MIGUEL ÂNGELO PARDAL
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Scientific Editors

Aquatic Ecology of the Mondego River Basin
Global Importance of Local Experience

Coimbra • Imprensa da Universidade

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THE EFFECT OF PRIMARY PRODUCERS DYNAMICS (MACROPHYTES AND MACROALGAE) ON *Hydrobia ulvae* POPULATION DYNAMICS

Abstract

Eutrophication in the Mondego estuary gave rise to qualitative changes in the benthic community, involving the replacement of eelgrass, *Zostera noltii*, by green algae, like *Enteromorpha* sp. and *Ulva* sp.. *Hydrobia ulvae*, is a dominant species concerning abundance and biomass. The objective was to compare to what extent differences in primary producers dynamics might affect *H. ulvae* life cycle, production and population dynamics. During the study period *H. ulvae* population exhibited both temporal and spatial density variations. The settlement was equal in the presence of both primary producers, and took place in March, June, July and September. However, the population was denser in the *Zostera noltii* meadows, when compared to the eutrophied area, were macroalgae where present. Life span was estimated as 21 months ± 3 months. Growth productivity (P) was estimated as 93.7 g. AFDW m^{-2} year^{-1} in the *Z. noltii* meadows, and 30.3 g. AFDW m^{-2} year^{-1} in the eutrophied area. Elimination productivity (E) was estimated as 300 g. AFDW m^{-2} year^{-1} in the *Z. noltii* meadows, and 97.5 g. AFDW m^{-2} year^{-1} in the eutrophied area. The average annual biomass ($\overline{B}$) (standing stock) of the population was estimated as 70.2 g. AFDW m^{-2} in the *Z. noltii* meadows, and 7.4 g. AFDW m^{-2} in the eutrophied area. P/$\overline{B}$ and E/$\overline{B}$ ratios were estimated as 1.3 and 4.8 in the *Z. noltii* meadows, and 4.5 and 13.2 in the eutrophied area, respectively. There is evidence that *H. ulvae* population structure and annual production are affected by primary producers dynamics, particularly by macroalgae blooms dynamics.

Introduction

As in most estuaries all over the world, eutrophication largely increased in the Mondego estuarine system since the eighties, probably as a result of excessive nutrient release into coastal waters (Pardal 1998). These processes are most related to the increase availability of growth limiting nutrients, namely nitrogen and phosphorus (e.g.

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Flindt et al. 1997, Pardal 1998, Martins 2000). The most visible feature of eutrophication in the Mondego estuary is the occurrence of seasonal green macroalgae blooms (*Enteromorpha* sp.) followed by the drastically reduction of *Zostera noltii* (Hornem) community (Marques et al. 1997, Pardal 1998, Martins 2000). This process has been giving rise to qualitative changes in the benthic community, and might be followed by changes in the species composition and trophic structure at other levels (e.g. macrofauna composition), (Marques et al. 1997, Pardal 1998). Through time, such changes may determine a selected new trophic structure (Marques et al. submitted).

The eutrophication process in the south arm of the Mondego estuary has been reported for several years (e.g. Marques et al. 1993a, b, 1997, Múrias et al. 1996, 1997, Flindt et al. 1997, Pardal 1998, Pardal et al. 2000, Martins et al. 1997, 1999, 2001, Martins 2000, Cabral et al. 1999, Lillebø et al. 1999, Lopes et al. 2000). A number of studies were carried out on the benthic communities (e.g. Pardal 1998, Lillebø et al. 1999), in which *Hydrobia ulvae* (Pennant 1777) was identified as a dominant species in the *Zostera noltii* meadows, exhibiting a stable population and significant biomass all over the year. Moreover, this species was found in the inner areas of the estuary, were the green macroalgae blooms usually occur (Pardal 1998, Lillebø 1996, Lillebø et al. 1999, Lopes et al. 2000, Shories et al. 2000), showing a clear dependence on the occurrence of macroalgae (Lillebø 1996, Lillebø et al. 1999). Moreover, a study concerning *H. ulvae* production along an eutrophication gradient in the south arm of the estuary (Lillebø et al. 1999) showed that *H. ulvae* standing stock decreased as a function of increasing eutrophication, while $P/\overline{B}$ and $E/\overline{B}$ ratios increased following the same gradient. Results also suggested that *H. ulvae* might be suffering a change in its adaptive strategy, becoming closer to a typical r strategist in the eutrophied areas (Lillebø et al. 1999).

The purpose of the present work was to evidence the effect of primary producers (macrophytes and macroalgae) dynamics on *H. ulvae* life cycle and production. Taking into account data from Lillebø et al. (1999), we compare *H. ulvae* population dynamics in a *Zostera noltii* meadows and in a eutrophied area, were usually macroalgae blooms of *Enteromorpha* sp. occur, in the south arm of the Mondego estuary.

Material and methods

Study Site

The Mondego estuary is a warm-temperate coastal system on the western coast of Portugal (Fig. 1). It consists of two arms, north and south, with very different hydrologic characteristics. The northern arm is deeper, while the southern arm is largely silted up, especially in upstream areas, which causes most of the fresh-water discharge to flow through the northern arm. Consequently, the water circulation in the southern arm is mainly dependent on tidal activity and on the usually small fresh-water input of a tributary, the Pranto River, which is controlled by a sluice (Pardal 1998).

Although, a large part of the southern arm intertidal area still remains more or less unchanged, exhibiting sand muddy bottoms covered by *Spartina maritima* and

Scirpus maritimus marshes and *Zostera noltii* meadows, macroalgae blooms of *Enteromorpha* sp. have been regularly observed during the last two decades (e.g. Marques et al. 1997, Pardal 1998, Lillebø 2000, Martins 2000). This is probably a result of excessive nutrient release into the estuary, coupled with longer persistence of nutrients (nitrogen and phosphorous) in the water column (Flindt et al. 1997, Marques et al. 1997, Pardal 1998). Such macroalgae blooms may not occur in exceptionally rainy years due to the occurrence of low salinity values for long periods, as a result of the Pranto river discharge (Pardal 1998). As a general trend, *Enteromorpha* biomass increases from early spring (February/March) up to July, when algae crash usually occurs. After summer a second smaller biomass peak may normally be observed in September followed by a decrease in winter (Pardal 1998, Martins et al. 2001).

