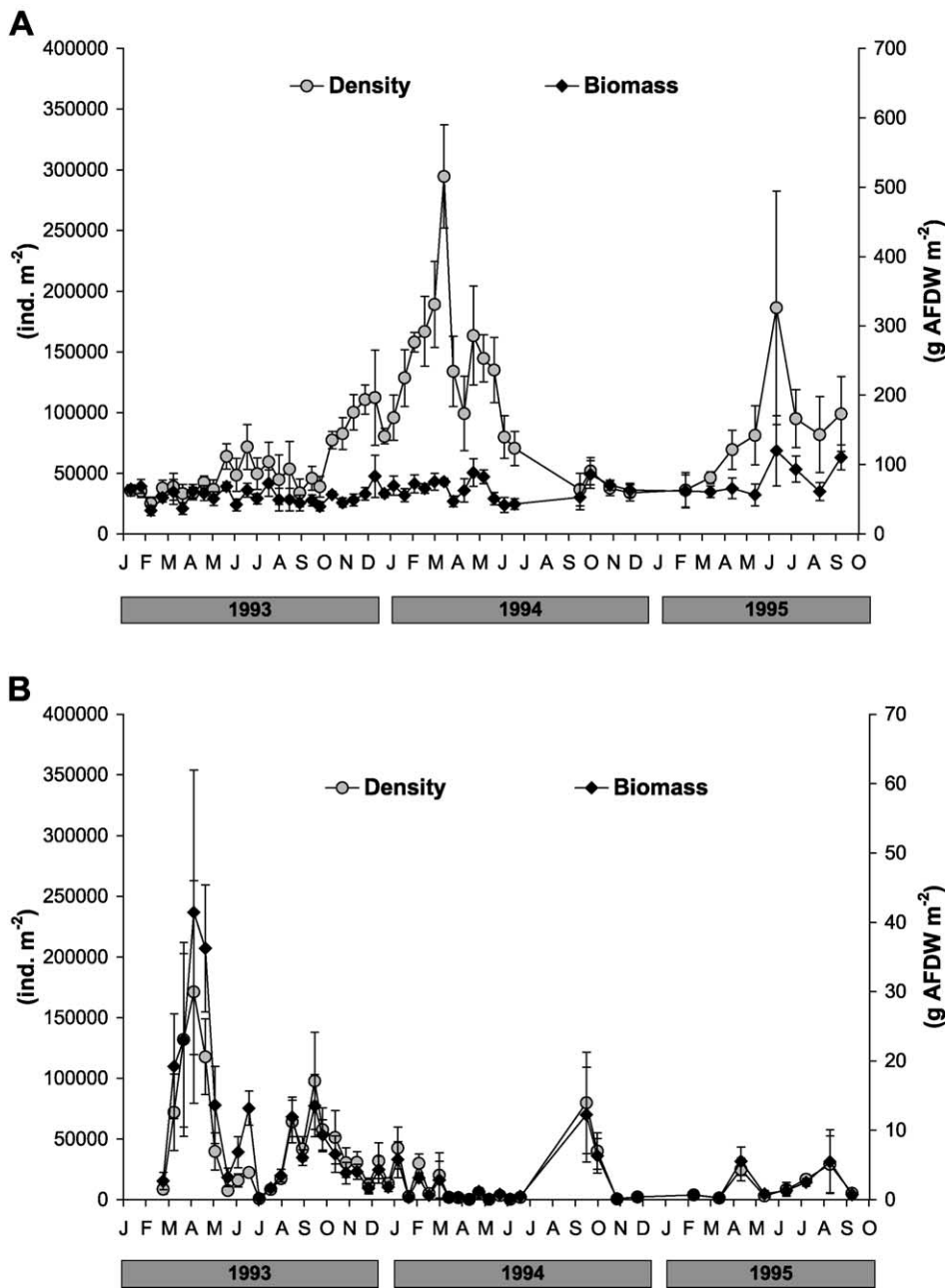


Fig. 3. Average *H. ulvae* density and biomass \pm standard error (SE), between January 1993 and September 1995. (A) *Z. noltii* meadows; (B) eutrophicated area.

In the eutrophicated area, the scenario was completely different, since green macroalgae (*Ulva* sp. and *Enteromorpha* sp., especially the latter) were the dominant primary producers (Fig. 2B). During the first 6 months, there was a typical spring algal bloom that completely covered the sediment, in which *Enteromorpha* sp. biomass reached maximum values of 419 g AFDW m⁻². This was followed by an algal crash, in early summer. On the contrary, in 1994, minimal biomasses of green macroalgae were recorded. This was due to a very rainy year and frequent freshwater discharges from the Pranto River, that gave rise to low salinity (e.g. 10 g l⁻¹), high turbidity of the water column and increased current velocities. Such conditions did not allow macroalgal fixation and inhibited their growth (Martins et al., 2001). In the spring and summer of 1995, considerable biomasses of *Enteromorpha* sp. (109 g AFDW m⁻², April 95) developed in the system but not in the same proportion as in the previous algal bloom.

