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Use of artificial collectors shows semilunar rhythm of planktonic dispersal in juvenile *Hydrobia ulvae* (Gastropoda: Prosobranchia)

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The pattern of planktonic abundance of juvenile *Hydrobia ulvae* was investigated in the Ria de Aveiro, Portugal, with the use of floating artificial collectors made of 'hoghair' filter, which were deployed for 2-day consecutive periods during 3.5 months. Abundance in the collectors followed a remarkably regular semilunar pattern, being higher during spring tides around full and new moons. Cross-correlation analysis between tidal range and captures in the collectors indicated a period of oscillation of the captures of 15 d, with maximum captures tending to occur on the day of the highest amplitude tides. The physical and behavioural mechanisms responsible for the pattern remain largely unknown. However, results from a simple model assuming that migration from the sediment to the water is dependent on current velocity suggest there is a minimum threshold in average current velocity integrated along the tidal cycle (and, therefore, in tidal amplitude) above which juvenile *H. ulvae* exhibit the floating behaviour. Artificial collectors may provide an effective and relatively easy and inexpensive technique for the study of dispersal of post-metamorphic molluscs.

INTRODUCTION

Gastropods of the genus *Hydrobia* are common inhabitants of estuaries of the temperate zone. These small gastropods form dense populations that can reach densities over 100,000 ind m^{-2} in intertidal areas (Fish & Fish; 1974; Bachelet & Yacine-Kassab, 1987) and constitute an important component of the estuarine food web (Drake & Arias, 1995). *Hydrobia ulvae* (Pennant) hatch as a short lived veliger that develops on the sediment or that has a free-swimming phase of two or three days. Consequently, dispersal during the larval phase is considered to be of little ecological significance (Fish & Fish, 1974). However, juvenile and adult *H. ulvae* are known to use tidal currents as a means of dispersal. Floating with the incoming tide can be achieved by several mechanisms, which include the secretion of mucous rafts, the use of air bubbles trapped in the shell opening or the extension of the foot to contact the water surface where it remains locked due to the surface tension (Newell, 1962; Anderson, 1971). A behavioural pattern synchronized with the tide has been described in this species, in which adult animals crawl over the sediment during the receding tide, burrow, resurface with the incoming tide, float and sink again to the sediment during high water. Over 95% of the captures from the plankton with the use of nets are juveniles (Armonies, 1992; Armonies & Hatke, 1995). Still, the extent of the horizontal movements along the estuary during the floating phase is not known (Newell, 1962; Anderson, 1971).

Floating artificial collectors made of 'hoghair' air-conditioning filter have been routinely used for the study of supply and settlement of crab megalopae (e.g. van Montfrans et al., 1990). In an exploratory study on the use of artificial collectors conducted in the Canal de Mira, Ria de Aveiro, Portugal (Meireles, 1998), the collectors captured large numbers of juvenile *Hydrobia ulvae* and revealed a remarkable semilunar pattern of abundance in the plankton. The objectives of the present paper are: (i) to examine the phasing of the rhythm of abundance in the collectors relative to the tidal range cycle; (ii) to analyse the size of the floating individuals, in order to distinguish possible direct settlement of veligers on the collectors from floating behaviour of juvenile snails; and (iii) to develop a set of simple numerical models, in order to identify the nature of the physical and behavioural mechanisms controlling abundance of juvenile *H. ulvae* in the water.

MATERIALS AND METHODS

Study area and field sampling

Ria de Aveiro is a coastal shallow lagoon located on the north-western coast of Portugal, separated from the sea by a sand bar (Figure 1). It can be classified as a bar-built estuary. Tides in the Ria de Aveiro are semi-diurnal, with a mean tidal range of 2.1 m at the inlet. Tides are slightly asymmetrical at the sampling sites, with flood duration exceeding ebb duration by 25 min on average. The delay of the tide at the sampling sites relative to the inlet varies between 20 and 40 min, according to tidal amplitude and phase (Queiroga, 1995). The sampling sites (Figure 1) were located at Canal de Mira, one of the branches of the Ria de Aveiro, at a distance of 2.3 to 6.6 km from the inlet. The sampling sites were originally chosen for a study on recruitment of crab (*Carcinus maenas*) megalopae. Coincidentally, both are located close to intertidal areas densely populated by *Hydrobia ulvae*.