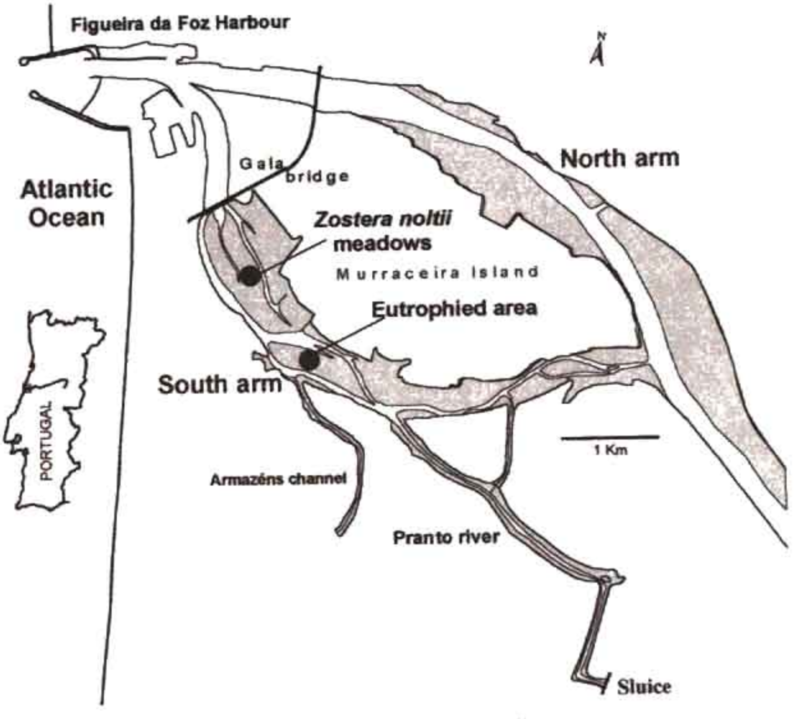


Fig. 1. The Mondego estuary with indication of the two study sites, *Zostera noltii* meadows and eutrophied area, were *Enteromorpha* sp. spring blooms usually occur, in the south arm.

Field Program

The benthic communities were sampled fortnightly from March 1993 to March 1994, at two study sites: *Zostera noltii* community and a eutrophied area, from where macrophytes disappeared while *Enteromorpha* blooms may occur (Lillebø et al. 1999). At each station 10 random samples were taken using a manual core, each replicate corresponding to 141 cm² and approximately 3 l of sediment. Samples were preserved in 4% buffered formalin, and later sieved through a 0.5 mm mesh size sieve. Animals were separated and kept in 70% ethanol. At each station and sampling date, salinity, temperature, and dissolved oxygen were measured in situ in low water pools. Sediment samples were also collected and subsequently analysed for organic matter content and granulometry. The organic matter was determined by loss on ignitions (8h at 450 °C), for each sampling date, and the granulometry was analysed seasonally and classified according to the nomenclature proposed by Brown and McLachlan (1990).

Laboratory Procedures

Hydrobia ulvae individuals were counted and their shell height measured to the nearest 0.1 mm. As a number of individuals had the shell damaged we determined other measures, such as the maximum width and maximum length unto the last spire, which were then converted to shell height. These conversions were based on the biometrics relationships of 339 individuals with intact shells (Figs. 2A and 2B), (Lillebø et al. 1999). The relationship between total length and ash free dry weight was also established to be use in production estimates. There were not any significant differences between equations established for each season based on analysis of variance (P = 0.05). Therefore, the data set of 191 individuals measured and weighted throughout the study was used to provide a single regression equation (Fig. 2C), (Lillebø et al. 1999). Individuals were dried at 60 °C for 72 h and weight to the nearest 0.01 mg. Ash-free dry weight was assessed after combustion of the samples for 8 h at 450 °C.

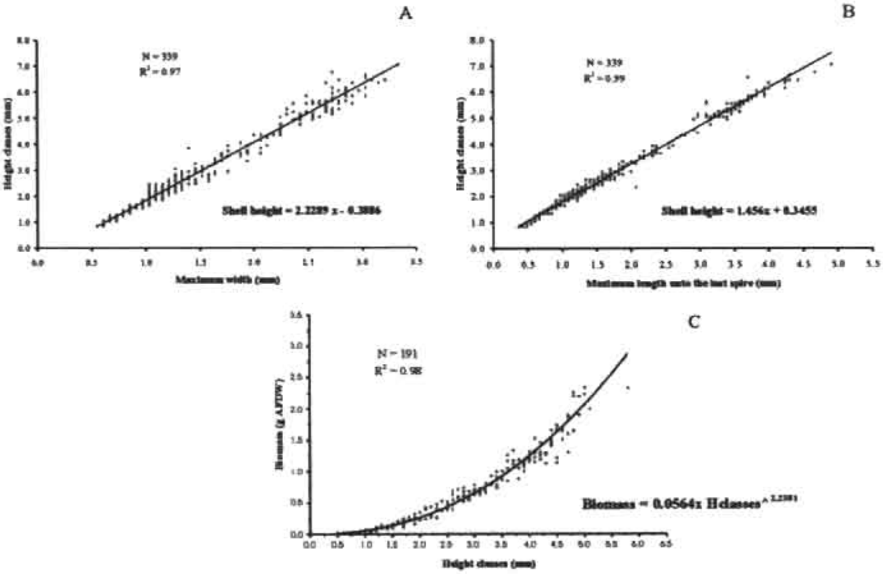


Fig. 2. *Hydrobia ulvae* biometric relationships.

Data analysis

Multiple regression models were developed to relate the variation of *Hydrobia ulvae* biomass with salinity, temperature, dissolved oxygen, organic matter content in sediments, and macroalgae and macrophytes biomass (Lillebø et al. 1999). The fitted regression models were expressed as: $Y' = a + b_1X_1 + b_2X_2 + ... + b_kX_k$.

Y' - are the values of a given dependent variable (e.g. biomass) predicted by the equation;

$X_1, X_2...X_k$ - are independent variables (e.g. salinity).

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 (F), and the t test for the regression coefficients, as described in Edwards (1984, 1985). Regressions were estimated using the Stepwise Forward Analysis method performed with the STATGRAPHICS 4.0 statistical package.

Growth rates were estimated by tracking recognisable cohorts along size-frequency distributions (0.02 mm classes) from successive sample dates. Size-frequency analysis was performed using the ANAMOD software package (Nogueira 1992), in which the analysis reliability was tested using the χ^2 and G tests (P= 0.05).

We estimated both growth (P) and elimination (E) production as derived by Allen (1971). Values of P and E for each cohort for a given time interval are expressed as:

$$P = [(N_t + N_{t+1})/2]\ (\overline{W}_{t+1} - \overline{W}_t) \qquad \text{for} \qquad \overline{W}_{t+1} > \overline{W}_t$$

$$E = [(\overline{W}_t + \overline{W}_{t+1})/2]\ (N_t - N_{t+1}) \qquad \text{for} \qquad N_t > N_{t+1}$$

N = number of individuals from cohort at each sample date; = mean individual biomass for each sample date; t and t+1 = consecutive sample dates.