3.2. Population density

H. ulvae density changed throughout the study period, following different patterns at the two sampling areas (Fig. 3). In the spring of 1993, when an algal bloom occurred, density was consistently higher at the eutrophicated area reaching a maximum value of 171 264 ± 91 670 ind. m⁻² (± SE) (7 of April 1993), while in the *Z. noltii* beds, the mean density was 33 480 ± 5147 ind. m⁻². On the contrary, in the spring of 1994 (when there were no macroalgae in the eutrophicated area), the highest densities were registered in the *Z. noltii* beds, reaching the maximum value of 294 667 ± 42 657 ind. m⁻² (23 of March 1994). During fall we observed a decrease of *H. ulvae* density in this area, which was followed by an increment at the eutrophicated area. This period corresponded to the appearance of macroalgae in the eutrophicated zone (Fig. 2B). In 1995, we could observe an intermediate situation relatively to the previous years. Some peaks of macroalgae were observed during spring/summer leading again to the dispersion of juveniles to the eutrophicated area, although at a smaller scale than in 1993 (e.g. 188 000 ± 96 377 ind. m⁻² (± SE) at the *Z. noltii* meadows compared to 12 321 ± 7076 ind. m⁻² at the eutrophicated area, 29 of June 1995).

The patterns of variation of density (*t*-test, *t*₉₅ = 4.05; *P* < 0.05) and biomass (*t*-test, *t*₉₅ = 15.03; *P* < 0.05) at the two sampling stations show significant differences (Fig. 3). At the eutrophicated area (Fig. 3B), the biomass pattern always follows the density pattern, while in the *Z. noltii* meadows (Fig. 3A), this does not always occur. At the macrophyte

Table 1

Temporal and spatial variation of the percentage of new benthic recruitments (referent to cohorts C5, C6, C9, C10, C13 and C14)

Cohorts	<i>Z. noltii</i> meadows (%)	Eutrophicated area (%)
C5 (March 1993)	1.0	99.0
C9 (March 1994)	98.9	1.1
C13 (March 1995)	49.6	50.4
C6 (June 1993)	65.5	34.5
C10 (June 1994)	97.0	3.0
C14 (June 1995)	35.0	65.0

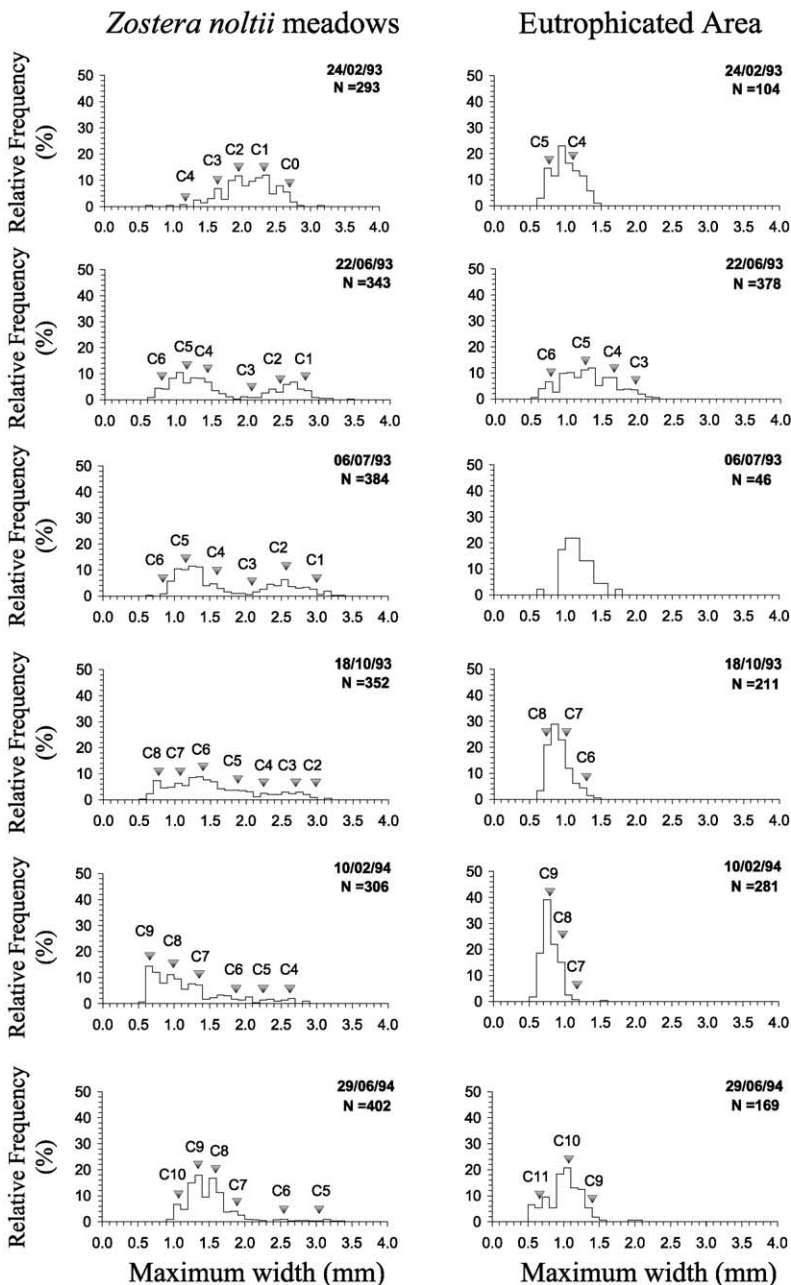


Fig. 4. *H. ulvae*. Size–frequency polymodal distribution at *Z. noltii* meadows and at the eutrophicated area. The cohorts (C) and the number of individuals (N) are represented in the figure.

