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Short communication

Differences in spatial structures between juveniles and adults of the gastropod *Hydrobia ulvae* on an intertidal mudflat (Marennes–Oléron Bay, France) potentially affect estimates of local demographic processes

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Abstract

Spatial structures of juvenile and adult cohorts of the gastropod *Hydrobia ulvae* were investigated over a surface area of several km^2 in an intertidal mudflat at the end of the recruitment period. Three cohorts (average shell lengths of 3.9 ± 0.89 mm, 1.8 ± 0.43 mm and 1.1 ± 0.18 mm for cohorts I, II and III, respectively) were identified by a statistical analysis and their spatial distributions were characterised. Cohorts of juveniles (cohorts II and III) showed a patchy distribution pattern, whereas the cohort of adults (cohort I) was homogeneously distributed over the study area. These marked differences in spatial distribution of cohorts are likely to have a strong effect on estimates of local demographic processes, and hence of population dynamics.
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Keywords: Spatial structure; *Hydrobia ulvae*; Gastropod; Population structure; Large-scale; Intertidal mudflat

1. Introduction

Many benthic invertebrates inhabiting intertidal areas are characterised by high dispersal during larval and post-larval stages (Butman, 1987; Lane et al., 1985; Beukema and De Vlas, 1989; Armonies, 1992; Olivier et al., 1996; Ellien et al., 2000) and are exposed to strong physical disturbances (Hall, 1994). Such processes are likely to generate spatio-temporal heterogeneity that may affect population and community dynamics (Palmer et al., 1996; Bouma et al., 2001; Norkko et al., 2001). In addition, this heterogeneity is likely to limit our ability to infer large-scale processes from local information only (Hewitt et al., 1998; Thrush et al., 2000; Defeo and Rueda, 2002).

The gastropod *Hydrobia ulvae* is one of the most common species inhabiting European intertidal mudflats (Fish and Fish, 1974; Newell, 1979; Bachelet and

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Yacine-Kassab, 1987; Sauriau et al., 1989; Sola, 1996). Several studies have shown that density changes and population structure of this species result both from demographic processes and hydrodynamics (Fish and Fish, 1974; Armonies and Hartke, 1995; Barnes, 1998; Haubois et al., 2002). Particularly, the population structure of *H. ulvae* is strongly influenced by large-scale movements of individuals that may lead to spatio-temporal differentiation between distribution patterns of juveniles and adults (Armonies and Hartke, 1995; Haubois et al., 2002). Spatial data are thus necessary to characterise the emergent spatial structures and their potential effect on the local assessment of the population structure.

The objective of this study was therefore to characterise the large-scale spatial structures of juveniles and adults of *H. ulvae*. The distribution of *H. ulvae* densities was investigated at the end of the recruitment period by a systematic sampling over several square kilometres. A statistical analysis was used to separate the mixed juveniles and adults cohorts at each node of the sampling grid. Results were further analysed by experimental variograms to characterise spatial structures of juvenile and adult density distributions.

2. Materials and methods

2.1. Study area and sampling strategy

Brouage mudflat is located in the eastern part of the Marennes–Oléron Bay (46°25′ N, 1°10′ W), along the French Atlantic coast (Fig. 1). This bare intertidal mudflat is more than 5 km wide; the sediment consists of silt and clay particles (Gouleau et al., 2000) and the tidal range reaches 6 m during spring tide.