Total values of P and E for each cohort are expressed as:

$$P = \sum_{t=0}^{t=n} [(N_t + N_{t+1})/2]\ \Delta\overline{W}$$

$$E = \sum_{t=0}^{t=n} [(\overline{W}_t + \overline{W}_{t+1})/2]\ \Delta N$$

Total values of P and E, for the population, are expressed as:

$$P = \sum_{n=1}^{N} P_{cn} \qquad \text{and} \qquad E = \sum_{n=1}^{N} E_{cn}$$

P_{cn} and E_{cn} are the growth and elimination production of the cohort n. $P/\overline{B}$ and $E/\overline{B}$ ratios were determined. $\overline{B}$ (mean population biomass) is expressed as:

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

T = period of study; N = number of cohorts in the period T; $\overline{B}_n$ = mean biomass of the cohort n; and t = duration of the cohort n.

Results

Macrophytes and macroalge biomass

Z. noltii biomass exhibited a seasonal variation in biomass. During fall and winter total biomass consisted essentially of rhizomes, and during spring and summer total biomass increased due to the growth of shoots (Fig. 3).

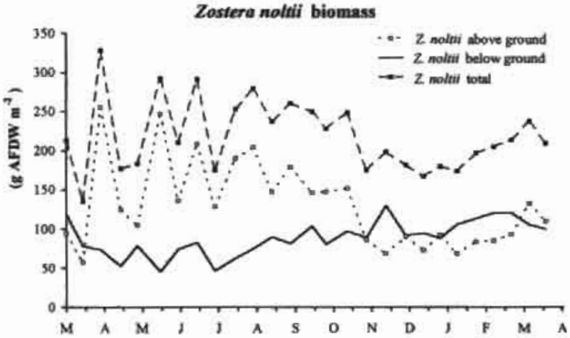


Fig. 3. *Zostera noltii* biomass in the south arm of the Mondego estuary between March 93 and March 94.

The composition of macroalge biomass was distinctive in each study site. Red macroalgae, essentially *Gracilaria* sp., were relatively abundant at the *Z. noltii* meadows (Fig. 4). In the eutrophied area, green macroalgae presented a typical spring bloom, with *Enteromorpha* sp. biomass reaching 413.19 g AFDW m^{-2} (April 7th 1993), followed by an algae crash in early summer (July 6th 1993) (Fig. 4). However, no algae bloom was observed in spring 1994 due to the fact that this was a particularly rainy year.

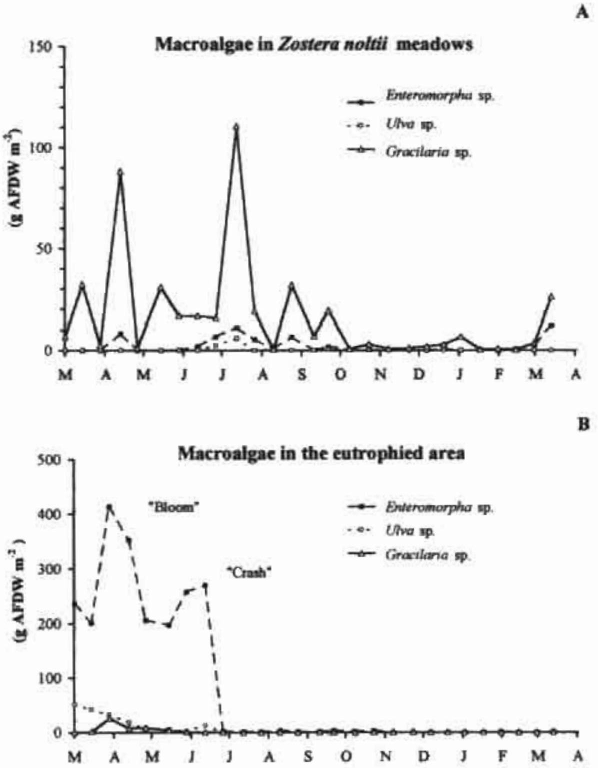


Fig. 4. Macroalgae biomass in the south arm of the Mondego estuary between March 93 and March 94. A – *Zostera noltii* meadows; B – eutrophied area.

Abundance

Population density changed throughout the period of study but the pattern of variation was distinctive for each type of dominant primary producer (macrophytes/macroalgae), (Fig. 5). Density was consistently higher at the *Zostera noltii* meadows, increasing gradually from November 1993 up to a maximum during spring in 1994 (approximately 288 000 ind. m^{-2}, March 23rd 1994). The population density in the eutrophied area reached a maximum of approximately 167 000 ind. m^{-2} (April 7th 1993), during the algae bloom, and a minimum of 699 ind. m^{-2} (July 6th 1993), after the algae crash (Fig. 5).

Environmental factors

Silt and clay were the main constituents of sediments at the *Z. noltii* meadows, while in area covered with algae, sediments mainly consisted of fine sand (table 1).The multiple regression analysis was performed taken into account *H. ulvae* biomass, primary producers biomasses, salinity, temperature and dissolved oxygen (Lillebø et al. 1999).

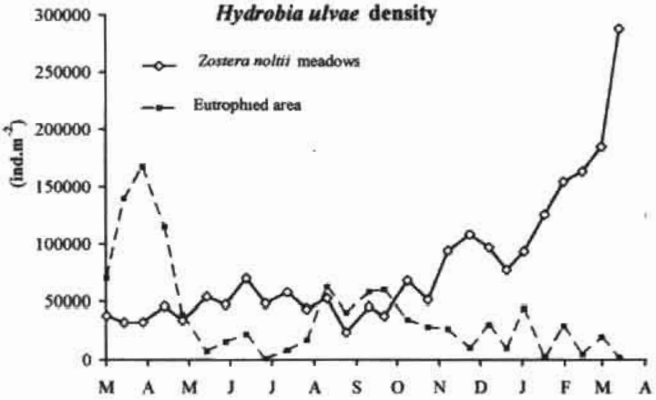


Fig. 5. Abundance of *Hydrobia ulvae* at *Zostera noltii* meadows and eutrophied area, in the south arm of the Mondego estuary between March 93 and March 94.

Table 1. Relative frequency of sediment granulometry classes determined seasonally in *Zostera noltii* meadows and in the eutrophied area, were *Enteromorpha* sp. spring blooms usually occurs, in the south arm of the Mondego estuary.

	Zostera noltii meadows			*Eutrophied* area		
Classes (mm)	June	April	Dec.	April	June	Dec.
> 2	0.29	0.94	3.86	0.42	0.11	0.03
> 1< 2	1.10	1.03	1.44	0.62	0.57	0.33
> 0,500 < 1,0	1.36	4.28	2.27	2.06	1.72	1.34
> 0,250 < 0,500	14.79	1.11	16.23	7.71	10.78	15.08
> 0,125 < 0,250	17.21	22.35	19.99	36.86	33.13	40.02
> 0,063 < 0,125	19.48	63.10	19.30	49.43	28.12	26.19
> 0.038 < 0,063	31.34	4.54	27.85	1.80	20.45	9.87
< 0,038	14.43	2.65	9.06	1.10	5.12	7.14

In the *Zostera noltii* meadows, *H. ulvae* biomass (g AFDW) was positively correlated with green algae (*Enteromorpha* sp.+ *Ulva* sp.), biomass (log+1) and negatively correlated with salinity and *Z. noltii* below ground biomass; ($P=0.000$; $r^2=0.70$).