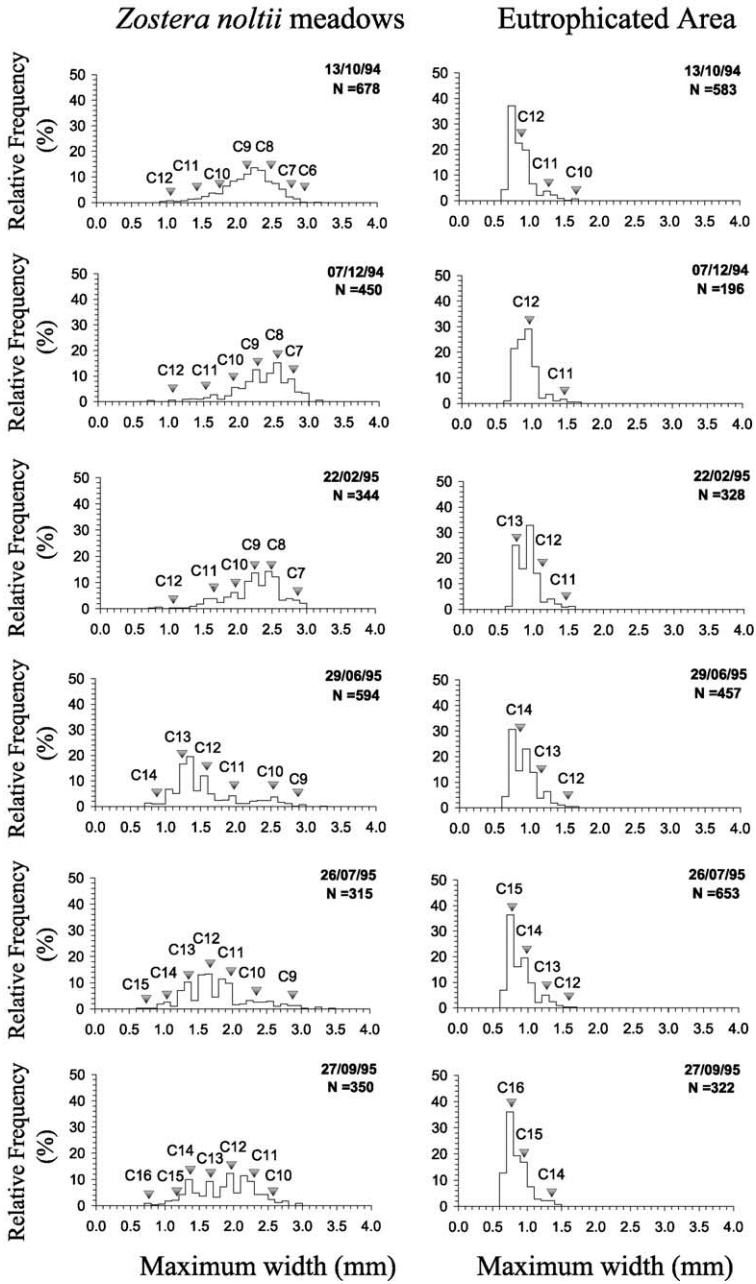


Fig. 4 (continued).

beds, *H. ulvae* biomass remained relatively constant through the study period, despite strong density oscillations. It is important to point out that at the eutrophicated area, *H. ulvae* biomass was much lower (one order of magnitude) than those registered in the *Z. noltii* beds. The only exception occurred during the algal bloom (spring of 1993), when similar biomasses were observed in both areas.

H. ulvae seems to respond rapidly to macroalgal biomass fluctuations and its presence at the eutrophicated area is controlled by the occurrence of seaweeds.

Based on the previous results, we hypothesized that, in the presence of macroalgae, recruitments would occur preferentially at the eutrophicated area. The opposite trend should