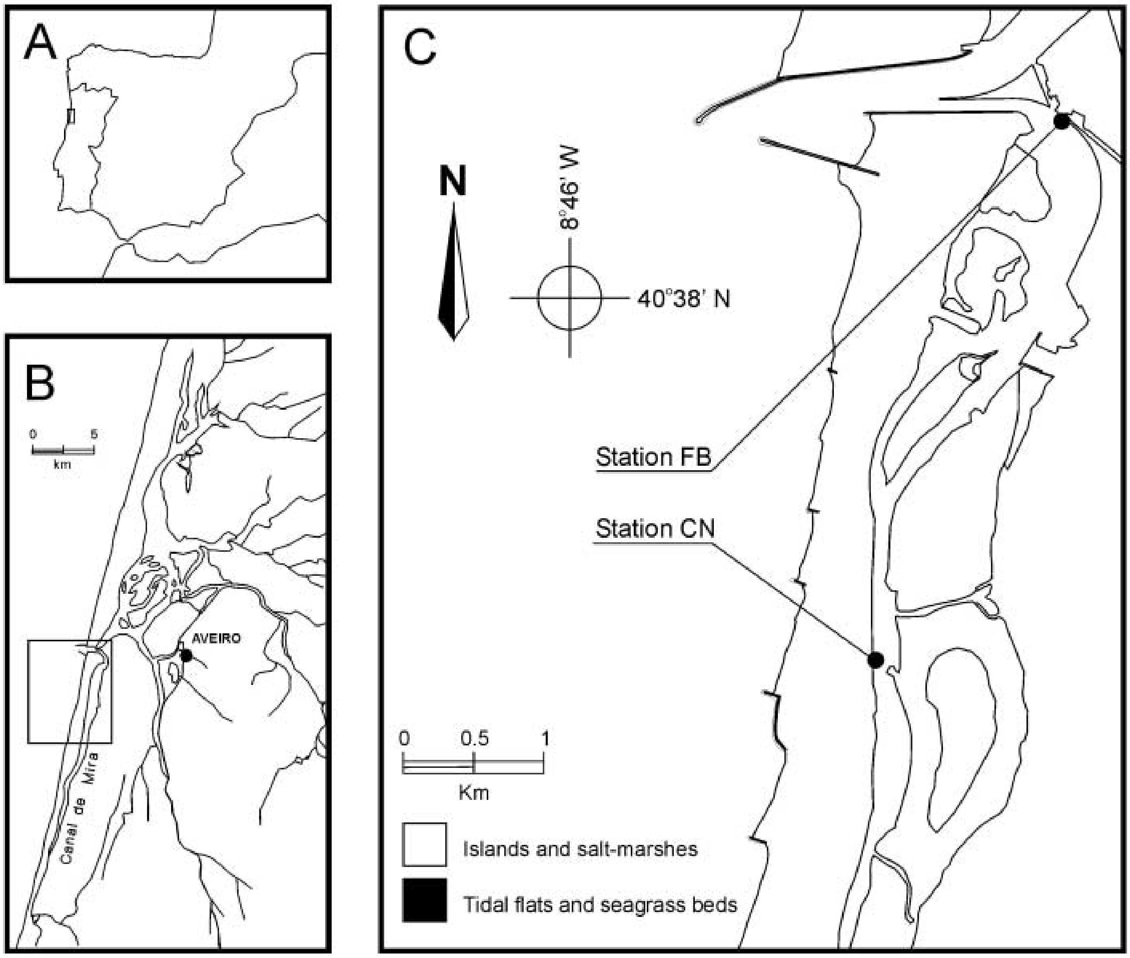

Figure 1. (A) Iberian Peninsula; (B) Ria de Aveiro; and (C) Canal de Mira, showing location of sampling stations.