H. ulvae biomass = 105 + 15.0 (ln+1 green algae) – 1.38 (Sal.) – 0.282 (Z. below ground)

Regarding the eutrophied area, we analysed separately the algae bloom and post-algae crash scenarios (Fig. 6). During the algae bloom *H. ulvae* biomass appeared positively correlated with green algae biomass, with organic matter content in sediments, and with dissolved oxygen, ($P=0.007$; $r^2=0.94$):

H. ulvae biomass = -74.2 + 0.0333 (green algae) + 0.150 (o.m.) + 1.89 (oxyg)

After the algae crash *H. ulvae* biomass appeared positively correlated with green algae biomass (*Enteromorpha* sp.+ *Ulva* sp.; ln+1) and dissolved oxygen ($P=0.001$; $r^2=0.63$):

H. ulvae biomass = - 53.6 + 27.0 (ln+1 green algae) + 4.71 8 (oxyg.)

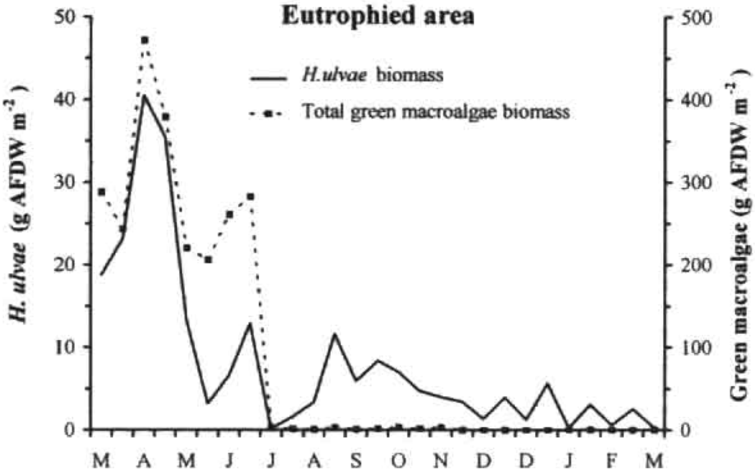
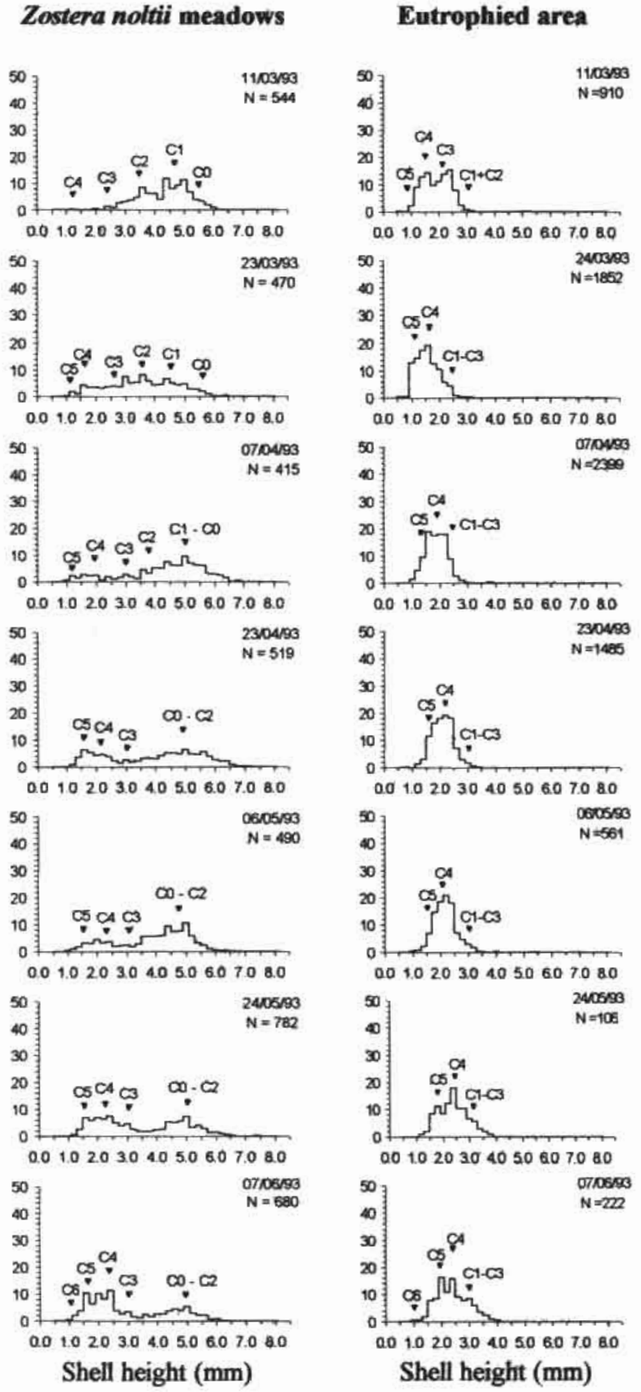


Fig. 6. Green macroalgae biomass and *Hydrobia ulvae* abundance variations in the eutrophied area, in the south arm of the Mondego estuary between March 93 and March 94.

Growth and Life Span

Size-frequency polymodal distributions were analysed for *H. ulvae* recognisable cohorts (Fig. 7). Significant differences in the population structure were observed for each type of dominant primary producer, respectively *Z. noltii* and *Enteromorpha* sp.. Individuals reached larger dimensions at the *Z. noltii* meadows when compared to the eutrophied area. Nevertheless, the same settlement pattern was observed, respectively in March, June, July and September (X^2 and G not significant, $P \leq 0.05$). New cohorts were detected with an average shell height of 1.11 mm at the *Z. noltii* meadows, and 1.10 mm at the eutrophied area.



Zostera noltii meadows
Eutrophied area
11/03/93 N = 544
C4 C3 C2 C1 C0
11/03/93 N =910
C5 C4 C3 C1+C2
23/03/93 N = 470
C5 C4 C3 C2 C1 C0
24/03/93 N =1852
C5 C4 C1-C3
07/04/93 N = 415
C5 C4 C3 C2 C1 - C0
07/04/93 N =2399
C5 C4 C1-C3
23/04/93 N = 519
C5 C4 C3 C0 - C2
23/04/93 N =1485
C5 C4 C1-C3
06/05/93 N = 490
C5 C4 C3 C0 - C2
06/05/93 N =561
C5 C4 C1-C3
24/05/93 N = 782
C5 C4 C3 C0 - C2
24/05/93 N =106
C5 C4 C1-C3
07/06/93 N = 680
C6 C5 C4 C3 C0 - C2
07/06/93 N =222
C6 C5 C4 C1-C3
0 10 20 30 40 50
0.0 1.0 2.0 3.0 4.0 5.0 6.0 7.0 8.0
Shell height (mm)
Shell height (mm)

