Journal of Experimental Marine Biology and Ecology 410 (2011) 87–100

Contents lists available at SciVerse ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Effect of vertical planktonic distribution of competent larvae on spat location in a soft-bottom intertidal zone: A case study for the softshell clam (*Mya arenaria*) and the blue mussel (*Mytilus edulis*)

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A R T I C L E   I N F O

Article history:
Received 19 May 2011
Received in revised form 14 October 2011
Accepted 15 October 2011
Available online 5 November 2011

Keywords:
Benthic distribution
Day/night cycle
Larvae
Mya arenaria
Mytilus edulis
Planktonic distribution

A B S T R A C T

Larval behavior and hydrodynamics may affect the vertical distribution of planktonic larvae and, in turn, spat location in the intertidal zone. This study describes the vertical profile of competent larvae in the water column and the distribution of spat on soft-bottoms, and quantifies the relationship between both distributions for the softshell clam (*Mya arenaria*) and the blue mussel (*Mytilus edulis*). Sampling was carried out in 2007 and 2008 along the coast of New Brunswick (Canada) in two tidally contrasted regions: Bay of Fundy (high tidal amplitude) and Northumberland Strait (low tidal amplitude). The planktonic larvae were collected with a pump at three depths. Spats were collected directly from the top layer of sediments as well as with two types of collectors. Sampling in the Bay of Fundy site took the day/night cycle into account. The distribution of planktonic larvae and spats in the intertidal zone was highly variable for both species. Overall, no general pattern in the larvae distribution was observed. The day/night cycle did not affect the distribution and abundance of planktonic larvae and spats. Only a few statistically significant relationships were observed between the abundance of spats in the intertidal zone and the abundance of planktonic larvae. Soft-bottom habitats are highly unstable and this characteristic may explain, in part, the absence of relationship between spat location and the vertical profile of planktonic larvae.

1. Introduction

Most marine benthic invertebrates have a complex life cycle that includes a planktonic larval stage and a benthic adult stage (Scheltema, 1986). Pre- and post-settlement processes are then important in determining population dynamics and the shape of coastal communities (Connell, 1985). The "supply-side ecology" approach championed during the 80s (Caffey, 1985; Connell, 1985; Gaines et al., 1985; Grosberg, 1982; Keough, 1983, 1984; Watzin, 1983) introduced various mechanisms influencing the larva before or during settlement that complemented classic post-settlement processes proposed earlier (e.g. dessication, competition, predation). The availability of competent larvae for settlement, which is influenced by many processes (Navarrete and Wieters, 2000; Rodriguez et al., 1993), affects settlement success and number of recruits (Caffey, 1985; Connell, 1985; Gaines et al., 1985; Grosberg, 1982; Minchinton and Scheibling, 1991; Miron et al., 1995).

The vertical position of larvae in the water column is mainly related to hydrodynamics and larval behavior (Ambrose et al., 1992; Armonies and Hellwig-Armonies, 1992; Butman, 1987; Dobretsov and Miron, 2001; Epifanio and Garvine, 2001; Hannan, 1984; Metaxas, 2001; Miron et al., 1995, 1996, 1999; Porri et al., 2007; Satumanatpan and Keough, 2001; Snelgrove et al., 1998; Woodin, 1986). Larvae may be neustonic (i.e. near the surface), suprabenthic (i.e. near the seafloor) or uniformly distributed in the water column. Vertical planktonic distribution of larvae may have an effect on spat location in the intertidal zone. The relationship between settled larvae and planktonic competent larvae in tidal systems, however, may be modulated by the shape of the tidal curve, which varies locally (Miron et al., 1995). Other hydrodynamic forces are also important in the intertidal zone (e.g. waves, turbulence, surface currents generated by winds). These forces have an effect on the behavior and distribution of planktonic larvae, and therefore, influence settlement (e.g. Armonies and Hellwig-Armonies, 1992; Hadfield, 1986; Porri et al., 2007). When currents are strong, larvae act as inert particles and are subject to passive transport (Butman, 1987). Larval habitat selection behavior is noticeable when currents are weak and is mainly observed near the settlement site, most often in the benthic boundary layer.