The collectors were made of 0.50×0.40 m pieces of 0.02 m thick hoghair that were wrapped around polyvinyl chloride (PVC) tubes 0.16 m in diameter and secured in place with Velcro and rubber bands, giving cylinders with an outer diameter of 0.2 m and a height of 0.4 m. The collectors were suspended vertically from the water surface using a float placed inside the tube. Three collectors were deployed at each of two stations in the Canal de Mira (Figure 1), from 15 April to 1 August 1997. This period encompasses the start of the egg-laying season at the Ria de Aveiro (C.M. Barroso, unpublished data). The settling surfaces were replaced every 2 d, during the morning, transported to the laboratory inside plastic bags and placed in buckets with fresh water for 20 min. After this period the hoghair pieces were washed with fresh water jets to another container and the material was sieved through a 500-μm sieve. The hoghair was air-dried before reuse. These procedures are similar to those used in studies that also employed the same type of collectors (van Montfrans et al., 1990). Surface water temperature and salinity were measured at both stations during the recovery of the collectors. The number of sampling sites and replicates and the sampling frequency were determined as a compromise between replication of sites and collectors, the need to use a sampling frequency appropriate for resolving the tide amplitude cycle, and logistic reasons.

Identification and size determination

Gastropods were identified according to Kermack & Barnes (1988). A subsample of a maximum of 20 *Hydrobia ulvae* from each station was taken every day of collection for size determination, by random sampling proportionally allocated to each of the three replicates according to the number of individuals caught in each replicate. Shell heights of 0.5 and 2.0 mm (Fish & Fish, 1974; Bachelet & Yacine-Kassab, 1987) were used to discriminate between larvae recently settled from the plankton, juveniles and adults. In order to evaluate whether the average size of floating *H. ulvae* changed throughout the tide amplitude cycle, a 2-way orthogonal analysis of variance (ANOVA) was employed, using station (CB and CN) and tidal range (spring and neap) as independent variables, followed by post-hoc comparisons according to the Student–Newman–Keuls procedure (Quinn & Keough, 2002). Average tidal range at the Ria de Aveiro is 2.0 m, and this value was used to distinguish between neap and spring tides, according to the expected values given by the tide tables published by the Instituto Hidrográfico. Before the analysis the data were transformed in order to normalize the distribution and homogenize variances. Since the variance of each group in the analysis was strongly correlated with the mean, the transformation applied was based on the Taylor's power law (Elliott, 1977). This transformation has the form $y' = y^{1-b/2}$, where b is the slope of the line relating the logarithm of the variance to the logarithm of the mean.

Periodicity of Hydrobia *abundance in the collectors*

Cross-correlations (Brockwell, 1996) were used to investigate the relationship between abundance in the collectors and tidal range as predicted from the tide tables of the Instituto Hidrográfico. Before the analysis the series were standardized to zero mean and unit standard deviation and the trend was removed by subtraction of the expected values according to a least squares linear regression.