Fig. 7a

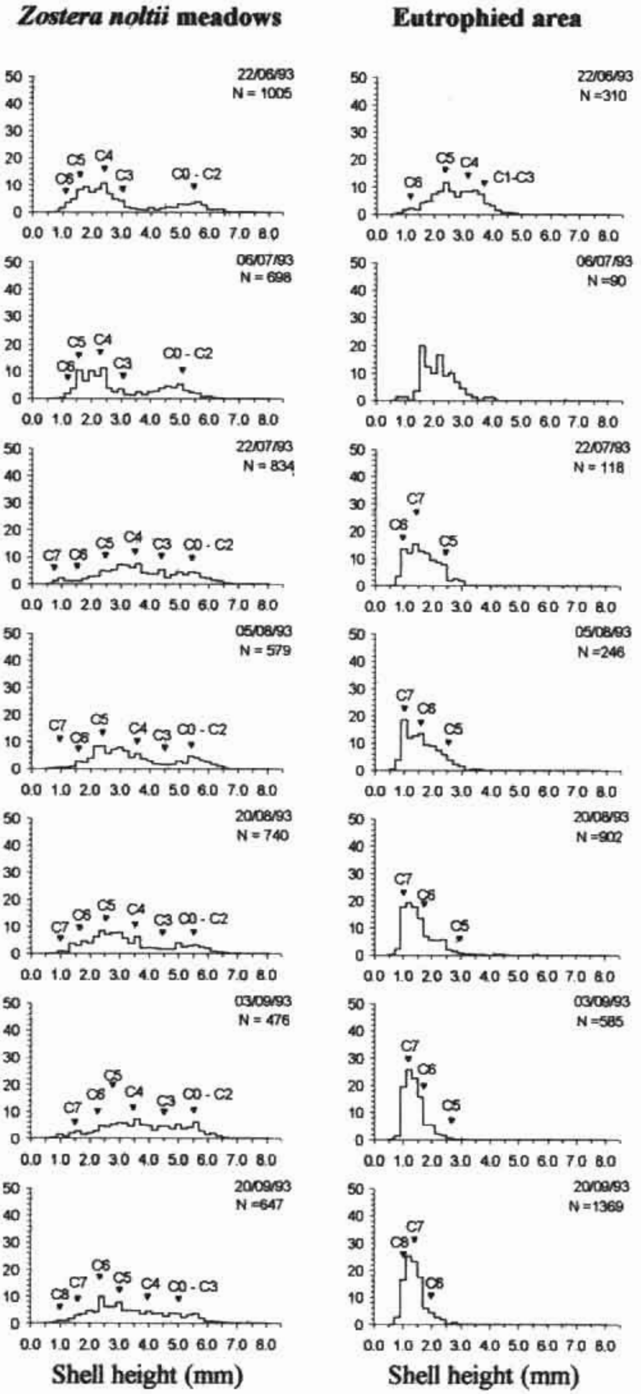

Zostera noltii meadows
Eutrophied area
22/06/93
N = 1005
C6 C5 C4 C3 C0 - C2
22/06/93
N =310
C6 C5 C4 C1-C3
06/07/93
N = 698
C6 C5 C4 C3 C0 - C2
06/07/93
N =90
22/07/93
N = 834
C7 C6 C5 C4 C3 C0 - C2
22/07/93
N = 118
C6 C7 C5
05/08/93
N = 579
C7 C6 C5 C4 C3 C0 - C2
05/08/93
N =246
C7 C6 C5
20/08/93
N = 740
C7 C6 C5 C4 C3 C0 - C2
20/08/93
N =902
C7 C6 C5
03/09/93
N = 476
C7 C6 C5 C4 C3 C0 - C2
03/09/93
N =585
C7 C6 C5
20/09/93
N =647
C8 C7 C6 C5 C4 C0 - C3
20/09/93
N =1369
C8 C7 C6
0 10 20 30 40 50
0.0 1.0 2.0 3.0 4.0 5.0 6.0 7.0 8.0
Shell height (mm)
Shell height (mm)

