Spatio–temporal differentiation in the population structure of *Hydrobia ulvae* on an intertidal mudflat (Marennes-Oléron Bay, France)

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Spatio–temporal changes in density, breeding cycle, growth and population structure of *Hydrobia ulvae* (Gastropoda: Prosobranchia) were studied by monthly sampling of a wide bare mudflat in Marennes-Oléron Bay. Four stations, located along a cross-shore transect and characterized by different geomorphological structures, were investigated from March 2000 to February 2001. *Hydrobia ulvae* was mainly distributed in the upper half part of the mudflat and no individuals were found in the lower part. The breeding cycle extended from March to December and showed two annual peaks, in spring and in autumn. Three cohorts were recruited during the year and showed high growth rates during summer; the parameters of the von Bertalanffy model describing the growth curves were equal to $k_{max}=0.47 \pm 0.5$ mm month^{-1} and $L_{\infty}=5.4 \pm 0.2$ mm. The snail population had similar size–frequency structure along the transect at the beginning of the survey but summer recruitment initiated spatial differentiation. Reproduction occurred in the middle part of the mudflat but recruits mainly settled down at the upper level of the mudflat; new cohorts appeared with increasing individual densities. The middle part of the mudflat was rather dominated by adult individuals which showed large density fluctuations.

INTRODUCTION

Hydrobia ulvae (Pennant) is one of the most common deposit-feeders in European intertidal mudflats (Newell, 1979). This snail feeds on different sources of organic matter at the mud surfaces (Newell, 1965; Jensen & Siegismund, 1980) and microphytobenthos, which is the main source of primary production in intertidal mudflats (Admiraal, 1984; Colijn & de Jonge, 1984; Blanchard & Guarini, 1998), have been reported to be its major source of nutrition (Fenchel et al., 1975; Lopez & Kofoed, 1980; Morrissey, 1988). In addition, *H. ulvae* may provide an important food source for secondary consumers like birds (Evans, 1987) and fish (Aarnio & Mattila, 2000). It is thus considered as an important link in the intertidal food web. In Marennes-Oléron Bay, where mudflats extend over ~60% of the whole bay area, *H. ulvae* can reach several thousands of individuals m^{-2} (Sauriau et al., 1989) and is supposed to have a strong impact on microphytobenthic biomass (Cariou-Le Gall & Blanchard, 1995). Nevertheless, the functional role of the species cannot be quantified because its population dynamics had not been studied. Studies of the population dynamics of *H. ulvae* in different areas (Fish & Fish, 1974; Bachelet & Yassine-Kassab, 1987; Barnes, 1990; Lillebo et al., 1999) revealed a latitudinal trend in the breeding cycle and growth. Several authors have also recorded temporal variations of the density which were not the result of recruitment or mortality processes (Sola, 1996; Barnes, 1998; Barnes & de Villiers, 2000) and Fish & Fish (1974) recorded a differential distribution between juveniles and adults. *Hydrobia ulvae* has a pelagic larval stage (Fish & Fish,

1974) and a floating capacity (Little & Nix, 1976). Armonies (1992) and Armonies & Hartke (1995) showed a high dispersion of juveniles of *H. ulvae* by a drifting behaviour, a phenomenon already reported for other benthic species (Armonies, 1994; Olivier et al., 1996; Blackmon & Eggleston, 2001). In addition, individuals may also be passively rolled by flooding tides which may induce temporal variation in natural abundances, more particularly during spring tides (Barnes, 1998). Consequently, densities are susceptible to show a spatio–temporal dynamics; this suggested that sampling at a single station is not adequate to understand processes involved in population density changes.

The objective of this study was to investigate the population dynamics of *H. ulvae* at different locations on a mudflat, to determine processes which can be estimated at a local scale and processes involving a larger scale. For this, the spatio–temporal evolution of the population structure of *H. ulvae* was investigated along a cross-shore transect during one year. Classical tools of population dynamics were used to estimate unknown parameters from observed samples. The breeding cycle was characterized by the percentages of individuals bearing egg capsules and population structure and growth were investigated by statistical analyses.

MATERIALS AND METHODS

Study area

Brouage mudflat is located on the eastern side of the Marennes-Oléron Bay along the French Atlantic coast
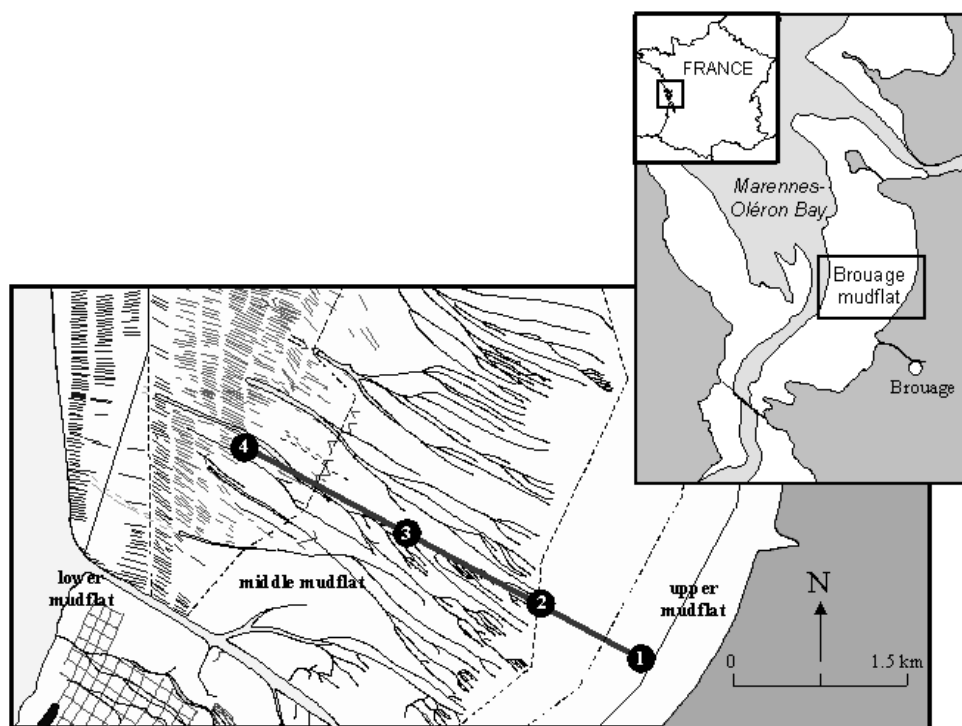
Figure 1. Position of sampling stations along a cross-shore transect on Brouage mudflat.