Modelling

The cross-correlation analysis detected a cycle of 15 days in the numbers of juvenile *Hydrobia ulvae* caught in the collectors deployed at both sampling stations, in which the largest numbers were recorded during spring tides. Changes in tide amplitude during the spring/neap cycle control changes in average current velocity during the tide cycle. Since the juveniles are benthic during a portion of the tide cycle and float during the rising tide, then the concentration in the water column is expected to be a function of the migration rate and of the current velocity. In the absence of detailed information on the behavioural reactions of the animals and in order to throw some light on the nature of the physical and behavioural mechanisms controlling abundance of juvenile *H. ulvae* in the water, we used a simple model to describe captures by the collectors in three different scenarios. All the scenarios have two simplifying assumptions in common. The first is that average current intensity fluctuations along the semilunar cycle follow a sinus function. This assumption is based on historical observations made close to the sampling sites throughout the lunar month (Queiroga, 1995). From those observations is was estimated that vertically averaged current velocity integrated through the tide cycle varies from 0.4 m s^{-1} during spring tides to 0.25 m s^{-1} during neap tides. The second is that the collectors filter the water. In reality they do not. Because of the inner PVC tube the water flows around the collectors and an unknown proportion of the juveniles that come into contact with the surface of the collector is caught. Under this assumption captures are proportional to the surface of the collectors that is exposed to the current (i.e. to the area of the projection of the cylindrical collector onto a tangent plane: $0.2 \times 0.4 = 0.08$ m^2) and to current velocity: the stronger the currents, the larger the number of juveniles that hit the collector. We have no data or any other information to further model this.

In Scenario 1, a constant net rate of migration from the bottom to the water column of 0.02 ind m^{-2} s^{-1} was assumed. This value was chosen in order to scale the simulated captures in the collectors to the values that were recorded at Station CN. Please note that this is an average value. It should be understood as the net number of juveniles leaving the bottom sometime during each of the two daily flood tides, divided by 86400 seconds. We calculated:

$$C = M/V \qquad (1)$$

where C is concentration of juveniles (ind m^{-3}), M is the net migration rate (=0.02 ind m^{-2} s^{-1}) and V is the current velocity (m s^{-1}).

$$Fv = 0.08/V \qquad (2)$$

where Fv is the filtered volume (m^3 s^{-1}) and 0.08 is the collector area that faces the current (m^2).

$$Cap = C \times Fv \times 84600 \qquad (3)$$

where Cap is the captures per collector per day (ind), Fv is the filtered volume and 86400 is the number of seconds in 1 day.

Scenario 2 assumed that migration rate is a linear function of current velocity. Since $C = M/V$ then $M = V \times C$ and C has to be constant. We set C to 0.06, in order to scale the captures in the collectors to the range of values that were observed at Station CN.

Scenario 3 assumes that migration rate is not a linear function of absolute velocity, but rather a linear function of the difference between average current velocity and average current velocity during neap tides:

$$M = (V - V_{\min}) \times 0.244 \qquad (4)$$

where $V_{\min}$ is the average current velocity during the least amplitude tides. Again, the constant 0.244 was chosen for scaling reasons. The filtered volume, Fv, and the captures in the collectors, Cap, for Scenarios 2 and 3 were calculated similarly to Scenario 1.

RESULTS

The number of *Hydrobia ulvae* specimens caught daily per collector (Figure 2) was two orders of magnitude higher at Station CN (maximum of 1150 ind col^{-1}) than at Station FB (maximum of 23 ind col^{-1}). Most of the individuals collected were juveniles with shell heights ranging