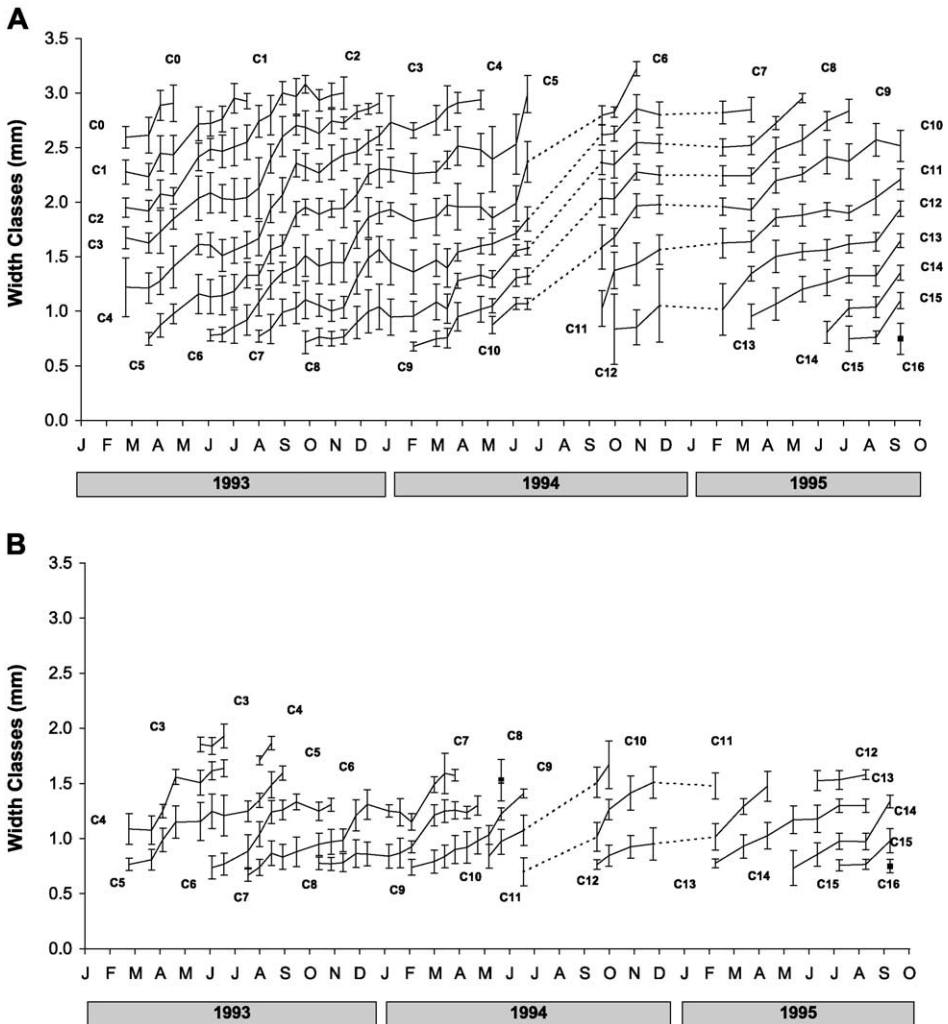


Fig. 5. Estimated growth of *H. ulvae* cohorts (average growth \pm standard deviation), between February 1993 and September 1995. (A) *Z. noltii* meadows; (B) eutrophicated area.

be expected when no macroalgae takes place. This hypothesis was indeed supported by our data (Table 1). For example, with respect to the new cohort recruited in March 93 (when an algal bloom occurred) we could see that most of individuals (99%) recruited at the eutrophicated area. On the other hand, in March 1994 (absence of macroalgae) almost all individuals (98.9%) recruited in the *Z. noltii* meadows. The same was observed for the cohort recruited in June 1994. An intermediate situation was observed in June 1995 when relevant biomasses of macroalgae occurred, individuals recruited preferentially (65%) at the eutrophicated area.

Stepwise multiple regression analysis was applied to *H. ulvae* density and biomass data of both sampling areas in order to examine the differences observed.

At the eutrophicated area, *H. ulvae* biomass ($H. ulvae$; $\ln + 1$) was positively correlated with green macroalgae biomass (*Ulva* sp. and *Enteromorpha* sp.; $\ln + 1$) ($P=0.002$); $R^2=20\%$).

$$\ln (H. ulvae \text{ biomass} + 1) = 1.56 + 0.194 \ln (\text{green macroalgae} + 1)$$

Nevertheless, at the *Z. noltii* meadows, no significant correlation was found between any of the environmental factors monitored and density or biomass of *H. ulvae*.

3.3. Population structure, growth and life span

Size–frequency distributions were analysed for recognisable cohorts (Fig. 4) showing significant differences in the population structure at the two areas. At the *Z. noltii* meadows, *H. ulvae* exhibited a stable and well-structured population. On the contrary, at the eutrophicated area, the population exhibited a great instability, which made it impossible to follow any cohort from birth to extinction. In general, we did not observe individuals larger than 1.7 mm (MW) (Fig. 5B).

Despite the relevant differences regarding the population structure in the two areas, *H. ulvae* presents the same settlement pattern, with four recruitments per year, respectively in March, June, July and September (Fig. 5). The long duration of the present study enabled us to identify and track the complete development of 4 distinct cohorts (C6, C7, C8 and C9) up to their extinction at the *Z. noltii* meadows. Field growth data from these cohorts were used to calibrate a model proposed by Gaschütz et al. (1980). The model parameters were estimated as shown in Table 2.

Table 2

Application of a growth mathematical model to data of cohorts C6, C7, C8 and C9, detected respectively in June of 1993, August of 1993, October of 1993 and February of 1994, in the *Z. noltii* meadows

Cohort	With seasonal adjustment						
	L_∞	T_0	K	D	C	T_s	r^2
C6	4.83525	−0.35423	0.48355	1	1.00927	0.17044	0.95480
C7	4.2831	−0.14230	0.64840	1	1.19080	−0.00095	0.96090
C8	4.4298	−0.10041	0.61585	1	0.89105	−0.21523	0.98971
C9	4.2532	−0.34285	0.59810	1	0.84185	0.42730	0.99344

The model parameters were estimated with seasonal adjustment.