(46°25′N 01°10′W). This intertidal area is more than 4 km wide and the sediment consists of silt and clay particles (95% < 63 μm). Three zones can be distinguished (Figure 1): (i) the upper mudflat (500 m wide) is flat, strongly affected by meteorological conditions and characterized by rapid changes of erosion/sedimentation events (Gouleau et al., 2000); (ii) the middle mudflat (3000 m wide) is typical of a ridge and runnel structure area; and (iii) the lower mudflat ($\sim$800 m wide) is used for mussel culture.

Sampling

The population dynamics of *Hydrobia ulvae* was investigated from March 2000 to February 2001 along a cross-shore transect which encompasses the main geomorphological units. At Station 1, in the upper mudflat, erosion structures appeared in spring and winter and observed crests and troughs were distinctively sampled. Stations 2 and 3 were located in the middle mudflat; ridges and runnels were both sampled. A fourth lower intertidal site was also sampled but never contained *Hydrobia* and is therefore not further mentioned. Six random replicates of 15 cm in diameter within 1 m^2 of mud were taken and the top 5 cm layer of sediment was sieved through a 500-μm mesh. The number of snails were counted and their shell length, from apex to anterior margin of the aperture, was measured. The breeding cycle was characterized in terms of percentage of individuals carrying egg masses.

Data analysis

Size–frequency distributions were established for each date, station and sedimentary structure using a 0.1 mm

size-class. A statistical analysis was performed on size–frequency histograms to separate different cohorts (groups of individuals recruited during a fixed period of time) from the mixed population of *H. ulvae*. This analysis relies on the assumption that the size distribution of a cohort follows a gaussian pattern. From the same observed size distribution K normal components were thus identified. Each component has been described by three parameters: μ (the mean), σ (the standard deviation) and p (the amplitude). The number of components K was fixed a priori, based on the biological cycle of the species (extension of the spawning period, time lag between spawning peaks and recruitments, life span of snails) and the definition of class resolution. Estimates of the K parameter sets $\hat{\theta}_k = \{\hat{\mu}_k, \hat{\sigma}_k, \hat{p}_k\}$ were performed without constraint by minimizing the maximum log-likelihood criteria, L_t (Hasselblad, 1966). At step t:

$$
\begin{cases}
\hat{q}_{t,nk} = \exp\left\{-(x_i - \hat{\mu}_{t,k})^2/(2\hat{\sigma}_{t,k}^2)\right\}/(\hat{\sigma}_{n,k}\sqrt{2\pi}) \\[2mm]
\hat{Q}_{t,n} = \sum_{k=1}^{K} \hat{p}_{t,k} \cdot \hat{q}_{t,nk} \\[2mm]
\hat{L}_t = \sum_{n=1}^{N} f_n \cdot \ln(\hat{Q}_{t,n})
\end{cases}
\tag{1}
$$

where x_i is the centre of the size class i.

The steepest descent algorithm was used (Tomlinson, 1970) after determining initial values, calculating observed frequencies f_n and rescaling size-classes (each size-class was equal to 1). Only the populations with N > 500 were analysed. Total abundances of each group were calculated from estimated cohorts by numerical integration which allowed checking of the density conservation through the modal analysis.

Growth

In order to describe the growth rate of *H. ulvae*, a dynamic model was fitted to the observed growth curves, obtained by tracking the estimated mean size of identified cohorts. The model is the von Bertalanffy equation:

$$\frac{dL}{dt} = k(t)(L_\infty - L) \qquad (2)$$

where L_∞ is an asymptotic fitted value representing the maximum mean individual size and $k(t)$ is a sinusoidal function representing the seasonal variation of the growth rate (Cloern & Nichols, 1972):

$$k(t) = k_{max}(0.5 + 0.5 \sin(\omega t + \varphi)) \qquad (3)$$

The parameter ω is fixed to correspond to a one-year periodicity. The 3-parameter vector $\theta\{k_{max}, L_\infty, \varphi\}$ was estimated using a Simplex Algorithm (Nelder & Mead, 1965) which minimizes an Ordinary Least Square criterion (Y_{OLS}):