A systematic sampling plan was designed to investigate a 1.50 x 1.75 km^2 area (Fig. 1) which includes a cross-shore transect previously investigated (Haubois et al., 2002). Thirty sites, divided into six parallel transects (named a, b, c, d, e, f), were sampled in November 2001. Sampling sites 1 and 2 were situated in the upper mudflat and sites 3, 4 and 5 were situated in the middle mudflat. *Hydrobia ulvae*

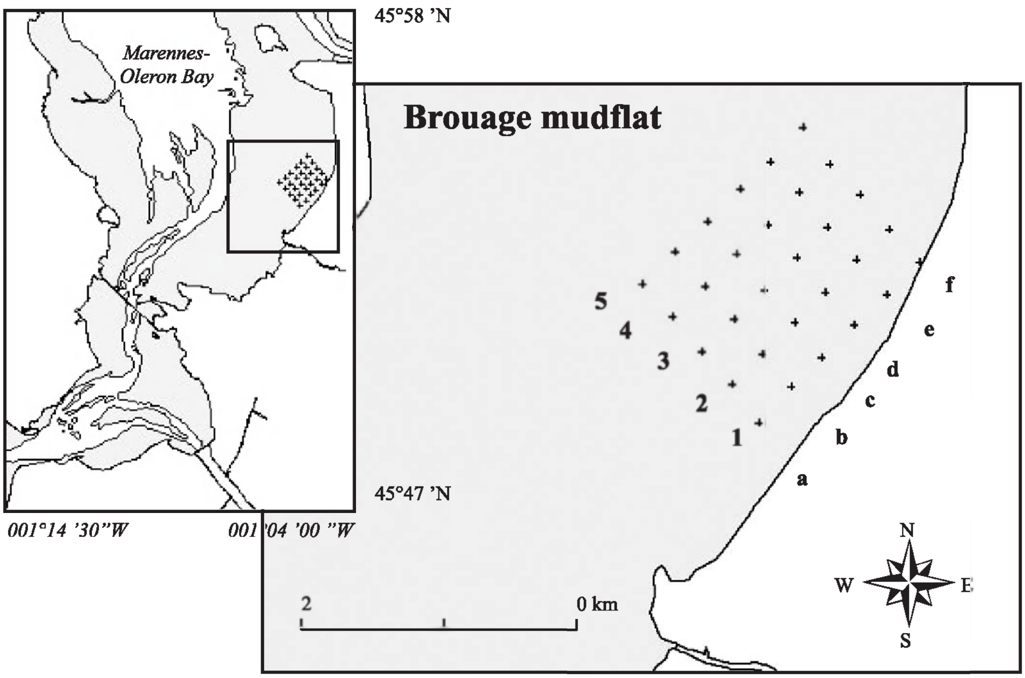

Fig. 1. Position of the sampling grid on Brouage mudflat (Marennes–Oléron Bay, France).

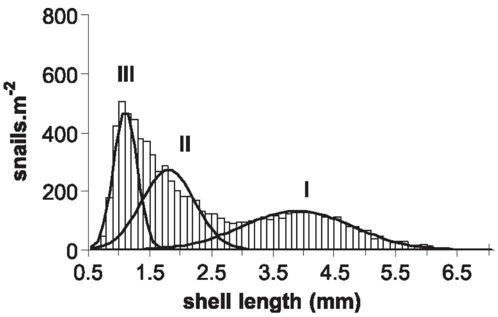

Fig. 2. Result of the cohort analysis performed on pooled data. Identified cohorts are labelled I, II and III.

was absent in the lower intertidal area and hence not sampled. Four random replicates (15 cm in diameter) were taken at each site within 1 m^2 of mud, and the top 5-cm layer of sediment was sieved through a 500-μm mesh. Individuals were sized and counted to estimate total density (snails m^{-2}) at each site.

2.2. Data analysis

Size-frequency distributions of the population were established for each site using 0.1-mm size class. A statistical analysis was then performed to separate the different cohorts (groups of individuals recruited at the same time). To obtain enough individuals to apply accurate statistics, data from all sites were pooled as though all samples belonged to the same population. The statistical analysis relies on the assumption that the size distribution of a cohort follows a gaussian pattern. The number of cohorts, $K=3$, was fixed a priori, based on previous results from the same area (Haubois et al., 2002). Three parameters were estimated for each cohort: μ_k (the mean), σ_k (the standard deviation) and p_k (the proportion of each cohort), with $k=1,\ldots,K$. Estimation of the K parameter vectors $\hat{\theta}_k=\{\hat{\mu}_k, \hat{\sigma}_k, \hat{p}_k\}$ was performed by minimising unconstrained maximum log-likelihood criteria, L_t (Hasselblad, 1966).