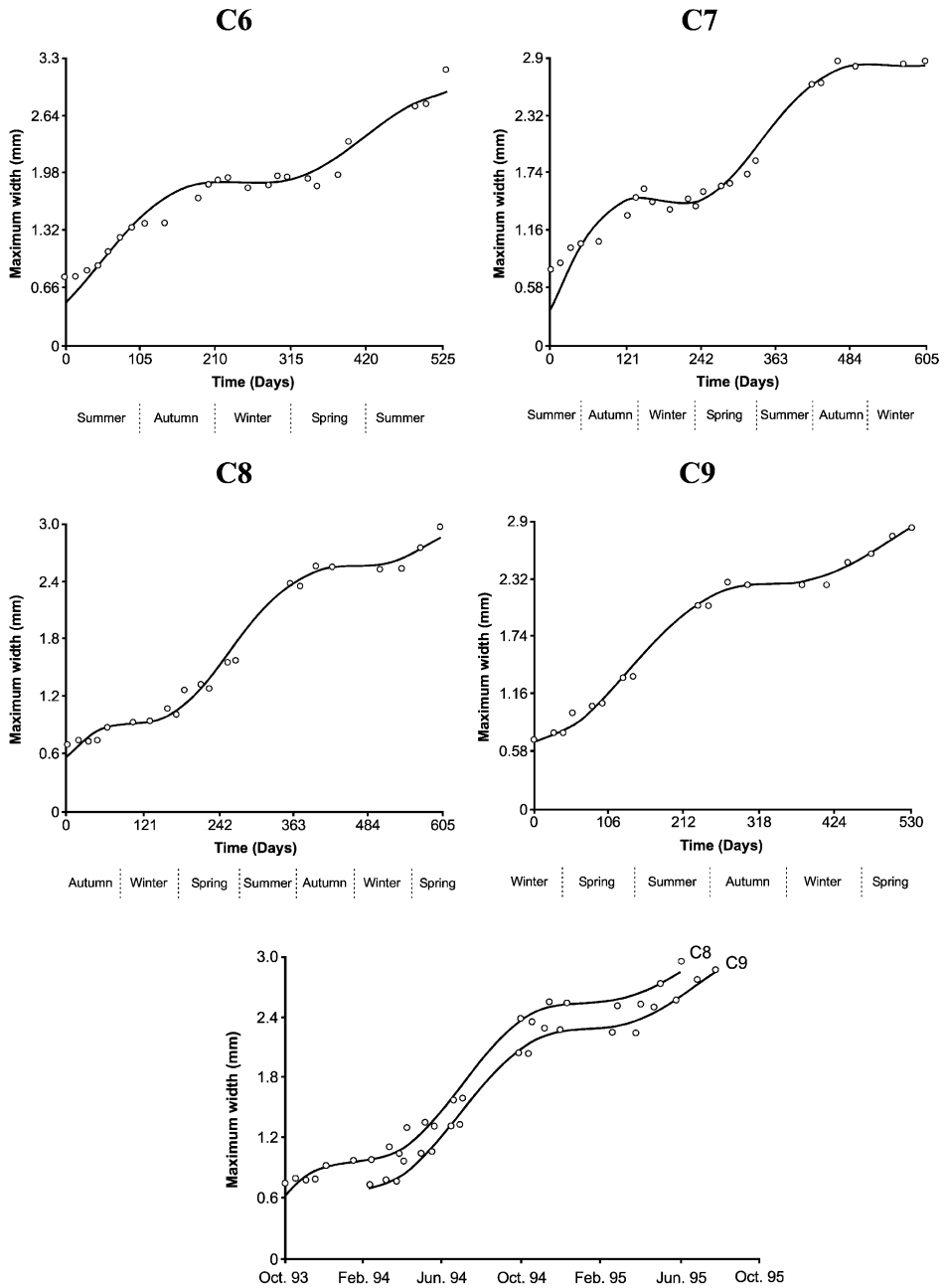


Fig. 6. *H. ulvae* growth models for the cohorts C6, C7, C8 and C9 at the *Z. noltii* meadows.

Based on the models developed for the four different cohorts, it is clear that *H. ulvae* has a continuous growth throughout life (Fig. 6). However, growth rates are higher during spring and summer, decreasing during winter.

The influence of seasonal factors on the cohorts growth rhythms seemed to be variable according to the time of the year in which recruitment takes place. For instance, cohort C9, detected in February of 1994, has an emphasized and protracted growth in the initial phase, reaching 1.3 mm (MW) after 4 months (Fig. 6). During winter, we observed a strong decrease in growth rates, which was followed by a marked increment in the next spring. On the contrary, cohort C8 detected in October of 1993 exhibited a slow growth during the first 6 months. Four months after the benthic recruitment, it reached only 0.9 mm (MW) approximately. However, in the next spring, cohort C8 recovered and after 12 months reached a width similar to the one attained by cohort C9 (2.3 mm) (Fig. 6).

The life span of the species was estimated as 16 to 20 months, depending on the time of recruitment, meaning that cohorts recruited in spring (March) have a life span of 16 months, those recruited in June and July have a life span of 17 to 19 months, and finally, autumn cohorts (September) have the longer life spans reaching approximately 20 months.

3.4. Breeding cycle

We attempted to study the breeding cycle in terms of presence/absence of egg capsules through time. In the Mondego estuary, two annual breeding periods were identified: the first and most important one occurred from February to June, peaking in March, April and the second took place in September–October (Fig. 7).