$$Y_{OLS} = \min \sum_{i=1}^{N} (L_{obs,i} - L_{sim,i})^2 \qquad (4)$$

where $L_{obs,i}$ corresponds to the estimated mean size of each cohort at time i (sampling dates); and $L_{sim,i}$ are the corresponding simulated values at time i. Numerical simulations were performed using a 4th-order Runge-Kutta
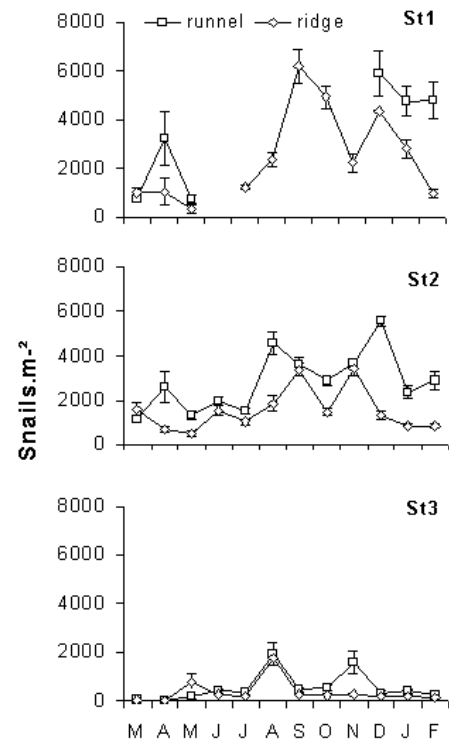

Figure 2. Abundance ±SE of *Hydrobia ulvae* along a cross-shore transect at three stations (Stations 1–3) and in both ridge and runnel structures between March 2000 and February 2001.
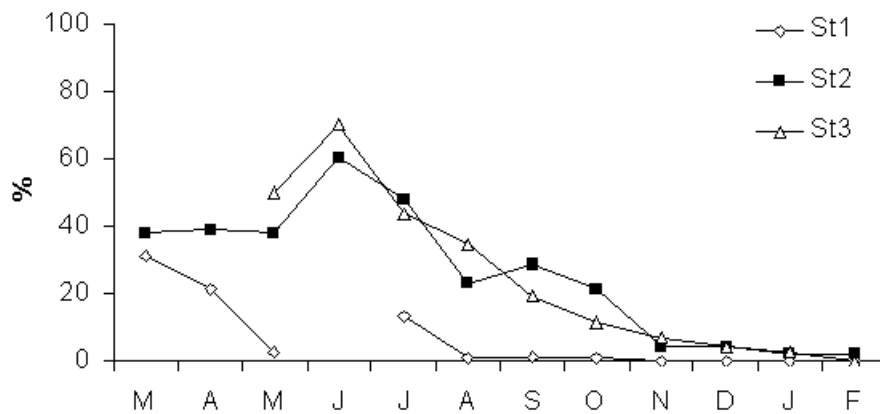

Figure 3. Percentage of *Hydrobia ulvae* bearing eggs capsules at Stations 1–3 along a cross-shore transect between March 2000 and February 2001.
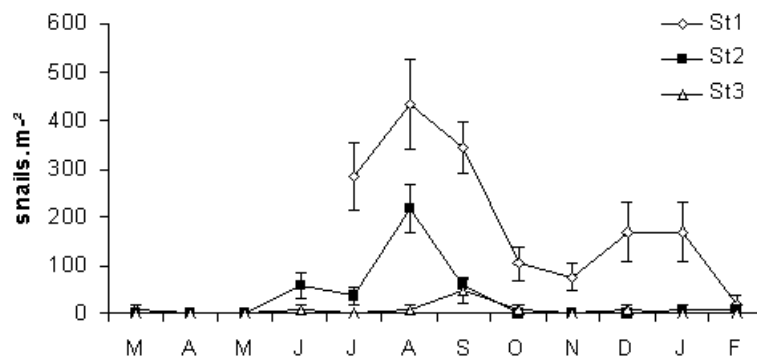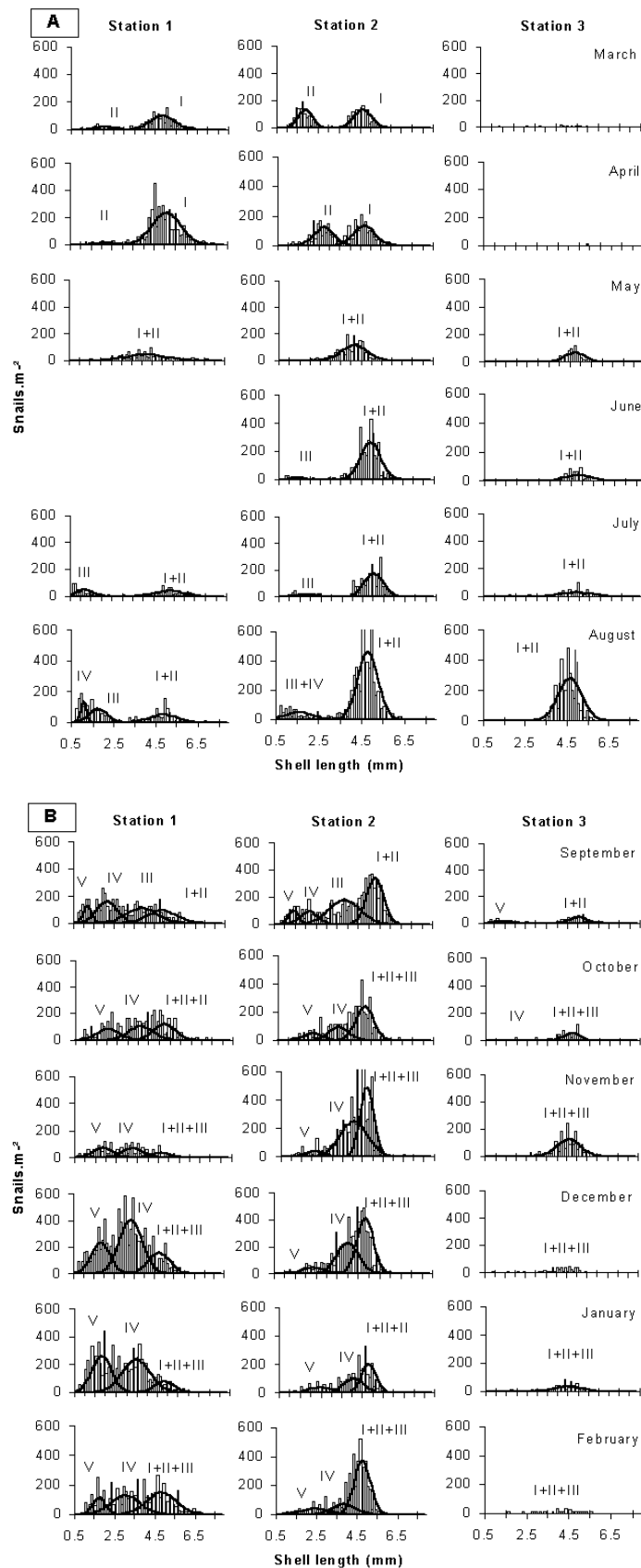