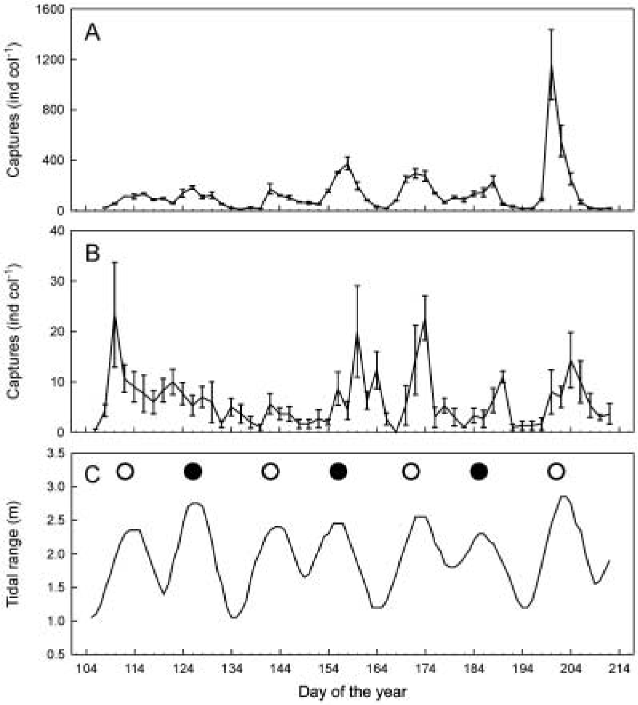

Figure 2. *Hydrobia ulvae*. Average abundance (±1 standard error; N=3) recorded in artificial collectors at (A) Station CN; (B) Station FB; and (C) tidal range during the sampling period. Open and closed circles at the top of panel C represent full and new moon.

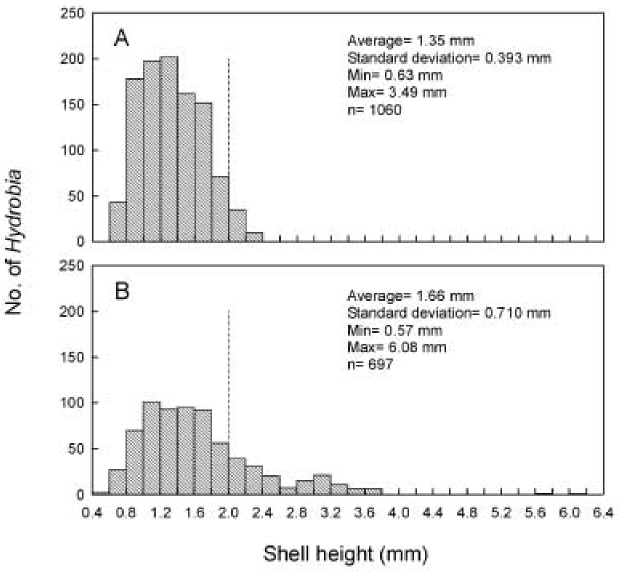

Figure 3. *Hydrobia ulvae*. Size–frequency distributions of individuals caught in the collectors at (A) Station CN; and (B) Station FB during the study period. Samples were made of a maximum number of 20 individuals collected every day. Sample statistics are also given. Dashed vertical line represents limit between juvenile and adult snails.

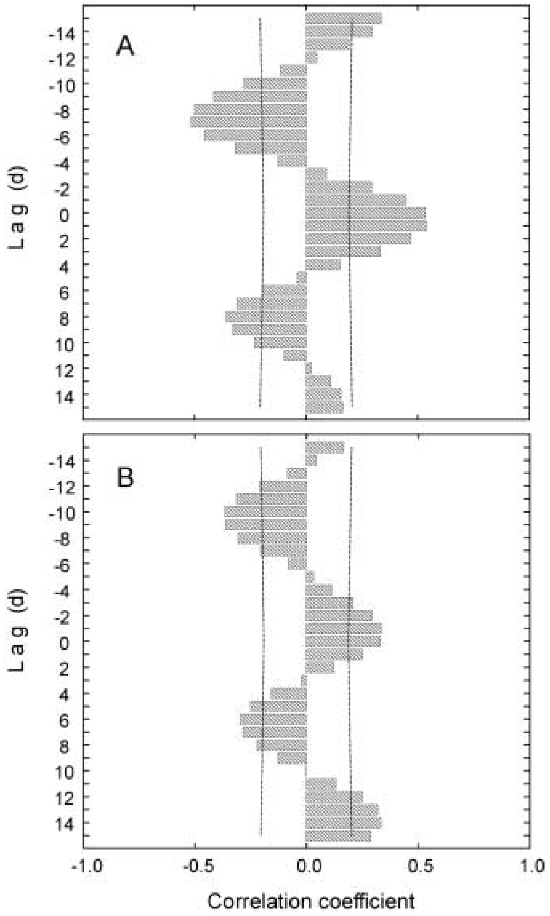

Figure 4. *Hydrobia ulvae*. Cross-correlograms between tidal range and abundance in the collectors at (A) Station CN; and (B) Station FB. Dashed line represents 5% confidence level.