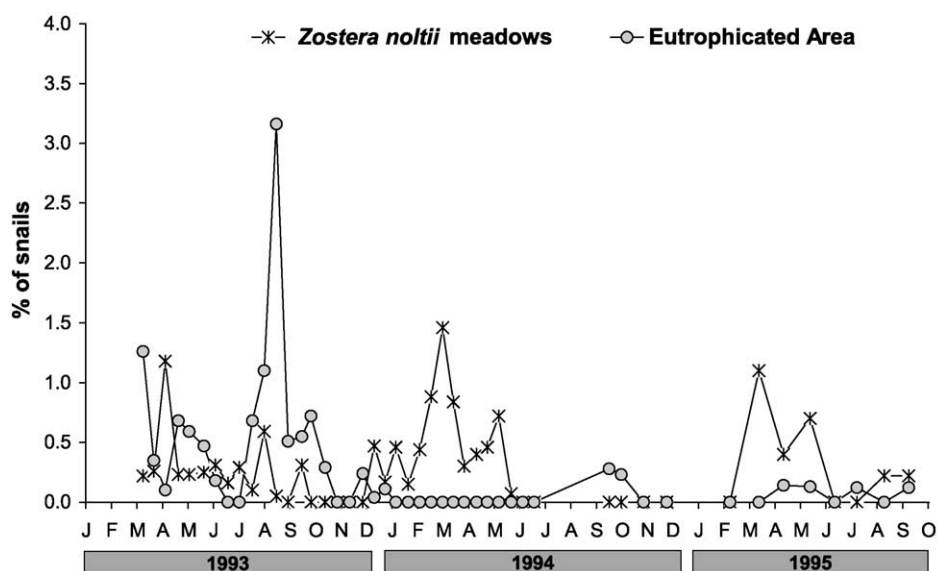


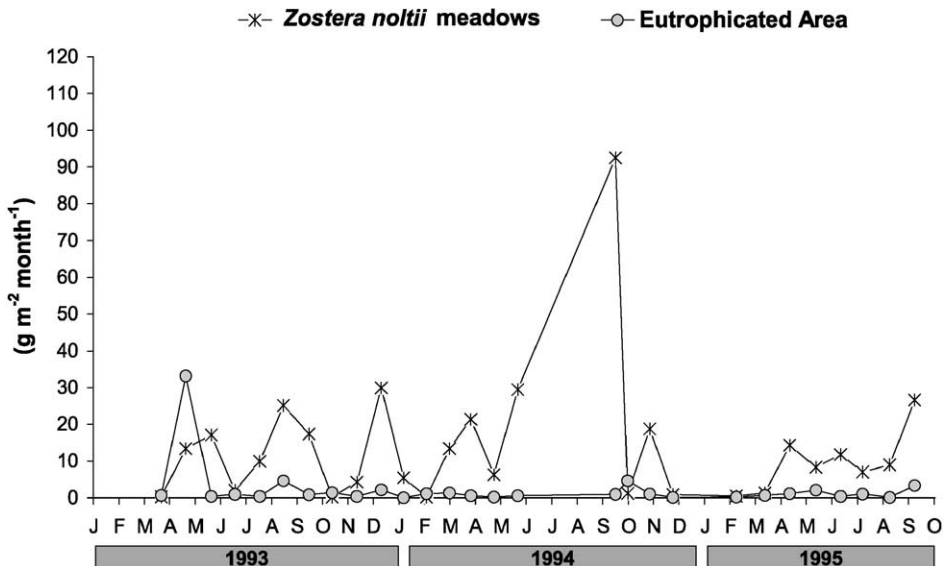
Fig. 7. Percentage of *H. ulvae* bearing egg masses at the two sampling stations, between January 1993 and September 1995.

Table 3

Comparison of growth production estimations for different European populations of *H. ulvae*

Location	Mesh size (mm)	\bar{B} (g AFDW m^{-2})	P (g AFDW $m^{-2} year^{-1}$)	P/\bar{B}	References
Grevelinger estuary, Netherlands	1	4.06–9.37	7.23–12.79	1.24–1.78	Wolff and De Wolf (1977)
Königshafen, Wadden Sea	0.5	12.83–25.21	14.00–40.81	1.09–1.62	Asmus (1984)
Gironde estuary, France	0.5	1.64–1.96	6.46–10.89	3.9–5.5	Bachelet and Yacine-Kassab (1987)
Bidasoa estuary, Spain	1	1.79–3.07	3.6–10.4	1.9–5.8	Sola (1996)
Mondego estuary, Portugal					
<i>Z. noltii</i> meadows					
1993	0.5	59.24	125.08	2.11	Present study
1994	0.5	74.14	202.54	2.70	Present study
Eutrophicated area					
1993	0.5	9.37	45.73	4.87	Present study
1994	0.5	2.38	10.87	4.56	Present study

It was possible to observe considerable differences in the percentage of snails bearing egg masses at the two sampling stations. For instance, in 1993 this percentage was clearly higher at the eutrophicated area. On the contrary, in 1994 and in 1995 the highest percentage of individuals carrying egg capsules was observed in the *Z. noltii* meadows.

Fig. 8. Monthly variation on *H. ulvae* growth production estimates.

Whenever significant quantities of macroalgae were registered at the eutrophicated area, we could observe an increment in the percentage of individuals bearing egg masses in this area, due to the dispersion of young specimens from *Z. noltii* meadows.

In the Mondego estuary, the percentage of snails bearing egg masses was very low (maximum of 3.2%—taking into account both areas). The mean number of egg capsules per snail ranged from 1 to 2. The number of eggs per capsule ranged from 3 to 24.

3.5. Production

The annual production estimations of *H. ulvae* at the two sampling stations showed that growth productivity (P) and mean population biomass (\bar{B}) were much higher at the *Z. noltii* meadows (Table 3). On the contrary, P/\bar{B} ratios were higher at the eutrophicated area. In this area, growth production reached the highest value in 1993, whilst in the *Z. noltii* meadows was superior in 1994. On the other hand, taking into account monthly production, we could observe that for a short period of time, during the algal bloom, production was higher at the eutrophicated area (Fig. 8).

4. Discussion

4.1. Population density

Population density exhibited considerable differences at the two sampling areas, as a result of different plant (macroalgae and macrophytes) dynamics and the dominant physical conditions at each area, since these constitute extreme places from different points of view (e.g. type of plant coverage, food resources, protection against predators) (Pardal et al., 2000; Martins et al., 2001).

The oscillations of density at the two areas may be conditioned by multiple factors, like for example the high reproductive potential of the species, more or less success in recruitment, mortality and dispersal capability inside the estuary. According to Thistle (1981 in Norkko and Bonsdorff, 1996a) and Norkko et al. (2000), hydrobiid snails are highly mobile, continuously moving to fresh patches of food. This constitutes the most probable explanation for the opposite density pattern exhibited by *H. ulvae* at the two sampling areas. For example, in the spring of 1993, during the macroalgal bloom, the mean population density was much higher at the eutrophicated area due to the combined effects of stronger benthic recruitments (99%) in this area and dispersion of juveniles proceeding from the *Z. noltii* meadows. A similar pattern was also recorded for the bivalve *Macoma balthica*, whose recruitment of juveniles may have been enhanced by the presence of weed filaments (Hull, 1987; Raffaelli et al., 1999). The hypothesis of dispersion of *H. ulvae* is in agreement with the observations from several authors (Smidt, 1951; Anderson, 1971; Armonies, 1992; Armonies and Hartke, 1995).