Table 1
Estimated parameters from cohort analysis

Cohorts	I	II	III
Mean size $\hat{\mu}_k$ (mm)	3.9	1.8	1.1
Standard deviation $\hat{\sigma}_k$ (mm)	0.89	0.43	0.18
Proportion $\hat{p}_k$ (dimensionless)	0.361	0.359	0.280
Estimated density $\hat{N}_k$ (snails m^{-2})	2944	2929	2285

As the 3 cohorts partially overlapped at the scale of the whole population (all sites pooled together), the proportions of individuals in each size-class belonging to the different cohorts were calculated. These proportions were then applied to the observed size-frequency distribution at each sampling site to

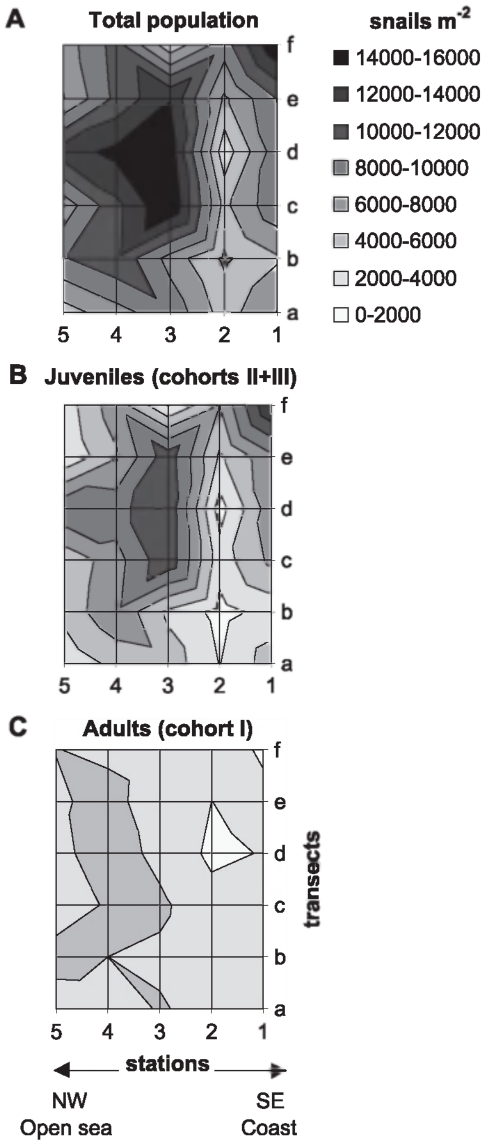

Fig. 3. Spatial distribution of *Hydrobia ulvae* in November 2001 on a sampling grid located in Brouage mudflat. (A) Spatial distribution of the total population densities (snails m^{-2}). (B) Spatial distribution of juvenile densities (cohort II+III). (C) Spatial distribution of adult densities (cohort I).

estimate locally the density of each of the three cohorts.

Spatial structures of cohorts were described by using experimental variograms (Legendre and Legendre, 1998). This method allows us to study the degree of dependence between two density estimates as a function of distance. The semi-variance, plotted as the ordinates, was thus calculated for each distance h:

$$\gamma_k(h) = \frac{1}{2n_k(h)} \sum_{\nu=1}^{n_k(h)} (\hat{N}_k(x_i + h) - \hat{N}_k(x_i))^2$$

where $n_k(h)$ refers to the number of pairs of estimated densities that corresponds to sites separated by the distance h; x_i refers to the sites ($i = 1, \ldots, 30$) and $\hat{N}_k(x_i)$ is the estimated density of cohort k at the site x_i. The semi-variance $\gamma_k(h)$ increases with h until 2 density estimates become independent. Then $\gamma_k(h)$ fluctuates randomly around a constant maximum value. The range of influence of the spatial structure is the distance where the semi-variance stops increasing.