Fig. 7b

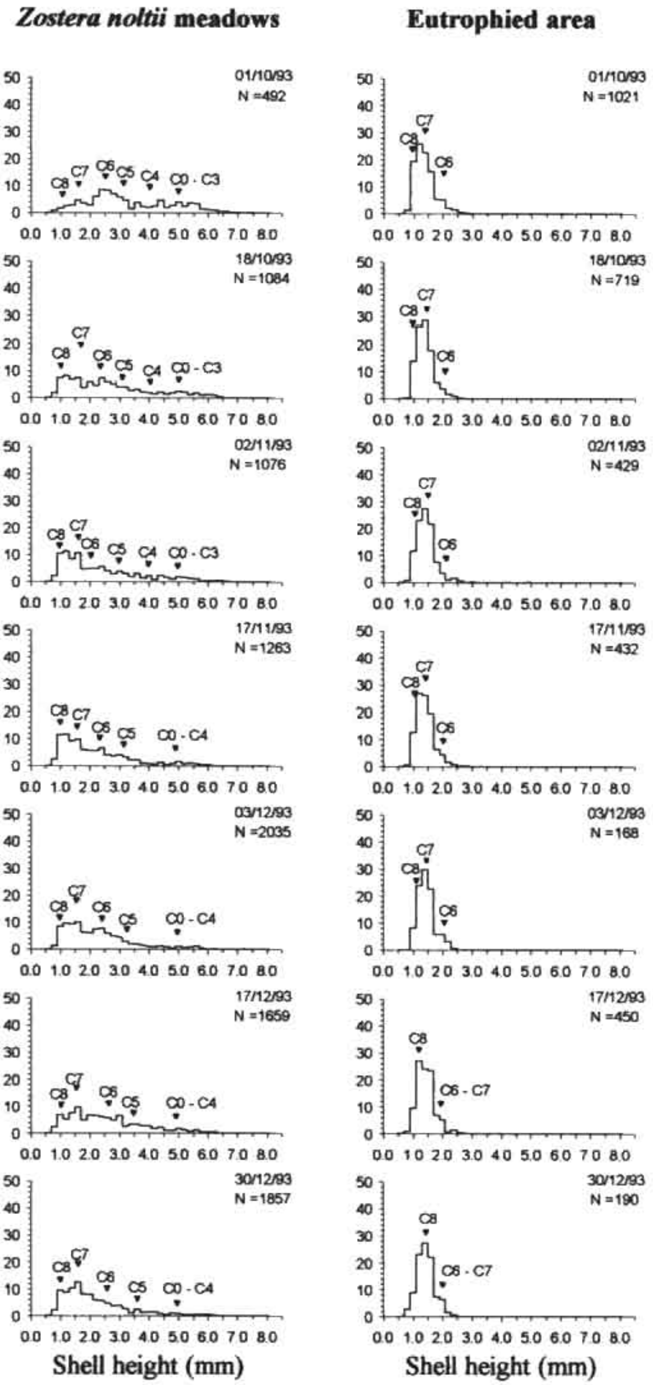

Zostera noltii meadows
Eutrophied area
01/10/93
N =492
C8 C7 C6 C5 C4 C0 - C3
01/10/93
N =1021
C8 C7 C6
18/10/93
N =1084
C8 C7 C6 C5 C4 C0 - C3
18/10/93
N =719
C8 C7 C6
02/11/93
N =1076
C8 C7 C6 C5 C4 C0 - C3
02/11/93
N =429
C8 C7 C6
17/11/93
N =1263
C8 C7 C6 C5 C0 - C4
17/11/93
N =432
C8 C7 C6
03/12/93
N =2035
C8 C7 C6 C5 C0 - C4
03/12/93
N =168
C8 C7 C6
17/12/93
N =1659
C8 C7 C6 C5 C0 - C4
17/12/93
N =450
C8 C6 - C7
30/12/93
N =1857
C8 C7 C6 C5 C0 - C4
30/12/93
N =190
C8 C6 - C7
0 10 20 30 40 50
0.0 1.0 2.0 3.0 4.0 5.0 6.0 7.0 8.0
Shell height (mm)
Shell height (mm)

Fig. 7c

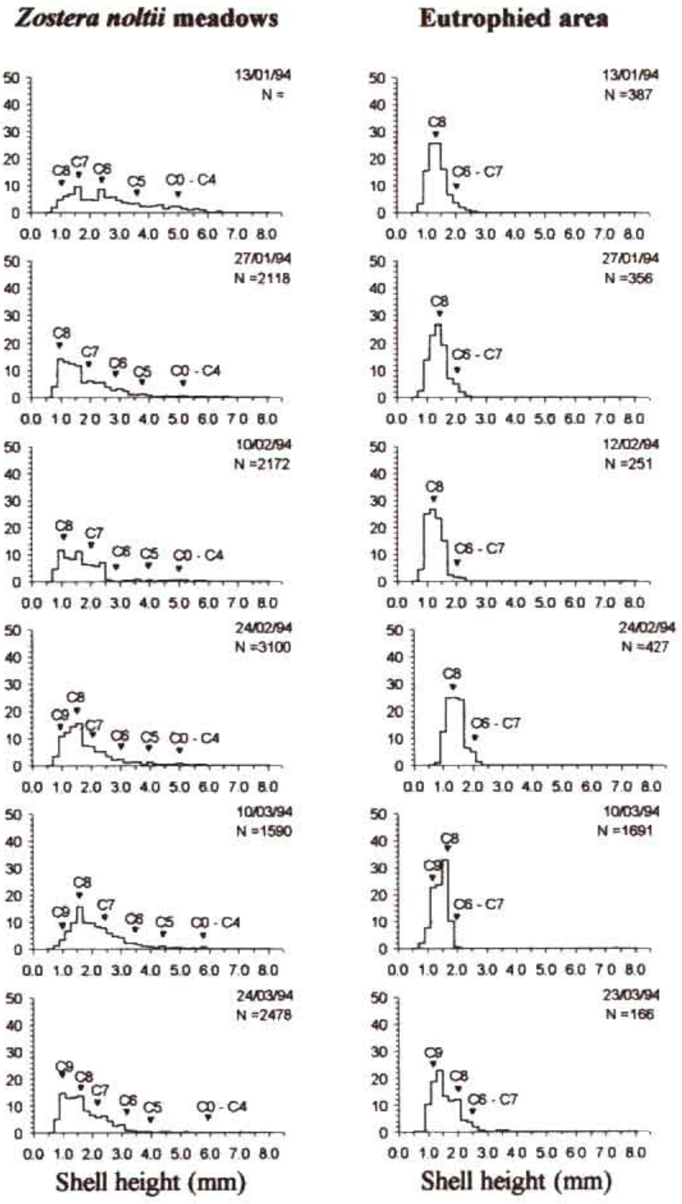


Fig. 7d. Size-frequency polymodal distribution of *Hydrobia ulvae* in the south arm of the Mondego estuary at *Zostera noltii* meadows and eutrophied area, between March 93 and March 94. Sampling dates are indicated. N = number of individuals analysed.

Growth was continuous through life (Fig. 8). Nevertheless, growth rates were highest in spring, decreased from early summer to mid fall, practically ceased in winter (Fig. 8), and gradually increased again until spring. Lower growth rates during winter were probably a result of lower temperatures. During the rest of the year, higher growth rates were probably a function of higher temperatures and also increased food resources.