Figure 4. Density of snails (individuals m^{-2}) ±SE smaller than 1 mm at Stations 1, 2 and 3.

Figure 5. (A) Size–frequency distribution of *Hydrobia ulvae* along a cross-shore transect between March 2000 and August 2000 at Stations 1, 2 and 3. Identified cohorts are labelled I through V; I+II means that cohorts I and II have merged in a single cohort; I+II+III means that cohort III has merged with the mixed cohort I+II; (B) size–frequency distribution of *Hydrobia ulvae* along a cross-shore transect between September 2000 and February 2001 at Stations 1, 2 and 3. Identified cohorts are labelled I through V; I+II means that cohorts I and II have merged in a single cohort; I+II+III means that cohort III has merged with the mixed cohort I+II.

Table 1. *Estimated parameters from cohort analysis.*

|		M	A	M	J	J	A	S	O	N	D	J	F
Station 1													
I	μ	4.1	5.1										
	s	0.6	0.7										
II	μ	2.0	2.2	4.2		5.2	4.8	4.8					
	s	0.5	0.5	0.9		0.7	0.6	0.8					
III	μ				1.1	1.7	3.6	4.7	4.5	4.7	4.8	4.8	
	s				0.4	0.4	0.8	0.5	0.5	0.5	0.5	0.7	
IV	μ					1.0	2.1	3.6	3.2	3.3	3.5	3.0	
	s					0.1	0.5	0.6	0.5	0.6	0.7	0.7	
V	μ						1.1	2.0	1.8	1.8	1.8	1.7	
	s						0.2	0.5	0.5	0.5	0.5	0.3	
Station 2													
I	μ	4.6	4.7										
	s	0.4	0.5										
II	μ	1.9	2.7	4.1	4.9	5.0	4.8	5.3					
	s	0.3	0.5	0.6	0.5	0.5	0.5	0.4					
III	μ				1.3	1.8		3.8	4.7	4.7	4.8	4.8	4.7
	s				0.4	0.6		0.7	0.4	0.3	0.4	0.4	0.4
IV	μ					1.5	2.1	3.4	4.0	4.1	4.1	3.8	
	s					0.6	0.4	0.5	0.7	0.5	0.5	0.6	
V	μ					1.4	2.1	2.1	2.4	2.4	2.4		
	s					0.2	0.4	0.5	0.5	0.6	0.7		
Station 3													
I	μ			4.7	4.8	4.8	4.6	5.0	4.6	4.6	4.3	4.5	
	s			0.5	0.6	0.6	0.7	0.4	0.5	0.6	0.9	0.6	

μ, means; s, standard deviations.
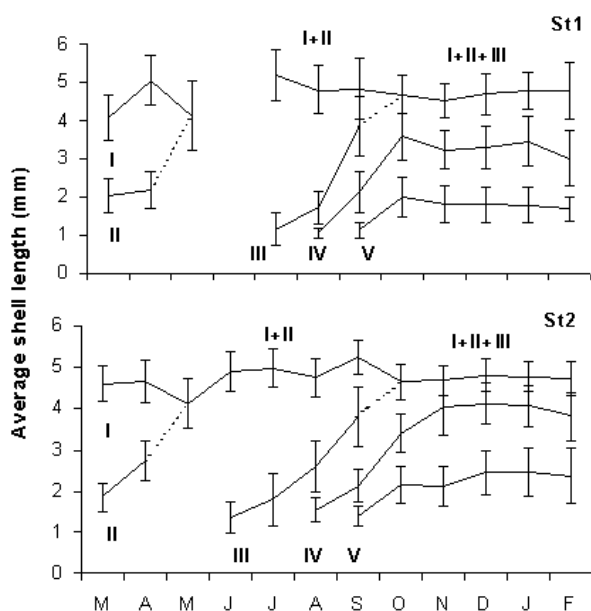
Figure 6. Average shell length (mm) of *Hydrobia ulvae* cohorts on Brouage mudflat between March 2000 and February 2001 at Stations 1 and 2. Cohorts are labelled I through V; I+II means that cohorts I and II have merged in a single cohort; I+II+III means that cohort III has merged with the mixed cohort I+II.

