Trophic cues promote secondary migrations of bivalve recruits in a highly dynamic temperate intertidal system

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Abstract. Post-settlement dispersal is a key process in the recruitment of bivalves. To assess the role of such secondary migrations and to identify potential associated triggers, we conducted an in situ sampling survey during the summer recruitment period on the bivalve assemblages of a coarse-sediment temperate tidal habitat in the Chausey archipelago (Normandy, France). The dynamics of drifters were studied using three types of settler traps (for example, bedload, pelagic, and sinking transports), and we monitored both the abiotic (hydrological and hydrodynamic conditions) and the trophic (nano- and pico-sized particulate organic matter [POM]; fatty acid composition of POM and sediment organic matter [SOM]) environmental parameters. Such an approach allows the discrimination of passive migration (due to sediment erosion by tidal currents and waves) from active migration (related to recruit behavior). Secondary migrations were observed in 25 bivalve taxa, and these mainly involved decreasing abundances of Mytilidae, Nuculidae, Semelidae, Mactridae, and Lucinidae individuals on the study site, highlighting the crucial role of these processes in highly dynamic coastal benthic assemblages. Surprisingly, the intense post-settlement dispersal observed at the end of the recruitment season was not synchronized with periods of high hydrodynamic stress but to a change in the structure of phytoplanktonic assemblages, particularly the nanoeukaryotic component. Such a response by bivalve recruits to a trophic pelagic cue—triggering secondary migrations—could result from an increased demand for energy required for active migratory behavior.

Key words: behavior; bivalve recruits; post-settlement dispersal; secondary migrations; trophic environment.

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INTRODUCTION

In temperate coastal areas, most benthic marine invertebrates exhibit a bentho-pelagic life cycle with a larval stage dispersing into the water column (Thorson 1950) followed by settlement and metamorphosis into a post-larva in the benthic boundary layer (BBL). Recruitment is usually defined as the colonization of the substrate through the early stages of life, but that term does not correspond to a precise event in the life cycle (Booth and Brosnan 1995). As summarized in Pineda et al. (2009), the recruitment of benthic invertebrates is controlled by larval pool dynamics, larval transport, and settlement and post-settlement processes. Larval and
settlement dynamics have been widely studied, and many reviews include descriptions of such processes (Pechenik 2006, Pineda et al. 2010, Thiyagarajan 2010). However, mechanisms explaining the high short-term variability observed in the early phase of benthic life are poorly understood. Post-settlement mechanisms correspond to the terminal phase of recruitment, and they include mortality of early juveniles due to several causes (Hunt and Scheibling 1997), particularly abiotic factors for intertidal species (Jenewein and Gosselin 2013). Another significant factor is the migration of recently metamorphosed post-larvae, also called the secondary migration (Günther 1992a, Olivier and Retière 2006), but this has been little studied in coarse-sediment habitats.

Mortality of post-larvae can be due to predation by shrimp (Beukema and Dekker 2005) or crabs, and this predation may be responsible for nearly 25% of the decreases in post-larval cockle abundance (Jensen and Jensen 1985). High densities of adults lead to a greater predator presence and therefore an increased predation pressure on younger individuals (Richards et al. 2002). Abiotic factors like heat and desiccation can also cause mortality of the smallest individuals, leading individuals to escape habitats with suboptimal conditions (Jenewein and Gosselin 2013). Post-settlement survival is strongly dependent on the previous pelagic larval experience and involves latent effect mechanisms (Pechenik 1990, 2006), which can, for example, originate from delays in metamorphosis (Bishop et al. 2006, Martel et al. 2014) or not finding suitable habitat according to the desperate larva theory (Knight-Jones 1953, Wilson 1953, Tremblay et al. 2007). The combined effects of settlement and post-settlement processes drastically affect the renewal potential of bivalve populations: Pedersen et al. (2008) estimated that losses of 85% and 71% in abundance between the number of larvae and post-larvae and between the number of post-larvae and adults, respectively. Surprisingly, post-settlement losses are often imprecisely attributed only to mortality, thus minimizing the role of secondary migrations in the recruitment process (Armonies 1994a). In fact, net emigration could cause an overestimation of juvenile mortality (Gosselin and Qian 1997).