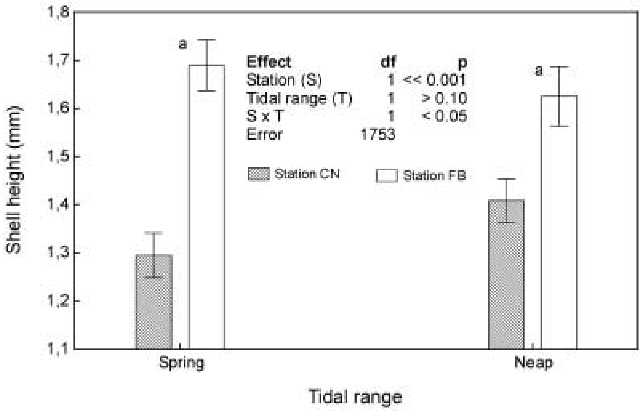

Figure 5. *Hydrobia ulvae*. Average size and 95% confidence interval (whiskers) of individuals caught in the collectors during spring and neap tides at Stations CN and FB. The inset table shows the results of the ANOVA of the effects of station and tidal range on the transformed values of shell height. Average size and 95% confidence intervals are based on non-transformed values. Post-hoc tests showed that all pairwise comparisons were significant ($P<0.05$), except in the pair marked with a.

from 0.5 to 2.0 mm: 95% of the total number collected at Station CN and 77% at Station FB (Figure 3). The remainder were adult individuals, as snails smaller than 0.5 mm were not collected. In both stations abundance in the collectors changed cyclically, being greater during high amplitude tides around full and new moons. Tidal range and abundance in the collectors were positively correlated (Pearson correlation coefficient of 0.55, $P<0.001$, for Station CN, and 0.30, $P<0.05$, for Station FB; Quinn & Keough, 2002). Cross-correlograms between tide range and captures in the collectors showed maximum correlation with time lags of −1–0 and 14–15 days at both stations, indicating that the highest abundances of floating *H. ulvae* tended to occur during the day of the highest amplitude tides (Figures 2 & 4). Salinity and temperature were not significantly related to captures in the collectors. The ANOVA of the effects of station and tidal range on size of the snails (Figure 5) showed significant effects of station ($P\ll 0.001$) and of the interaction ($P<0.05$), and post-hoc comparisons indicated all pairwise comparisons were significant ($P<0.05$) except that between spring and neap tides at Station FB. Besides a significant larger size at Station FB, the analysis showed that at Station CN larger juvenile snails were collected during neap tides.

The results of the simulations are represented in Figure 6, in which panel A shows the estimated current velocity common to all three scenarios. In Scenario 1, where migration rate does not change with current velocity, concentration of juveniles in the water is exclusively a function of current velocity: with low velocities a given amount of water that is flowing over a given area of the sediment receives a certain number of juveniles; with high current velocities the same amount of water will receive a lower number of juveniles because it flows faster over the same area of sediment, resulting in a lower concentration. The effect of lower concentrations in the water during spring tides is compensated by larger amounts of water that the collectors ‘filter’, so that, all else being constant,