Algorithm. We have added the estimation of initial conditions to the process of global optimization of the vector θ.

RESULTS

Spatio−temporal distribution of Hydrobia ulvae

During the overall sampling period, *Hydrobia ulvae* mainly occurred in the upper part of the mudflat (Stations 1 & 2), with lower densities in the middle part at Station 3 (Figure 2; Kruskal−Wallis test adjusted for ties, $P<0.001$ for both ridges and runnels). Maximum abundances were observed at Stations 1 and 2 with mean annual densities of $4334 \pm 892 \, \mathrm{ind \, m^{-2}}$ and $4380 \pm 556 \, \mathrm{ind \, m^{-2}}$, respectively. At Station 3, the mean annual density only reached $902 \pm 290 \, \mathrm{ind \, m^{-2}}$. In general, three periods can be distinguished: (1) from March−July, densities of *H. ulvae* remained low with about $2000 \, \mathrm{ind \, m^{-2}}$ at Stations 1 and 2 and about $100 \, \mathrm{ind \, m^{-2}}$ at Station 3; (2) from August−December, *H. ulvae* showed higher densities, especially at Stations 1 (maximum of $6215 \, \mathrm{ind \, m^{-2}}$ in September) and 2; (3) from December to February densities decreased. *Hydrobia ulvae* abundances were significantly higher in runnels than on ridges at Station 1 when bedforms could be distinguished (1-sample *t*-test, $P=0.020$) and at Station 2 (1-sample *t*-test, $P=0.003$).
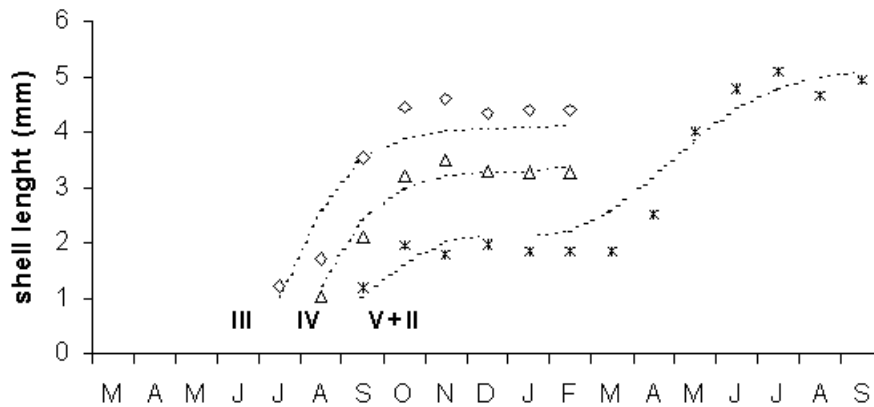
Figure 7. Reconstructed annual growth curves (✳) from observed data (symbols, data from the different Stations 1, 2 and 3 were pooled together): assuming a steady state, values of cohort II (corresponding to March–September 2000) were moved at the end of data from cohort V (September 2000–February 2001). A dynamic model, based on von Bertalanffy equation including a variable growth parameter, was then fitted to the observed data to estimate the asymptotic maximum length (L_∞) and the maximum growth rate (k_{max}) over the annual cycle.

Breeding cycle and recruitment

The breeding period of *H. ulvae* on Brouage mudflat extended from March–November and the individuals carrying egg capsules were mostly found in the middle part of the mudflat (Stations 2 & 3, see Figure 3). At these stations, the spawning peak occurred between May and July with a maximum value in June (with ~60% of snails carrying egg capsules); a secondary peak occurred at Station 2 between September and October. At Station 1, the observed pattern was different with a much lower percentage of snails carrying egg masses and a shorter period of reproduction (March through July only).

Abundance of snails smaller than 1 mm (Figure 4) showed that recruitment mainly occurred at Station 1 in the upper mudflat and to a lesser extent at Station 2. At Station 1, two maxima occurred: in August with 434 ± 94 ind m^{-2} and in December with 180 ± 53 ind m^{-2}. At Station 2, the recruitment was characterized by a single peak in August with 219 ± 71 ind m^{-2}. At Station 3, a few recruits appeared in September (47 ± 28 ind m^{-2}).
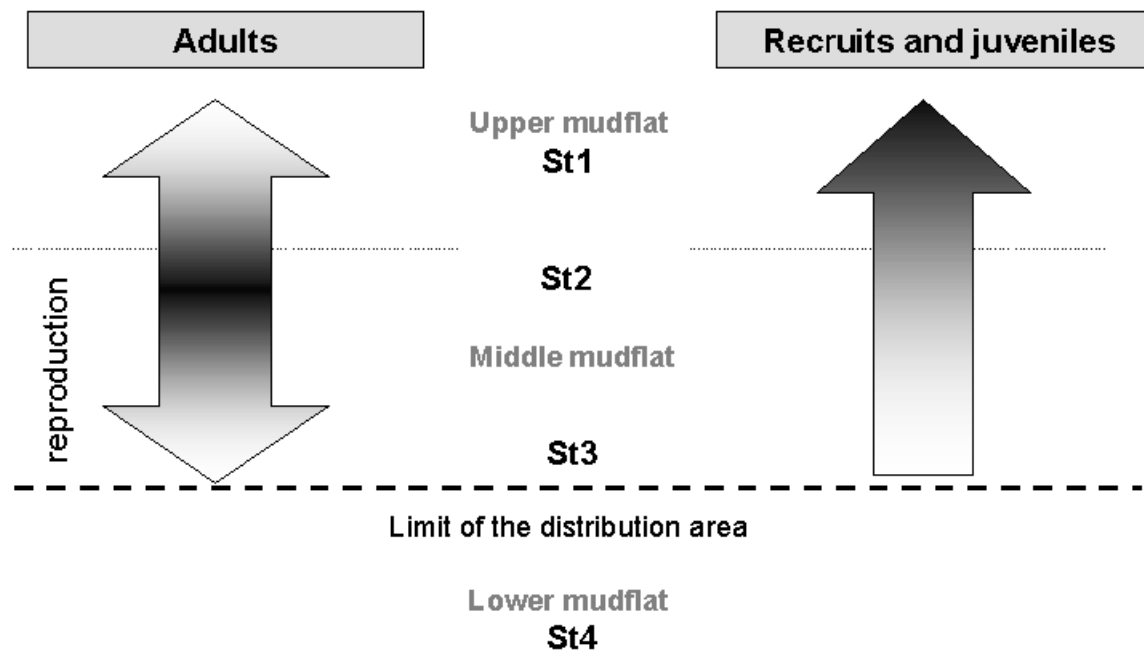
Population structure