Secondary migrations have been observed for many bentho-planktonic invertebrate species including bivalves (Butman 1987) and can strongly modify initial primary settlement patterns (Olivier et al. 1996b, Olivier and Retière 1998, Huxham and Richards 2003). Secondary migrations couple both passive (i.e., related to BBL flows) and active behavioral processes, like the production/secretion of byssus/mucus or crawling (Sigurdsson et al. 1976, Butman 1987, Caceres Martinez et al. 1994, Olivier et al. 1996a, Nakamura 2013). These mechanisms have been observed in coastal habitats with fine sediment (Beukema and de Vlas 1989, Armonies and Hellwig-Armonies 1992, Günther 1992a, Armonies 1994a, Olivier et al. 1996a, Olivier and Retière 1998, Hiddink et al. 2002) and hard substrates (Hunt and Scheibling 1996, Navarrete et al. 2008, Le Corre et al. 2013), but a small number of studies have focused on the highly dynamic systems of coarse sediments (Hewitt et al. 1997), which are known to be dominated in biomass by bivalve species (Cugier et al. 2010). Some of these studies led to the establishment of different theories describing post-settlement migration processes, such as the theory of primary-secondary settlement (Bayne 1964, Buchanan and Babcock 1997) or the continuous settlement-relocation model (Navarrete et al. 2015). These theories have sometimes been challenged (McGrath et al. 1988, Caceres Martinez et al. 1994, Lasiak and Barnard 1995), and evidence indicates that mechanisms of post-settlement migrations are strongly dependent on the considered environments, on the life history, and on the traits of the species studied. As proposed by Pilditch et al. (2015), secondary migrations, via exchanges of post-settlers, could dominate connectivity between spatially distinct communities, therefore influencing the maintenance of biodiversity.

The aim of our work was to monitor secondary migrations in a coarse-sediment habitat in a highly dynamic tidal environment using fine-scale environmental and trophic characterization to quantify and understand these processes for different bivalve species. We hypothesized that the trophic condition, particularly the quality of food used by young settlers, is a major component explaining the post-settlement dispersal behavior of all bivalves present in this habitat (more than 20 bivalve species). The metabolic requirements of the young bivalve stages depend mainly on lipids accumulated from food (Webb...
and Chu 1983). Three major fatty acids from microalgae (eicosapentaenoic acid (20:5n-3), docosahexaenoic acid (22:6n-3), and arachidonic acids (20:4n6)), called essential fatty acids (EFA), modulate the performance and survival of young bivalve stages by their energetic, structural, and bioactive roles (Langdon and Waldock 1981, Delaunay et al. 1993, Bassim et al. 2015). To our knowledge, the composition and nutritional quality of food have never been tested as a factor acting on the secondary migrations observed in bivalves. To test this hypothesis, we simultaneously monitored (1) dynamics of secondary migrations in bivalves, including bedload, resuspension, and advection transport into the water column, and (2) the detailed characterization of the environment including abiotic variables (i.e., hydrodynamic stress, temperature, salinity) and the pelagic and benthic trophic resources characterized by fatty acid composition and flow cytometry analyses.

Materials and Methods

Study site
The Chausey archipelago, located in the Normand-Breton Gulf in the western part of the English Channel, has a spring tidal range of ~14 m and an area of 4500 ha including rocky shore and sand flats; thus, it is a highly fragmented environment (Godet et al. 2009). Such fragmentation generates highly variable physical conditions at local spatial scales and several soft-bottom benthic habitats with high species richness (Godet et al. 2010). The Chausey tidal flats are mostly the coarse sand Glycymeris glycymeris (dog cockle) habitat (Godet et al. 2009). Especially in Sound’s fishing reserve (48°52’49.8” N 1°49’56.6” W), where we positioned the experimental area (Fig. 1) to avoid any disturbances related to recreational activities such as hand-rake fishing. Within this area, three contiguous experimental plots (20 × 20 m) designated A, B, and C were delineated at approximately mean neap low water, between 2.9 and 3.5 m above the chart datum.

Recruit traps
To collect recruits migrating by bedload transport on the sediment, drifting in suspension into the water column, or sinking from the water column, we developed benthic, pelagic, and epibenthic traps (Fig. 1). Traps were deployed in the field from June to October 2014 for experimental periods that were approximately synchronized with spring tide periods (three-week intervals; 16 June, 26 June, 16 July, 9 August, 26 August, 12 September, and 10 October 2014). Four traps of each type were set in a regular pattern on each of the three experimental plots for a total of 36 traps; the order of trap type was randomly selected, and they were distant by a minimum of 5 m (Fig. 1). Benthic and epibenthic traps were set for 48 h and pelagic traps for 24 h for each experimental sampling period to limit desiccation and loss of plankton net contents.