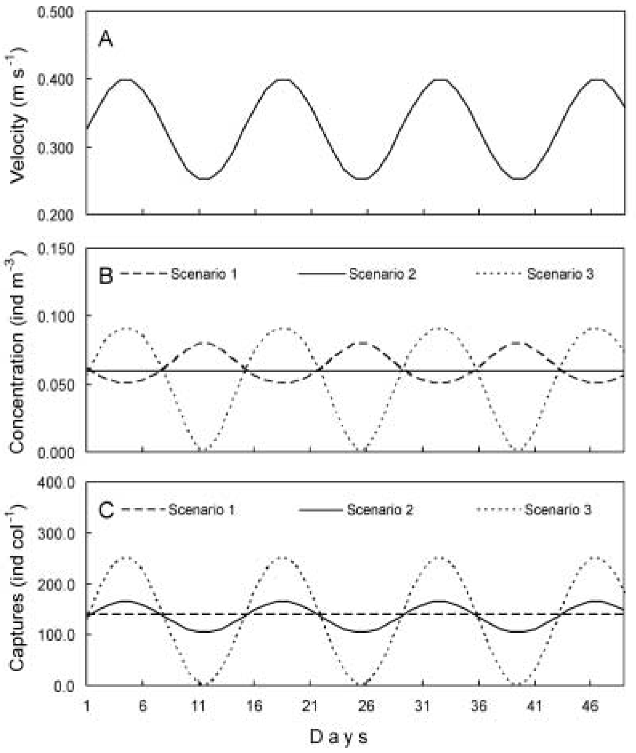

Figure 6. *Hydrobia ulvae.* (A) Average current velocity series used for input to the model; (B) simulated concentration in the water column; and (C) captures in the collectors for Scenarios 1, 2 and 3. See text for further explanation of Scenarios 1, 2 and 3.

both effects cancel out and the numbers of juveniles caught by the collectors do not change. In Scenario 2, where the migration rate was set to vary linearly with current velocity, the model shows a constant concentration in the water over time and a cyclic change in the numbers collected. The numbers captured by the collectors do not approach zero during neap tides contrary to the observations. The change in the captures during the spring/neap cycle is only due to the high current velocity during spring tides, which cause the anchored collectors to 'filter' greater volumes of water. Scenario 3 also shows a cyclic change in the captures, which now is caused by variations in concentration in the water. The captures in the collectors reach zero during the least amplitude tides. A verification of the validity of Scenario 3 can be made by referring to Figure 2, panels A and C. This figure shows that observed values at Station CN reached zero or very close to zero during the neap tides around days 137, 164 and 194, when tidal range was below 1.3 m. When tidal range during neap tides was over 1.3 m, around days 120, 148 and 180, observed values did not reach zero.

DISCUSSION

The present study constitutes the first account of a semi-lunar pattern of abundance of drifting *Hydrobia ulvae* and indicates that floating behaviour in these snails is more frequent during spring tides. Individuals smaller than 0.5 mm were not collected, and only 4% were smaller than 0.8 mm. The highest growth rates of *H. ulvae* reported in the literature are 0.033 mm d^{-1} (Bachelet & Yacine-Kassab, 1987). Considering that the average time the snails spent on the collectors was 1 d, it is extremely unlikely that veligers, with maximum sizes reaching 0.4 mm (Fish & Fish, 1974), could settle on the collectors directly from the plankton and grow to the sizes recorded in the present study. Therefore, the individuals recorded must be considered juveniles that engaged in rafting behaviour, and not veligers that settled from the plankton on the collectors. The behavioural and/or physical mechanisms that may account for such a pattern remain to a large extent unexplained. A former study of the migratory rhythms of juvenile molluscs in the Wadden Sea (Armonies, 1992) detected a diel pattern in *H. ulvae*, where the highest activity was recorded during the day, but failed to show any longer-trend period. Increasing evidence shows that intertidal and shallow subtidal animals respond to internal clocks synchronized with the tidal cycle, which control their level and type of activity (Palmer, 1995). Moreover, salinity, hydrostatic pressure and turbulence changes associated with the tide can control swimming reactions in these animals (e.g. Forward & Tankersley, 2001). The repertoire of floating-enhancing behaviours previously described for *H. ulvae* (Newell, 1962; Anderson, 1971; Fish & Fish, 1974) indicates that behavioural factors may be involved in the fortnightly pattern, but the extent to which these reactions are controlled by natural clocks or by responses to external stimuli is not known. In this respect it is noteworthy that both an internal rhythm and responses to water cover and light intensity have been demonstrated to affect the crawling behaviour of adult *H. ulvae* (Barnes, 1986).