Size–frequency analyses presented in Figure 5A,B and Table 1 (estimated parameters of cohorts) revealed that a maximum of five cohorts were identified, namely I, II, III, IV and V. According to the assumption of cohort analysis, the estimate of the standard deviation of each cohort (characterized by a gaussian distribution) did not change throughout the sampling year, except when densities were too low or when different cohorts merged in a single one.

In March 2000, cohorts I and II co-occurred at Stations 1 and 2 (with an estimated mean size of 4.3 and 1.9 mm, respectively; Table 1). In May, cohorts I and II merged in a single one (estimated mean size of 4.3 mm) and individuals were present at all three stations. Cohort III and cohort IV are recruited in July and August respectively, only at Stations 1 and 2. The last recruitment of the year (cohort V, estimated mean size of 1.3 mm) occurred in September at all three stations, but mainly at Stations 1 and 2. In October, cohorts I, II and III merged in a single one (estimated mean size of 4.6 mm). Then, the major characteristics of the population structure were maintained until February 2001: three cohorts (I+II+III, IV, V) co-occurred at Stations 1 and 2 with a predominance of juveniles at Station 1 and adults at Station 2; only the oldest cohort was recorded at Station 3.
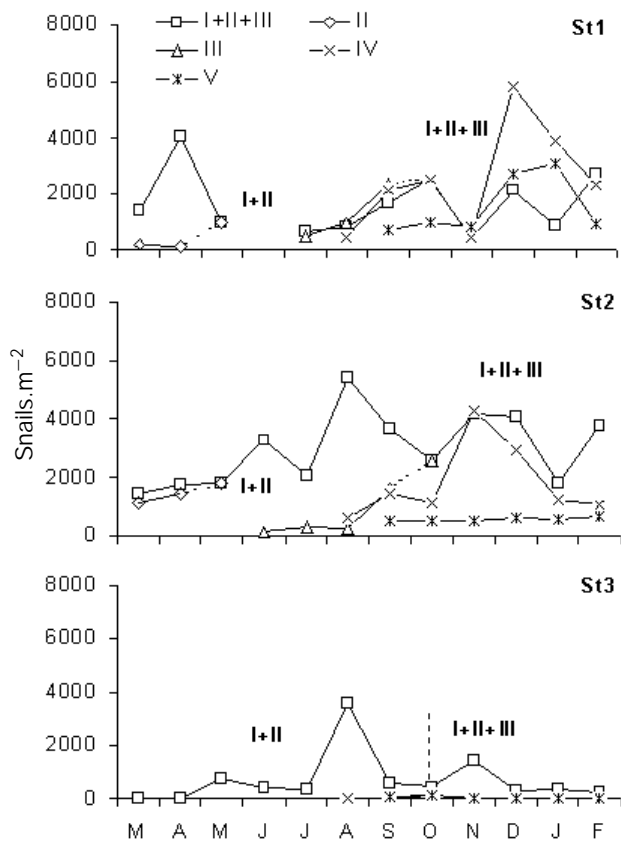
Figure 8. Abundance of each cohort at Stations 1, 2 and 3 between March 2000 and February 2001. Cohorts are labelled I through V; I+II means that cohorts I and II merged in a single cohort; I+II+III means that cohort III has merged with the mixed cohort I+II.

Figure 9. Spatio–temporal differentiation in the population structure of *Hydrobia ulvae* on Brouage mudflat.

Growth

Growth curves of the different cohorts were built using the mean individual shell length at different dates (Figure 6), obtained from the results of the cohort analysis (Table 1). The maximum mean shell length of the population was ~ 5 mm. Only cohort III, which appeared in June, reached a size close to the maximum in October (4.7 mm at Station 1, 4.6 mm at Station 2); cohorts IV and V, recruited later in the summer, stopped their growth in October at a shell length of ~ 3.5 and 2 mm, respectively. There was no growth during the winter time from October 2000 until February 2001.