3. Results

Results of the statistical analysis used to estimate K cohorts of individuals from the overall population are presented in Fig. 2 and Table 1 (estimated parameters of cohorts). The 3 identified cohorts were named I, II and III in the time order of their recruitment: cohort I corresponded to adult individuals and represented 36.1% of the total population; cohorts II and III corresponded to juveniles and represented 63.9% of the total population (35.9% and 28%, respectively).

The spatial distribution of the *H. ulvae* population showed two aggregates of high densities (Fig. 3A). The first one was located in the central part of the study area with maximum values of 16 071 and 15 081 snails m^{-2} at sites 3c and 3d, respectively. The second one was observed in the northern part of the upper mudflat from site 1c to site 1f, with densities in the range of 9535 to 15 714 snails m^{-2}. These structures were mainly due to juveniles (cohorts III + II) (Fig. 3B): their contribution to total density was 77% in the central aggregates (36% for cohort III and 41% for cohort II) and the northern aggregate consisted mainly of individuals from cohort III (Fig. 4). Estimated densities of adult individuals (cohort I) varied in the range of 1654 to 5181 snails m^{-2} with a mean value of 3225 ± 971 snails m^{-2} (Fig. 3C). Higher densities were recorded in the lower half of the sampled area (between stations 3 and 5).

Linear correlation among cohort density estimates was performed and showed that densities of juvenile cohorts (III and II) were spatially correlated ($P < 0.01$), and hence they were pooled for the semi-variance calculations. In contrast, the densities of cohorts III + II (juveniles) and I (adults) were not significantly correlated ($P = 0.39$). Results of the semi-variance calculations (Fig. 5) suggest that spatial structures were different: the maximum (= sill) of the semi-variance was reached for a mean distance of 500 m

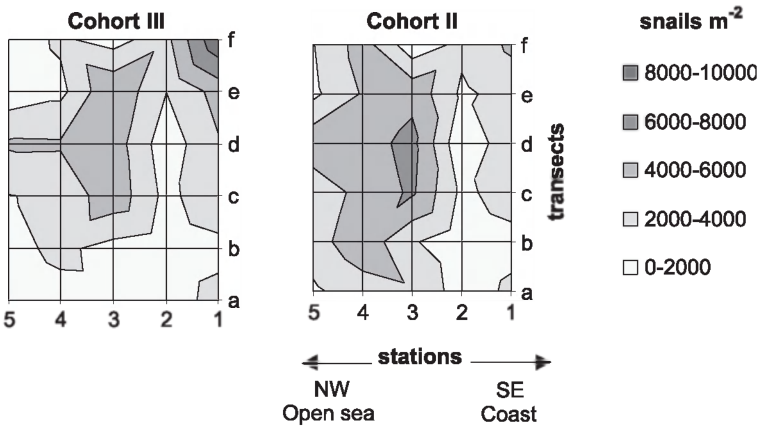

Fig. 4. Spatial distribution of cohorts III and II and their densities in November 2001.

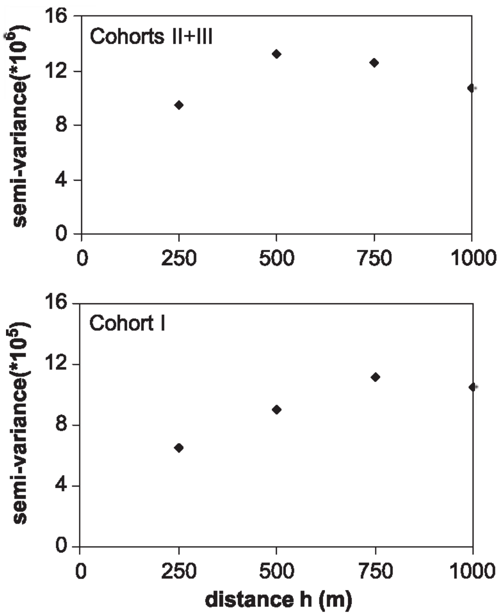

Fig. 5. Experimental variograms for juveniles (cohort II + III) and adults (cohort I).