Our results confirm the idea that the presence of *H. ulvae* at the eutrophicated area depends on the occurrence of green macroalgae, demonstrating the opportunistic behaviour of the species from the alimentary point of view. In fact, *H. ulvae* individuals

(mainly juveniles) move to the eutrophicated area only when fresh abundant patches of food occur there (e.g. 1993). On the contrary, when conditions are not favourable, most of the population remains in the *Z. noltii* meadows (e.g. 1994).

Similar responses to these were observed in the Ythan estuary. Hull (1987) also reported positive effects of macroalgal mats on *H. ulvae*, from a small-scale experimental plots (10 weeks), but not after 22 weeks, since the weed had been largely removed or buried by wave action at that time.

4.2. Population structure

Our study confirmed that *H. ulvae* presents four annual recruitments in the Mondego estuary, which is in agreement with the findings from Lillebø et al. (1999). However, these results do not agree with other authors, like for example, Walters and Wharfe (1980), Bachelet and Yacine-Kassab (1987), Curras and Mora (1990) and Sola (1996). Differences observed may be related to environmental conditions, namely latitudinal position and to different sampling methods (e.g. mesh size).

At the *Z. noltii* meadows, the population appeared to be stable and well structured, including individuals of all age classes, while at the eutrophicated area, during most of the time, only juveniles (<1 mm width) and young individuals (1–1.5 mm width) were found. Rarely, we detected some adults (>1.5 mm width), in general associated to the presence of macroalgal mats. The most probable explanation for the absence of adults at the eutrophicated area is predation by waders and/or fishes. During most of the time, this area is characterized by bare sediments. Therefore, *Hydrobia* individuals become very exposed, being an easy target for waders. Several studies support this hypothesis (e.g. Múrias et al., 1996; Cabral et al., 1999; Lopes et al., 2000), claiming that *H. ulvae* constitutes a preferential prey for several waders. According to Cabral et al. (1999), *H. ulvae* was the main prey for *Charadrius alexandrinus* (59.04%), being also an important prey for *Charadrius hiaticula* (26.32%), *Pluvialis squatarola* (24.55%) and *Calidris alpina* (31.97%), in the Mondego estuary. Other studies (Evans et al., 1979; Worrall, 1984; Dekinga and Piersma, 1993) confirm the hypothesis of predation, revealing that most of the *H. ulvae* taken were between 2 and 4 mm shell height (corresponding to 1–2 mm MW). This provides one explanation for why, at the eutrophicated area, during the periods without algae, we could not observe individuals larger than 1.5 mm maximum width (corresponding to 3 mm shell height). Moreover, some fish are known to feed upon *H. ulvae*, for example, *Trisopterus luscus*, *Pomatoschistus minutus*, *Platichthys flesus* (Summers, 1980; Aarnio and Mattila, 2000), all abundant species in the Mondego estuary.

4.3. Growth

In the Mondego estuary, the highest growth rates of *H. ulvae* were observed during spring/summer, decreasing in autumn and practically ceasing in winter. This agrees with a previous study carried out in the Mondego estuary (Lillebø et al., 1999) and with studies in other European estuaries. For example, in the Bidasoa estuary (Spain), the maximal growth rates were observed between May and July, being still elevated during August and

September (Sola, 1996). Planas and Mora (1987) observed in the Ria de Pontevedra (Spain) the same growing seasons as in the Bidasoa estuary. In the Medway estuary (UK), Walters and Wharfe (1980) observed rapid growth rates until autumn. According to Bachelet and Yacine-Kassab (1987), the maximal growth rate in the Gironde estuary (France) was observed in July and the minimal growth, almost zero, from August to the following May.

In the Mondego estuary, by tracking of cohorts we recorded maximum widths of 2.0–2.2 mm (corresponding to 4.0–4.5 mm shell height), 12 months after benthic recruitment. In the Wadden Sea, Smidt (1951) and in the Gironde estuary, Bachelet and Yacine-Kassab (1987) registered shell lengths of 2 mm during the first winter and 4 mm during the second winter. Fish and Fish (1974), in Wales, obtained similar results to those of the Gironde estuary, registering shell lengths of 1.5–2.5 mm for *H. ulvae* populations groups with 1 year. In Spain, Planas and Mora (1987), recorded mean lengths of 3.0–3.5 mm for 1-year-old snails. Sola (1996) registered higher growth rates, since before the end of the year, cohorts recruited in February–March reached a length of 4.0–4.7 mm while cohorts recruited in July reached a length of about 2.5 mm in the same period.

Results from the Mondego estuary are closer to those obtained by Sola (1996), which is understandable if we consider the nearby locations of the Bidasoa and Mondego.

4.4. Life span

Lillebø et al. (1999) estimated the life span of *H. ulvae* to be 21 ± 3 months. Nevertheless, that study was carried out within a period of 13 months, which did not allow following cohorts from their benthic recruitment until their disappearance. In the present study, we could assess in a more accurate way the life span of this species (16 to 20 months).