Of the three modelled scenarios, Scenario 1 is clearly the most unrealistic. This scenario assumed that migration rate is independent of average current velocity and constant. This is what would be expected if the floating behaviour exhibited by juvenile *Hydrobia ulvae* during the flooding tide was due solely to an internal rhythm. The lack of fit between the results of the model, which predicts constant captures through time, and the cyclic nature of the observations clearly indicates that migration rate is not exclusively controlled by an internal mechanism. Therefore, migration rate must somehow be related to tidal amplitude and current intensity. Both Scenarios 2 and 3 predict cyclic captures. Under Scenario 2, the concentration of *H. ulvae* in the water does not change and the variation in captures is only due to a large amount of water that flows past the collectors during spring tides. Moreover, the amplitude of the predicted oscillations is low when compared with the observations. Scenario 3 seems to be more adjusted to the observed values since it shows higher amplitude oscillations and a decrease to zero during the lower amplitude tides, which are due to changes in concentration of juveniles in the water. The simulated sinusoidal current velocity function that was used in the model does not show the inequalities of current velocity depicted by true tides (compare Figure 2, panel C, with Figure 6, panel A). The fact that the number of *Hydrobia ulvae* actually captured in the collectors decreases very close to zero during extreme neap (tide range <1.3 m) but not so much during less extreme neap tides, indicates that there is some threshold average current velocity (and, therefore, tidal amplitude) value below which juvenile *H. ulvae* do not migrate to the water column. This low threshold, which is incorporated into Scenario 3, must be at a current velocity close to the one observed during extreme neap tides.

The positive correlation between abundance in the collectors and tidal range, as well as the results of the simulations, suggests three possible explanations for the observed pattern: (i) increasing turbulence during high amplitude tides, caused by stronger tidal currents, could re-suspend larger numbers of individuals in a purely passive pattern; (ii) increased active floating behaviour as a response to larger rates of pressure change during flood; or (iii) since population density in the Ria de Aveiro increases towards the upper intertidal zone (C.M. Barroso, unpublished data), neap high tides would not cover an important proportion of the population and the juveniles would be prevented from migrating to the water. All three explanations are consistent with Scenario 3 and with the existence of a minimum threshold in average current velocity and tidal range above which migration to the water occurs. The data on the size of snails, however, seems to invalidate explanation (i) above, since smaller snails were collected during neap tides at Station CN. Neither the prevalence of the different types of behaviours according to size or maturity class is sufficiently described in *Hydrobia ulvae*, nor is the influence of internal and external tide-synchronized controls described in gastropods. Therefore, further interpretation of the nature of the mechanisms that result in the pattern obtained in the present study is not possible.

Another consideration on the ecological significance of the floating behaviour of *Hydrobia ulvae* is the phase of the tide cycle where it takes place. The available studies indicate that floating occurs during the flood, but the sampling schedule adopted in the present study, which integrates settlement on the collectors during 2-day periods, cannot resolve differences between phases of the tide. Escape of local adverse conditions and colonization of new areas have been considered advantages of a post-metamorphic dispersal phase in benthic invertebrates lacking free-swimming larvae (Martel & Chia, 1991), while dispersal away from hatching areas may reduce intraspecific competition in dense populations of juveniles (Armonies, 1992). Floating behaviour can provide alternative food resources for *H. ulvae*, because these gastropods feed during the floating phase (Newell, 1962). Whichever the mechanisms or selective advantages that underlie the pattern of planktonic occurrence detected in the present study, such a clear pattern indicates a strong ecological significance. Although the proportion of the population that engages in floating during each spring/neap cycle has not been determined, the fortnightly periodicity revealed by the data also indicates that considerable dispersal of juvenile *H. ulvae* may take place over short time scales. This issue should be accounted for in studies of secondary production, as cautioned also by Armonies & Hartke (1995), since it may alter considerably the estimates of juvenile density at individual sampling sites. The use of artificial collectors of the type used in the present study provides an inexpensive and relatively easy way to investigate these processes in this group of animals.

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