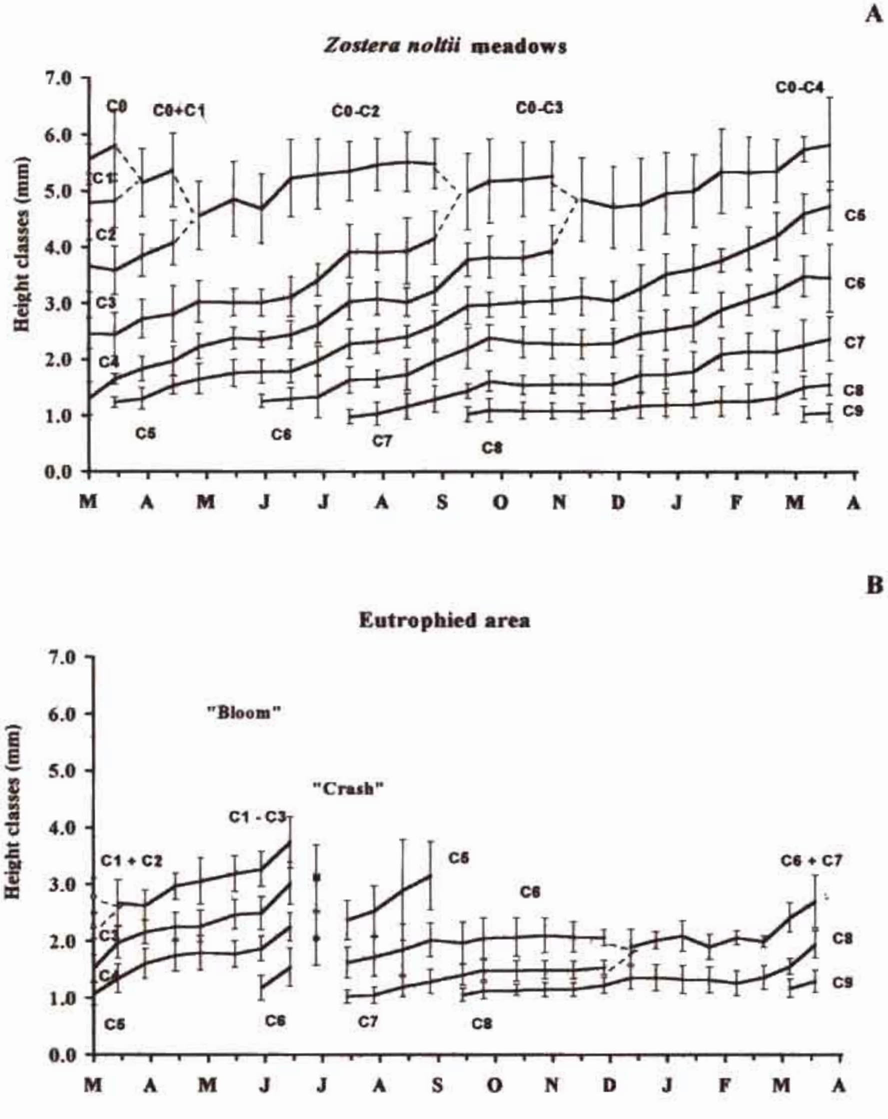


Fig. 8. Estimated growth (field growth data) of *Hydrobia ulvae* cohorts or groups of cohorts, average total length ± standard deviation during the study period. Broken lines indicate probable cohort merging. A - *Zostera noltii* meadows, B – eutrophied area.

Life span was estimated at 21 months ± 3 months. Individuals presented a mean shell height between 3.78 mm (std ± 0.30) and 4.75 mm (std ± 0.43) after the first year, and 5.84 mm (std ± 0.82) after 21 month.

Life Cycle

The reproductive period was studied taking into account the occurrence of egg masses, which are fixed on live shells of it congeners (Fish and Fish 1974). The percentages of the population carrying egg masses in the two study sites were low (Fig. 9). Therefore, data from three study sites, along an eutrophication gradient in the south arm (Lillebø et al. 1999), were also pooled together for the analysis (Fig. 9). Two main reproductive peaks are recognisable in the Mondego estuary population, in spring and in late summer.

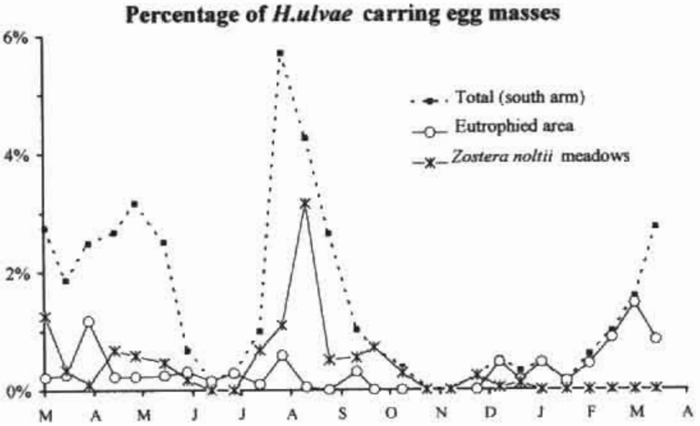


Fig. 9. Percentage of *Hydrobia ulvae* caring egg masses in the south arm of the Mondego estuary between March 93 and March 94.

Production Estimates

Relationships between height and ash free dry weight (g AFDW) (Figure 2C) were used to estimate production taking into account cohorts growth and mortality. Growth productivity (P) was estimated at 93.7 g. AFDW m^{-2} $year^{-1}$ in the *Z. noltii* meadows, and 30.3 g. AFDW m^{-2} $year^{-1}$ in the eutrophied area. Elimination productivity (E) was estimated at 300 g. AFDW m^{-2} $year^{-1}$ in the *Z. noltii* meadows, and 97.5 g. AFDW m^{-2} $year^{-1}$ in the eutrophied area. The average annual biomass ($\overline{B}$) (standing stock) of the population was estimated at 70.2 AFDW g. m^{-2} in the *Z. noltii* meadows, and 7.4 g. AFDW m^{-2} in the eutrophied area. $P/\overline{B}$ and $E/\overline{B}$ ratios were estimated respectively at 1.3 and 4.8 in the *Z. noltii* meadows, and 4.5 and 13.2 in the eutrophied area. Taking into account the two scenarios considered at the eutrophied area, we estimated $P/\overline{B} = 5.3$ and $E/\overline{B} = 14.4$ during the algae bloom, while after the algae crash $P/\overline{B} = 3.3$ and $E/\overline{B} = 11.4$.

Discussion and conclusions

The comparative study of *H. ulvae* population dynamics at *Zostera noltii* meadows, and at a eutrophied area during a typical *Enteromorpha* sp. spring bloom and a post-algae crash situation, provided an opportunity to assess the effect of different primary producers dynamics in the life cycle and production of this species. Moreover, production estimates contributed to evaluate the role of this species with regard to estuarine food web, and the effect of primary producers dynamics to the energy flow in the system.

Spatial distribution and abundance

At the Mondego estuary, densities were clearly higher than, for instance, those observed by Curras and Mora (1990) in "ria del Eo" (Spain), and Sola (1994, 1996) in Bidasoa estuary (Spain), which may be due to the fact that these authors used a 1.0 mm mesh size sieve. In fact, this mesh size is not effective in capturing individuals smaller than 1.5 mm (Bachelet and Yacine-Kassab 1987). Nevertheless, Planas and Mora (1987) observed a maxinum abundance of 100 028 ind. m^{-2} in "ria de Pontevedra", Spain.

Hydrobia ulvae densities were clearly different in the presence of each type of dominant primary producer, probably as a function of *Z. noltii* and *Enteromorpha* sp. dynamics. The *Z. noltii* meadows presented a stable and dense *H. ulvae* population thought the study period, which is consistent with results from other authors (Walters and Wharfe 1980), possibly as a result of the greater stability provided by macrophytes, in comparison to green macroalgae. Moreover, *Z. noltii* meadows are constituted by muddy sediments, with higher organic matter content, which may regulate distribution and abundance of *H. ulvae* (Barnes 1979).

At the *Z. noltii* meadows, *H. ulvae* density increased from early winter 1993 to a maximum in spring 1994. This is not in agreement with observations carried out by other authors, e.g. Curras and Mora (1990) in the "ria del Eo", Spain, where the maximum density occurred in spring and summer and the minimum during winter. Nevertheless, our data may be related to the fact that no algae bloom occurred at the eutrophied area in spring 1994. As a result, the usual alternative macroalgae habitat was not available and juvenile's byssus-drift dispersion (Armonies 1992) probably did not occur. This may as well explain the low population density observed in the eutrophied area in spring 1994. In fact, there were two distinctive scenarios in the strongly eutrophied area. During the algae bloom the population density was much higher (167 510 ind. m^{-2} in April 7th 1993) than in the *Z. noltii* meadows in the same period. This may be related to habitat heterogeneity and food resources (Soulsby et al. 1982, McLusky 1988, Everett 1994). During the algae crash, when anoxic conditions occurred in the sediment surface, the population suffered a sudden and drastic reduction, from 21 818 ind. m^{-2} (June 22nd) to 699 ind. m^{-2} (July 6th). After the algae crash, although the population was able to recover (62 863 ind. m^{-2} in August 20th), it could not come to the initial values again. Such recovery may have resulted from new settlements and/or the byssus-drift dispersion of *H. ulvae* juveniles (Armonies 1992, Armonies and Drake

1995). In the present study, *H. ulvae* showed a remarkable capacity to re-colonise the disturbed area. Furthermore, other authors have reported its dispersion capacity (Sola 1994, 1996) and tolerance to adverse conditions (Planas and Mora 1987, Sola 1994).