In order to model *H. ulvae* growth over a complete annual cycle, and assuming a steady state, growth curves were reconstructed by moving data of cohort II from March to September 2000 (see Figure 6), at the end of data from cohort V (Figure 7). This representation clearly shows the shape of the growth curve as a function of the time of recruitment; obviously, the growth rate changed as a function of seasons. A dynamic model, based on von Bertalanffy equation and including a variable growth parameter, was then fitted to the observed data to estimate the asymptotic maximum length (L_∞) and the maximum growth rate (k_{max}) over the annual cycle. The estimated parameters of the von Bertalanffy growth function are not significantly different from Station 1 to Station 2 (statistical test proposed in Blanchard et al., 1997); $f_{obs}=0.92$ and $P=0.65$). Then, it turned out that L_∞ was 5.4 ± 0.2 mm and k_{max} was 0.47 ± 0.5 mm month^{-1}.

Cohort density fluctuations

The abundance of each cohort showed large fluctuations during the sampling period (Figure 8), but the three stations were characterized by different patterns. At Station 1, all cohorts fluctuated, while at Station 2 cohorts with an average shell length larger than 3 mm showed larger fluctuations. Indeed, the largest cohorts (I+II and I+II+III), with an average shell length of 4.7 ± 0.2 mm, showed density fluctuations in the range 1500–6000 ind m^{-2} (the density significantly increased between May (1830 ± 218) and June (3490 ± 325), and between July (2235 ± 224) and August (5621 ± 624); Figure 8, Student *t*-test, $P<0.05$) whereas densities of younger cohorts remained lower than 1500 ind m^{-2} until October. Similarly, cohort IV was subjected to large changes in abundance when its average shell length exceeded 3 mm, while cohort V had a rather constant low density (~ 500 ind m^{-2}), with an average shell length of about 2 mm. At Station 3, only the largest cohort was present and showed occasional fluctuations in August (up to 3570 ind m^{-2}) and in November (up to 1430 ind m^{-2}).

DISCUSSION

Distribution, reproduction, recruitment and growth: comparison with other areas

On Brouage mudflat, the population of *Hydrobia ulvae* was mainly distributed in the upper parts of the mudflat (Stations 1 & 2 of the present study; Figure 2), above the mean neap low-tide level. However, this distribution may differ between different areas: for instance, in the Gironde estuary, Bachelet (1987) recorded maximum densities at the mean tidal level during autumn, but in the lower part of the intertidal area during summer. On the other hand, Armonies & Hartke (1995) also recorded maximum densities in the upper part of the mudflat, with a seaward extension during recruitment periods.

The Brouage population exhibited an extended spawning period since egg capsules were present most of the year with two peaks, in late spring and autumn

(Figure 3). Such a pattern was also observed in several sites of southern Europe: the Gironde estuary in France (Bachelet & Yassine-Kassab, 1987), the Bidasoa estuary in Spain (Sola, 1996) and the Mondego estuary in Portugal (Lillebo et al., 1999). Further north, populations from the Baltic Sea and the British Isles exhibit shorter spawning periods with a single peak in spring (Anderson, 1971; Lappalainen, 1979).

Despite the continuous flux of recruited juveniles from June to February (Figure 4) three cohorts between June and September were identified (Figures 5A,B & 6); another recruitment occurred in December but densities were too low to separate this cohort from the others. After spawning, about a two-month time lag (corresponding to the embryonic development, the pelagic larval stage and the post-larval growth) is necessary to detect new recruits on a 500-μm mesh (Fish & Fish, 1974; Bachelet & Yacine-Kassab, 1987). Accordingly (Figures 4 & 5), cohort III, recruited in July, may correspond to the increasing phase of spawning in May; cohort IV, recruited in August, may correspond to the spawning peak in June; cohort V, recruited in September, may correspond to the decreasing phase of spawning in July; individuals recruited in December may correspond to the slight renewal of spawn which occurred in September. Three annual cohorts were also recorded in the Gironde estuary (Bachelet & Yassine-Kassab, 1987).

The present study is the first to provide a dynamic model based on von Bertalanffy equation which quantitatively estimates growth parameters of *H. ulvae*. The growth rate changed during the annual cycle as a function of the time of recruitment (Figure 7) and was maximum during summer at about 0.47 mm month^{-1}. When cohorts were recruited in late summer or autumn, the growth curve was characterized by two phases because growth ceased during the winter (Figure 7). However, in every case, the maximum mean shell length was ~5 mm. These characteristics are similar to southern European sites: for instance, Bachelet & Yassine-Kassab (1987) in the Gironde estuary and Sola (1996) in Spain have also recorded a two-phase growth for cohorts recruited in summer, with a similar average shell length. On the other hand, populations in northern Europe show lower growth rates. In the Anse Lostrouc'h (Finistère, France) Barnes (1996) have recorded similar maximum average shell-length (between 4 and 5 mm) but the recruited cohort showed low and constant growth rates and reached the pool of larger individuals after about eight months. In the Dovey estuary (Anderson, 1971), the annual recruited cohort reached a shell length of 2 mm after one year.