The relationship between the abundance of competent larvae in the water column and the number of settled larvae has been observed in various invertebrate species (e.g. Dobretsov and Miron, 2001; Hurlbut, 1991; Miron et al., 1995). These studies showed that, in relation to the intertidal level, there was a high correlation between the abundance of planktonic larvae and the abundance of recruits. Most of these studies, however, were carried out on sessile species that settle on hard-bottom surfaces. Soft-bottom environments have a different

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0022-0981/$ – see front matter
doi:10.1016/j.jembe.2011.10.019

dynamic since the sediment is unstable, may be easily eroded and expose endobenthic organisms to resuspension (Armonies, 1996; Armonies and Hellwig-Armonies, 1992; Butman, 1987; Commito et al., 2005; Emerson and Grant, 1991; Günther, 1992; Hunt, 2004; Lundquist et al., 2004; Matthiessen, 1960; Roegner et al., 1995; St-Onge and Miron, 2007; St-Onge et al., 2007; Turner et al., 1997).

The response of larvae to light can also influence settlement and recruitment. In bivalve species, veliger larvae are usually attracted to light (photopositive). They then tend to maintain themselves near the surface mainly to feed. Once competent, they become photonegative and tend to get closer to the seafloor to settle (Gallager et al., 1996; Thorson, 1950). Laboratory studies carried out to verify the effect of light on invertebrate larval behavior showed, for instance, that scallop (*Placopecten magellanicus*) larvae have a neustonic distribution during night time (Gallager et al., 1996; Manuel et al., 1996, 2000). This particular behavior was also observed in the field in stratified waters (Tremblay and Sinclair, 1988). Day/night cycle could therefore affect settlement by modifying the behavior of larvae (Gallager et al., 1996). Settlement during night time may, for instance, diminish predation on settling individuals compared to settlement during day time (Enright, 1977; Irvine, 1997).

The purpose of this study was to document (1) the vertical distribution of competent larvae in the water column and (2) the intertidal distribution of spats in a soft sediment habitat. This was carried out by sampling two bivalve species, *Mya arenaria* and *Mytilus edulis*, in two tidally contrasted regions. To examine the relationship between the vertical distribution of competent larvae in the water column and the distribution of spats in the intertidal zone, we tested the following hypotheses:

H1. The location of spats in the sediments is influenced by the vertical distribution of competent larvae in the water column;

H2. This relationship is influenced by the day/night cycle.

To explain the distribution of spats and juveniles in the intertidal zone, LeBlanc and Miron (2006) suggested that competent larvae of the softshell clam, *M. arenaria*, were distributed homogenously in the water column. Accordingly, the number of spats in the intertidal zone should increase from high to low intertidal level due to differences in immersion time (Miron et al., 1995). Thus, we predict that the number of spats will be higher in the low intertidal zone. However, that relationship could vary as a function of the strength of the tidal regime. A week tidal regime, for instance, could allow larvae to display a more active behavior and increased swimming abilities compare to larvae under a strong larval regime where they act more like inert particles. Habitat selection behavior could then modify distribution patterns. Finally, we predict that settlement for both species will be higher during night time since night time settlement should diminish predation compared to day time settlement.