Within the BBL, benthic traps collect recruits that are moved by bedload transport as well as those sinking or drifting in the water column (Todd et al. 2006). Each trap is made of food grade polyvinyl chloride (PVC) and includes an outer tube permanently buried into the sediment that contains an inner tube with a circular collar. The collar consists of a circular plate attached to the inlet of the inner tube (internal diameter, 8 cm; total length, 80 cm; 50.3 cm² opening area) to avoid sediment scouring at the opening. The resulting length/opening ratio of 10 prevents any bivalve resuspension from the tube (Butman 1987, 1990, Armonies 1994a). Outer tubes were deployed one month before the start of the experiment to avoid potential BBL disturbances related to their placement. To quantify sinking recruits from the water column to the sediment, epibenthic traps were used. These protruded 15 cm from the sediment surface and are similar to the benthic traps but with no collar on the inner tube. Pelagic traps, which collect only recruits drifting into the water column (advection transport), are similar to those used by Günther (1992a, b) and Armonies (1994a, b) on tidal flat of the Wadden Sea. Briefly, the plankton net has a 20 cm diameter circular opening (314.1 cm² opening area) rotating freely on one axis and positioned 30 cm above the bottom. The 250 μm square mesh size of the net ensures that all bivalve post-larvae whose size at metamorphosis is on average 300 μm are sampled (Bayne 1971). After 48 h or 24 h of operation, depending on trap type, trap contents were fixed in 4% buffered formalin until laboratory analysis.
Fig. 1. Top: location and map of the study area on the Chausey archipelago showing the study area and the three experimental plots. Middle: position of recruit traps (triangles, pelagic traps; circles, benthic traps; and cylinders, epibenthic trap). Traps were placed in a regular pattern, but the order of trap type was randomly chosen. Bottom: diagram of recruit trap designs and associated transport types.
**Bivalve recruitment dynamics**

Bivalve meiofauna recruitment dynamics were monitored from June to October 2014 during each of the experimental sessions by the random sampling of eight sediment cores (5.4 cm diameter × 1 cm depth; 0.018 m² total surface area) within each of the experimental plots. The resulting material was sieved on 200-µm-square and 1000-µm-square meshes to keep only the meiobenthic fraction (between 200 and 1000 µm) and fixed in 4% buffered formalin before further processing.

**Monitoring of environmental parameters**

One YSI 6920 V2 multiparameter probe (YSI, Yellow Springs, Ohio, USA) was deployed from May to October 2014 next to the three experimental plots at 10 cm above the seabed. This probe recorded sea temperature (°C), salinity, chlorophyll a concentration estimated by fluorescence (µg/L), turbidity (NTU), and pressure for water level every 5 min. Due to instrument maintenance, data were not acquired between 1 August and 8 August. Sediment temperature at 2 cm in the sediment was simultaneously recorded using one HOBO U23 Pro v2 data logger (Onset, Bourne, Massachusetts, USA) per experimental plot.

Sediment grain-size distribution was determined before, during, and at the end of the season (13 May, 29 July, and 10 October 2014). Sediment samples were desalted and dried before being sieved through a sieve column (25 sieves log-spaced between 0.063 and 4 mm), and mass was determined for each fraction. Median grain size was computed with GRADISTAT (Blott and Pye 2001).

**Hydrodynamic parameters**

Currents were measured near the seabed with an acoustic doppler velocimeter (ADV) (Nortek Vector; 128 s bursts at 8 Hz every 30 min). The ADV measured 2.6 cm³ between 0.16 and 0.20 m above the seabed, depending on seabed elevation changes during the deployment. Waves were measured with an acoustic wave and current profiler-acoustic surface tracking (AWAC-AST) 1 MHz (Nortek), which was looking upward from the seabed; wave bursts were recorded for 8.5 min every 30 min. The AWAC also measured current profiles every 10 min in 0.5 m cells with the first cell centered at 1.25 m above the seabed. Sediment transport rates (kg m⁻¹·s⁻¹) and combined current-wave bed shear stresses (N/m²) were computed with the program Sedtrans05 using the Van Rijn method (Neumeier et al. 2008). The following parameters were used for the computation: current from the ADV (mean of each burst), waves from the AWAC-AST, salinity and temperature from the YSI multiparameter logger, and a median grain size of 0.353 mm (median of nine sediment samples). The bedform prediction by Sedtrans05 for once step was used as initial value for the next time-step.