Environmental factors

H. ulvae biomass at the *Zostera noltii* meadows was positively correlated with green algae biomass and negatively correlated with *Z. nolti* below ground biomass and salinity. Although, *Enteromorpha* sp. and *Ulva* sp. biomass were very low this positive correlation can be explained by the fact that an organic enrichment may favour algae development (Hull 1987, Lavery et al. 1991, Hardy et al. 1993, Shories and Reise 1993, Everett 1994, Pardal 1998). In addition, grazing activity on periphyton and epiphyte may favour the macrophytes (Howard and Short 1986, Philippart 1995) and therefore food resources were always available for *H. ulvae* (Fenchel et al. 1975, Jensen and Siegismund 1980, Graham 1988, Morrisey 1988). The negative correlation with *Z. noltii* below ground biomass may be explained by the fact that leaves and root-rhizomes showed opposite peaks during the study period. Furthermore, Asmus and Asmus (1985) observations in the Wadden Sea showed that epiphytic diatoms density, which constitute a main food item for *H. ulvae* (Fenchel et al. 1975), always followed *Z. noltii* leaves biomass. The negative correlation with salinity cannot be explained as a cause-effect relationship, since *H. ulvae* tolerates a wide salinity range (10 to 35) (McLusky 1988). In fact, *H. ulvae* abundance and biomass increased from winter 93 to spring 94 and as this was a very rainy period salinity values decreased, being lower in spring 94.

At the eutrophied area and during the algae bloom, *H. ulvae* biomass was positively correlated with the green macroalgae biomass, with organic matter content in sediment and with oxygen concentration. While, after the algae crash it was positively correlated with *Enteromorpha* sp. and *Ulva* sp. biomass and oxygen concentration. A positive correlation with macroalgae biomass makes sense since algae covered habitats can provide food resources and shelter (Hull 1987, Walters and Wharfe 1980, Everett 1994). In fact, Drake and Arias (1995) showed that algae biomass was the most important factor for hydrobiid species temporal and spatial patterns in the Bay of Cadiz, Spain. The positive correlation between the sediment organic matter contents and *H. ulvae* biomass can be related to the fact that in this area organic matter could be a limiting factor (Hull 1987). A possible explanation for the results regarding the oxygen concentration in this area resides in the fact that, during the bloom, due to respiration, a huge green macroalgae biomass may have induced anoxic conditions during nocturnal periods, which strongly affected the *H. ulvae* population, causing its decline. As we always measured oxygen concentrations during the day such conditions could not be detected but it was clear that *H. ulvae* biomass followed the decrease of green macroalgae biomass. In fact, Everett (1994) found dissolved oxygen concentration in the algae-sediment water interface to be significantly lower than in overlying water column, and Hull (1987) observed that sediments under algae matts had significantly lower redox potentials, when compared to bare bottom sediment.

Also, in the Bay of Cadiz, Drake and Arias (1995) found that *H. ulvae* abundance was highest in the sites with the greatest water renewal.

Growth, life span, and productivity

The settlement pattern of *H. ulvae* in the Mondego estuary was alike at the two study sites, with settlements occurring in March, June, July and September. This is not entirely coincident with results obtained by Bachelet and Yacine-Kassab (1987), Curras and Mora (1990) and Sola (1994, 1996), but differences may arise from contrasting geographic environmental conditions. Another possible explanation could be related to sampling periodicity, to the fact that we used 500 mm mesh size sieve, while the other authors used 1000 mm, which may cause a certain bias, or even to the methodology applied in cohorts detection. Nevertheless, it is possible to establish some correspondence between the settlements attending to the mean shell height of the cohorts.

Two main reproductive peaks, but very small when compared two other authors (Fish and Fish 1974, Drake and Arias 1995), were recognisable in the Mondego estuary population. Although, this result may not be consistent with the settlement pattern of *H. ulvae*, only a very small proportion of egg capsules were observed on snail shells. In the Mondego estuary *H. ulvae* egg capsules were mainly observed on macroalgae and *Z. noltii* leaves, but they were not quantified. Nevertheless, contrasting with the scarcity of egg capsules, *H. ulvae* abundance and population structure shows a successful reproduction and recruitment of this species.

Through cohort recognition and tracking it was possible to assess growth and to estimate life span at 21 months ± 3 months. The estimate for the Mondego estuary population was similar to the estimate for the Medway estuary, U. K. (Walters and Wharfe 1980). But slightly higher than for the "ria de Pondevedra", Spain (Planas and Mora 1987) and for the "ria del Eo", Spain (Curas and Mora 1990), and lower than estimates for the Dovey estuary, U. K. (Fish and Fish 1974) and for the Girond estuary, France (Bachelet and Yacine-Kassab 1987).

The *H. ulvae* standing stock was lower at the eutrophied area, while $P/\overline{B}$ and $E/\overline{B}$ ratios were higher at the eutrophied area. This was obviously related with the size of individuals found in each sampling area, in relation with the dynamics of macroalgae mats. Probably as a result from higher exposure to predators (Múrias et al. 1996), *H. ulvae* individuals were considerable smaller than in the *Z. noltii* meadows.

The *H. ulvae* $P/\overline{B}$ estimates in the Mondego estuary were of the same order of magnitude as estimates for the same species in similar habitat, *Z. noltii* meadows (Sprung 1994). Nevertheless, in the eutrophied area these estimates were higher. In this area, and considering the two distinctive situations, $P/\overline{B}$ and $E/\overline{B}$ estimates reflect that macroalgae dynamics induce unstable environmental conditions, which can be expressed as: exposure to anoxic conditions during the algae crash and predators, and consequently, *H. ulvae* population structure is altered probably as reduction of life expectancy.

In the Mondego estuary *Hydrobia ulvae* production was very high when compared to Ria Formosa, Portugal (Sprung 1994) and also when compared with estimates of secondary production of whole intertidal benthic communities (Sprung 1994). Nevertheless, *H. ulvae* P/$\overline{B}$ in the *Z. noltii* meadow can be compared to Sprung (1994) estimate for the whole intertidal benthic communities, attending to the fact that *H. ulvae* represents more than 80% of the total benthic macrofauna biomass in the Mondego estuary (Pardal 1998).

The present results show the generalised notion that macrophytes beds form highly productive systems, which have an important role in estuarine productivity. Moreover, evidence is shown that *H. ulvae* population structure and annual production were affected by the induced instability of macroalgae bloom dynamics.

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