for juveniles ($\hat{N}_{II+III}(x_i)$) while it was reached for a mean distance of 750 m for adults ($\hat{N}_I(x_i)$). In addition, the sill was about 10 times greater for juveniles than for adults, suggesting that the spatial distribution of adults was more homogeneous than for juveniles.

4. Discussion

The present study of the spatial distribution of juveniles and adults of *H. ulvae* complements the seasonal survey of population dynamics performed by Haubois et al. (2002) which pointed out that the local population structure of *H. ulvae* (at any single point over the mudflat) is strongly determined by large-scale movements of individuals. These movements generated a spatial differentiation in the density distribution of juveniles and adults at the scale of a cross-shore transect; spatial data were thus necessary to characterise the emergent spatial structures and their potential effect on the estimation of population demography and dynamics which is usually performed locally.

Based on the study of Haubois et al. (2002), we can determine the periods of recruitment of the 3 identified cohorts in the present work: cohort I was composed of individuals mostly recruited in 2000 and in the early summer of 2001; cohort II was composed of individuals recruited in late summer 2001, and cohort III was composed of the youngest individuals, which were recruited during autumn 2001. The analysis of the spatial distribution patterns of these cohorts indicated marked differences between juveniles and adults: the distribution of juveniles (cohorts II + III) was strongly aggregated whereas that of adults was more homogeneous (Figs. 3 and 5).

The fact that such differences in large-scale spatial structures exist precludes the possibility of inferring characteristics of the population structure from local information only. Indeed, the size-frequency distribution appears strongly influenced by the location of the sampling site. For example, in 3 sites separated by only a few hundred metres (Fig. 6), the total abundance of snails and the relative contribution to the 3 cohorts were found to be very different: at site 3d, in the centre of a patch, juveniles largely predominated while at site 5e, outside the patch, adults predominated. As those spatial structures resulted from indi-

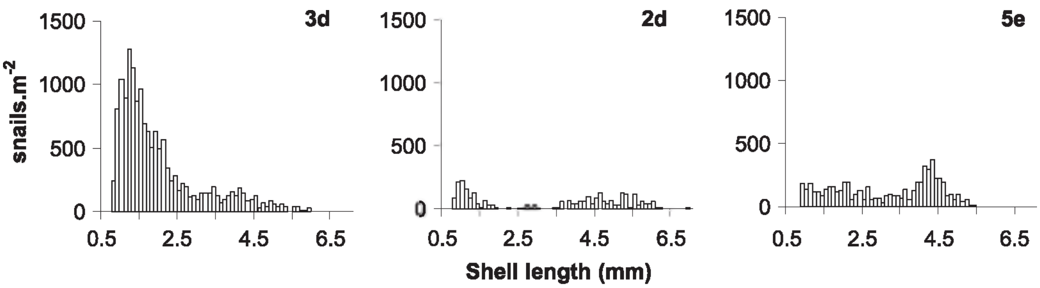

Fig. 6. Size-frequency distribution of *Hydrobia ulvae* at sites 3d, 2d and 5e in November 2001.

vidual functional responses to biological and physical processes, we conclude that (i) juveniles and adults respond differently to these underlying processes, and (ii) spatial structures are likely to exhibit spatio-temporal dynamics.

In conclusion, our study confirms the necessity of characterising and quantifying spatial structures as well as their dynamics, both for juveniles and adults, to obtain reliable estimates of demographic processes.

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