Differentiation in the population structure of Hydrobia ulvae

The fact that the same growth rate was found at Stations 1 and 2 suggests that we observed the same population along the cross-shore transect during the whole sampling period. Thus, growth of *H. ulvae* can be estimated from any station on the mudflat. On the contrary, this population exhibited a strong spatio–temporal differentiation in its size–structure, which appears as a strong feature of *H. ulvae* populations on intertidal mudflats. Indeed, similar findings were also observed by Fish & Fish in the Dovey estuary (1974) and by Armonies & Hartke (1995) in the Wadden Sea. In Brouage mudflat, recruitment events induced this differentiation in the population structure with a clear predominance of juveniles in the upper mudflat (Station 1 from June; Figure 5) and adults in the middle mudflat (at Station 2 and more particularly at Station 3). Taken together with the large fluctuations in the cohort densities observed at all stations, this feature emphasizes the fact that the local population structure (at any single site) is strongly influenced by large-scale movements, which make the interpretation of population dynamics particularly difficult and preclude the calculation of cohort mortality and population secondary production. As the spatial distribution of species involves both physical and biological processes (Newell, 1979), differential responses to these processes during the life cycle of *H. ulvae* must be taken into account to understand its population structure.

Recruitment pattern: we can hypothesize that the recruitment pattern along the transect mainly results from hydrodynamic processes. According to the density of mature individuals along the transect (Figure 3), the maximum density of recruits was expected to occur in the middle part of the mudflat (at Stations 2 & 3). As a result of larval dispersion, recruitment mainly occurred in the upper level (Station 1), to a lesser extent at Station 2, and almost no recruitment was observed at Station 3. Furthermore, the December recruitment was only detected at Station 1 (Figure 4) where reproduction stopped in August. Therefore, there seems to be a preferential settlement due to an importation of post-larvae at Station 1 from other sites (Stations 2 & 3 might be such sites, but it can be any sites even from outside the transect). This hypothesis is well supported by the fact that planktonic larvae are considered as passive particles (Hannan, 1984; Butman, 1989; Eckman, 1990), and as such the spatial pattern of recruitment is strongly influenced by physical factors (Eckman, 1983; Snelgrove, 1994; Emerson & Grant, 1991). This is probably the case at Brouage mudflat where maximum flood velocities occur in the lower part of the mudflat and decrease towards the shore (Le Hir et al., 2000), thus producing an onshore residual flux of particles (Bassoulet et al., 2000) and very likely a preferential accumulation and settlement of post-larvae in the upper mudflat. Bouma et al. (2001) have reported similar explanations for the observed recruitment pattern of *Cerastoderma edule* and *Macoma balthica*.

However, compared to other European sites—e.g. the Gironde estuary in France (Bachelet & Yassine-Kassab, 1987), and the Bidasoa estuary in Spain (Sola, 1996) with ~10,000 ind m^{-2}—the upper part of Brouage mudflat had a very low recruitment level with only ~500 ind m^{-2}. This 20-fold difference calls for two complementary explanations. The first one, based on Rhoads (1970) and Woodin (1976) studies, stipulates that new recruits of *Hydrobia* overcome a detrimental effect (through predation, interspecific competition) of the high densities of *Scrobicularia plana*, *Macoma balthica* and *Abra tenuis* populations characteristic of Station 1 (Sauriau et al., 1989). The second one suggests that the upper mudflat was not the main site for recruitment and that we only observed a residual recruitment, the main site not being covered by our transect. This hypothesis is supported by the fact that juveniles of a larger size appeared in the upper parts of the

mudflat (Stations 1 & 2) during several months following the initial recruitment event (Figure 8). This sequential arrival of juveniles could be the result of a secondary dispersal by drifting behaviour (Armonies, 1992; Armonies & Hartke, 1995) from a primary settlement site, as it was reported for several benthic invertebrates (Armonies, 1994; Olivier et al., 1996; Blackmon & Eggleston, 2001) and particularly for *H. ulvae* in the Wadden Sea (Armonies & Hartke, 1995). This behaviour responds to unfavourable biological and/or physical conditions (Olivier et al., 1996; Blackmon & Eggleston, 2001) but the direction of transport is strongly influenced by hydrodynamics (Armonies & Hartke, 1995).

Distribution pattern of adults: snail abundances were higher at Station 2 than at Station 1 (Figure 5) and individuals larger than 3 mm seemed to be imported from other parts of the mudflat (Figure 8). These snails were transported by currents but the determinism—resuspension induced by currents or active lifting into the water column—and the scale of their displacement cannot be determined in the present study. This also clearly demonstrates that the population structure cannot be understood from local information only. Moreover, within Station 2, the population was often rather contained in runnels (see Figure 2) which act as drainage structures during the ebb tide and also constrain the water flow during flood tide. Snails accumulated preferentially in these structures and were thus susceptible to move upwards and downwards around Station 2. The presence of runnels probably facilitates movements of *Hydrobia* in the middle part of the mudflat and might play an important role in the transport and exchange of individuals.

At Station 1, the lower abundance of adults may result from: (i) a differential mortality with higher loss rates at Station 1 (due to higher predation by birds or to higher parasitism than at Station 2); and (ii) active resuspension of adults to escape unfavourable conditions.

CONCLUSION

The population of *Hydrobia ulvae* on Brouage mudflat shows similar breeding and growth characteristics than that of other populations in southern Europe. Our study confirms the existence of large movements of *H. ulvae*, at the scale of the ecosystem, and shows a spatial differentiation in the population structure likely due to differential responses to physical and biological processes during the life cycle. Particularly, the spatial pattern of recruits and juveniles seems to be strongly influenced by hydrodynamics. These hypotheses, summarized in Figure 9, need to be tested by a modelling approach and an identification of the spatial structures of *H. ulvae* population at the end of the recruitment period. This should allow the larval dispersion pattern by hydrodynamical processes and mass transfers of individuals at the scale of the mudflat to be investigated.

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