These results are not in complete agreement with those obtained by other authors. For example, Fish and Fish (1974) in the Dovey estuary suggested that *H. ulvae* could live for about 24–30 months. According to Walters and Wharfe (1980), in the Medway estuary, few snails survived beyond 12–18 months. In the Gironde estuary, the life span of *H. ulvae* was estimated at 8–19 months (Bachelet and Yacine-Kassab, 1987). More to the south at the Ria de Pontevedra (NW Spain), Planas and Mora (1987) concluded that *H. ulvae* could live for about 12–30 months, while at the Bidasoa estuary (Spain), Sola (1996) estimated that snails could live for about 12–15 months.

We can accept that such differences regarding *H. ulvae* life span might be related to the latitude of each study area, with southern latitudes corresponding to higher water temperatures, higher growth rates and consequently shorter life spans, when compared to northern areas. However, different estimations may also be related to different sampling techniques (e.g. mesh size used), which are definitely selective relatively to the size or age of individuals and eventually to the duration of the studies.

In our opinion, monitoring programmes shorter than 24 months (usually just an annual cycle) could give rise to less accurate estimations of the life span because they imply the use of composed cohorts. This is particularly clear when distinct cohorts have different life spans as shown in this study.

4.5. Breeding

The pattern observed may be explained by the process of dispersion of *H. ulvae* individuals inside the estuary (corresponding to a rapid response to macroalgal dynamics). It is generally accepted that *H. ulvae* shows a preference for laying egg masses on live shells of its own species (Fish and Fish, 1974). However, in the Mondego estuary, the percentage of snails bearing egg capsules was very low (maximum of 3.2%), when compared to the ones observed at the Bidasoa (80%) (Sola, 1996), Gironde (40%) (Bachelet and Yacine-Kassab, 1987) and Dovey (40%) (Fish and Fish, 1974) estuaries. The reduced percentage of individuals bearing egg capsules recorded in the Mondego estuary may be explained based on personal observations that this species lays egg masses preferentially on other substrates like: bivalves shells, algae or even *Z. noltii* leaves.

Despite the low percentage of snails bearing egg masses, we could identify two distinct breeding periods in the Mondego estuary. This agrees with results regarding more southern populations (Fish and Fish, 1974; Bachelet and Yacine-Kassab, 1987; Planas and Mora, 1987; Barnes, 1990, 1994; Sola, 1996; Lillebø et al., 1999).

As has been pointed out by Bachelet and Yacine-Kassab (1987), there is a relationship between the breeding periods and the geographical position. According to these authors, more northern populations from the Baltic to the Wadden Sea are characterized by a short spawning period in spring (May–July), while more southern populations present two distinct breeding periods each year, in spring and late summer, probably as a response to more favourable temperature conditions.

4.6. Production

With regard to the annual production of *H. ulvae*, P (growth production) and \bar{B} (standing stock) showed higher values at the *Z. noltii* meadows. However, if we consider data on monthly production, looking carefully to the dynamics of the two areas, we may recognize that for a short period, during the macroalgal bloom, the production was higher at the eutrophicated area. This implies that during this period, the eutrophicated area played a very important role providing *H. ulvae* food resources and shelter. On the other hand, P/\bar{B} ratios (Table 3) were always clearly higher at the eutrophicated area, which was characterized by the dominance of young individuals in the population. These have higher growth rates and contributed therefore to the higher P/\bar{B} ratios observed, corresponding to a larger energy flow relatively to the standing stock.

Our P/\bar{B} estimations were quite similar to those obtained for other European systems (Table 3). For example, in the Bidasoa estuary, the P/\bar{B} ratios were in the range of 1.9–5.8 (mesh size = 1 mm) (Sola, 1996), while in the Gironde estuary, Bachelet and Yacine-Kassab (1987) calculated P/\bar{B} ratios in the range of 3.9–5.5 (mesh size = 500 μm). However, most of P/\bar{B} ratios calculated for more northern populations (Wadden Sea, Netherlands) are within a narrow range of variation: 1.1–1.8 (Wolff and De Wolf, 1977).

Growth production (P) estimations in the Mondego estuary (range = 125.08–202.54 g AFDW $\text{m}^{-2} \text{year}^{-1}$ in the *Z. noltii* meadows; 10.87–45.73 g AFDW $\text{m}^{-2} \text{year}^{-1}$ in the eutrophicated area) were much higher than those calculated by Bachelet and Yacine-

Kassab (1987) in the Gironde estuary (6.46–10.89 g AFDW m⁻² year⁻¹), Sola (1996) in the Bidasoa estuary (3.6–10.4 g AFDW m⁻² year⁻¹) and Wolff and De Wolf (1977) in the Grevelinger estuary (7.23–12.79 g AFDW m⁻² year⁻¹) (Table 3).

5. Conclusions

In conclusion, this work shows that: (a) different *Hydrobia*'s cohorts have dissimilar growth rhythms and life spans, which was not described yet in previous studies; (b) the benthic recruitment of veliger larvae is spatially dependent on the presence of macroalgal blooms and also confirms the pelagic drift (Armonies, 1992; Armonies and Hartke, 1995) inside the estuary; (c) in the short term, *H. ulvae* seems to benefit from the occurrence of macroalgae, however, in the long run, eutrophication will have a strong negative impact on the population structure and annual production. In fact, at the eutrophicated area, *H. ulvae* shows an unstable population structure, registering productions much inferior to those observed at the *Z. noltii* meadows. On the other hand, the success of *H. ulvae* seems to depend from the *Z. noltii* meadows, since reproductive adults were almost exclusively found in this area. Therefore, this species depends on this habitat to maintain a stable and well-structured population.

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