2. Methods

2.1. Study sites and species

The study was carried out in 2007 and 2008 from mid-July to early-August off the coast of New Brunswick (Canada) in two highly contrasted tidal regions: the Bay of Fundy (high tidal amplitude) and the Northumberland Strait (low tidal amplitude) (Fig. 1). The Bay of Fundy is characterized by lunar semi-diurnal tides with a period of 12.4 h. Mean tidal height is 7 m. The Northumberland Strait has a complex tidal regime, with diurnal tides of 2.5 m at its western end and semi-diurnal tides at its eastern extremity. One site in each tidal region was chosen to describe the distribution pattern of planktonic larvae and spats in the sediments and the relationship between the two stages in the life cycle. Two bivalve species were used as proxies to study the relationship: the softshell clam (*M. arenaria*) and the blue mussel (*M. edulis*). The study sites were chosen based on the occurrence of a clam population and accessibility (LeBlanc and Miron, 2005, 2006) while trying to minimize physical differences (e.g. sediment characteristics) (LeBlanc and Miron, 2006). All sites were also strewn with mussel beds. In the Bay of Fundy, the sampling site was Blockhouse beach near the town of Saint Andrews. This site is a west-facing sheltered beach at the mouth of the Saint Croix River estuary that opens onto the Passamaquoddy Bay. The beach has an intertidal zone 500 m long. In the Northumberland Strait, the sampling site was Côte-à-Fabien in Kouchibouguac National Park (KNP). This site is a north-facing beach with a narrow intertidal zone of 45 m. Both sites are dominated by a high percentage of sand (≥60%) regardless of the intertidal level (Landry, 2010; LeBlanc and Miron, 2006). No spatial pattern emerged from both sites regarding organic matter content (Landry, 2010). Mean percentages in Kouchibouguac varied between 1.81% and 4.90% in 2007 and between 1.02% and 11.41% in 2008 (Landry, 2010). Mean organic matter content in Saint Andrews varied between 1.20% and 4.42% in 2007 and between 0.01% and 6.16% in 2008 (Landry, 2010).

The spawning period of the softshell clam is usually from June to September depending on the region (Ropes and Stickney, 1965). The softshell clam veliger metamorphoses into a pediveliger at around 170 μm (Aucoin et al., 2005). Peak abundance of blue mussel larvae occurs at the end of May (Aucoin et al., 2005). A second peak may be observed around mid-June. The veliger larva metamorphoses to a pediveliger larva at around 260 μm (Aucoin et al., 2005). At our study sites, spawning usually occurs at the beginning of July (LeBlanc and Miron, 2006).

The presence of larvae in each tidal region was monitored using 5 min plankton trawls (63 μm) every 3 days starting mid-June for both 2007 and 2008. Sampling started once softshell clam larvae were present in samples. Samples were taken at the beginning, middle and end of the softshell clam settling period which lasts approximately two weeks. The tidal pattern in Saint Andrews allowed us to conduct one sampling during day time and one sampling at night time on the same date. In 2007, sampling was carried out during the 1st, 7th and 14th day of the softshell clam settling period: KNP: 23 July, 30 July and 7 August; Saint Andrews: 26 July, 3 August and 12 August. Two sampling days were added for each site in 2008: KNP: 22 July, 24 July, 28 July, 31 July and 5 August; Saint Andrews: 28 July, 31 July, 4 August, 7 August and 11 August. Wind speed and direction data were gathered during the sampling periods for both sites from Environment Canada's website: (http://www.climat.meteo.gc.ca/climateData/canada_f.html).

2.2. Sampling design

2.2.1. Distribution of planktonic larvae

The vertical profile of planktonic competent larvae was described at high tide. A buoy was installed at low tide at the low intertidal watermark of each study site. At the following high tide, plankton samples were taken by boat at the buoy. The depth of the water column at high tide was 7.0 m at Saint Andrews and 2.5 m at Kouchibouguac. Plankton samples were collected by using a pump at three depths: near the surface, at mid-depth and near the seafloor. The mid-depth samples were pumped at 3.5 m below the surface at Saint Andrews and 1.25 m at Kouchibouguac. Water was pumped for 11 minutes at each depth to collect 400 L of water. The water was sieved through a 63 μm plankton net to collect the larvae. Nine samples were taken at each sampling session (3 water depths × 3 replicates). Samples were put in 500 ml bottles and preserved with 70% ethanol. Larvae were identified, measured, and counted using an *Olympus CK40* reversed microscope.

2.2.2. Distribution of spat in the intertidal zone

Three intertidal levels were used at each site to collect spats: high, mid and low intertidal levels. Each level was chosen to have an