**Trophic environment**

Four replicates of four liters of surface water were sampled 2 h after low tide at about 200 m from the study site (48°52’51.5” N 1°50’09.8” W) during each sampling period for fatty acid composition determination and for flow cytometry analyses. Water was pre-filtered through a 20-µm mesh to focus on nano- and pico-sized particulate organic matter (Möynihan et al. 2016), which are preferentially retained by early bivalve recruits (Raby et al. 1997). Samples were then filtered onto precombusted GF/F 47-mm microfiber filters (Whatman) that were stored at −80°C until fatty acid analyses. Samples of 4.5 mL of prefiltred seawater were fixed with glutaraldehyde (Sigma-Aldrich Saint-Louis, Missouri, USA) at a final concentration of 0.1%. The samples were frozen and stored at −40°C until flow cytometry analysis.

For each of the seven sampling periods, four sediment cores (5.4 cm diameter × 1 cm depth; 0.018 m² total surface area) were collected at low tide then stored individually in a Petri dish and frozen at −80°C until fatty acid composition analysis in order to quantify benthic trophic environment.

**Laboratory procedures**

To extract benthic recruits, we used the elutriation methods modified from Burgess (2001) on material originating from sediment cores and benthic traps (Toupoint et al. 2016). Briefly, sediment was mixed with a Ludox solution (HS-40) in a vial placed on a vortex for 5 min. The organic matter, including the meiofauna, was separated from the sediment by density difference. The supernatant, which contains the meiofauna, was then rinsed with pure water onto a 200-µm sieve. Bivalve recruits were sorted and identified to the lowest taxonomic level under a dissecting microscope, and only settled metamorphosed individuals...
were considered as recruits. For this study, postlarvae were considered as settled metamorphosed individuals, characterized by well-visible dissoconch shell and/or gills.

Flow cytometry samples (4.5 mL of prefiltred seawater fixed with glutaraldehyde) were analyzed by using an Epic Altra flow cytometer (Beckman Coulter, Fullerton, California, USA) and v1.2b Expo32 software (Beckman Coulter, Fullerton, California, USA). Two planktonic communities were determined according to their autofluorescent properties using a 488-nm laser (blue): eukaryotes and cyanobacteria, which fluoresce at 690 nm (red) with chlorophyll and 570 nm (orange) with phycoerythrin, respectively. Plastic microbeads were added to each sample (1 and 2 μm microspheres, plain YG Fluoresbrite, Polysciences) to distinguish size classes in each group: picoplankton (0.2–2 μm) and nanoplanckton (2–20 μm) (Tremblay et al. 2009).

Lipids associated with sediment and water-column samples were extracted according to the modified Bligh and Dyer (1959) method (Meziane et al. 2006). The detailed analysis method is described in Moynihan et al. (2016). Fatty acid methyl esters were quantified by gas chromatography analysis (Varian 3800) using a flame ionization detector. Fatty acid identification was performed using coupled gas chromatography–mass spectrometry (Varian 450-GC; Varian 220-MS) and comparison of gas chromatography retention times with those of standards (SupelcoVR). An internal standard (23:0) was used to determine the proportion of each fatty acid. The proportion of EFA is used as an indicator of the nutritional quality of pelagic (POM) and benthic trophic resources (SOM).

Statistical analyses

For each of the dominant taxa of bivalve recruits, turnover (day$^{-1}$) was calculated as the ratio between the number of organisms collected per surface area of the sediment trap opening for one day (Nb·m$^{-2}$·day$^{-1}$) and the recruit density on the sediment (Nb/m$^2$) for the same period, as described in Armonies (1994b). Temporal variations in benthic and pelagic turnover were tested using a repeated-measures ANOVA followed by Tukey’s HSD post hoc test once assumptions of homoscedasticity and normality had been verified with Levene and Shapiro–Wilk tests, respectively.

Environmental variables exhibiting relevant temporal variations were selected to perform linear regression analyses. These variables serve thus as proxies for four major classes of environmental parameters: the plankton assemblage structure (picoeukaryotes, nanoeukaryotes, and bacteria concentrations), the quantity and quality of the food resource (EFA content of POM and sediment, chlorophyll a concentration), the abiotic environment (water temperature, turbidity, and suspended matter concentration), and the hydrodynamic stress (sedimentary transport). As expected for an offshore archipelago with no freshwater input, salinity was found to be stable throughout the season and was therefore not used in multiple regression analyses. Several proxies were tested during preliminary analyses, and these 10 variables were selected for their relevance as environmental proxies. Moreover, since multiple regression analyses are sensitive to the correlations between the explanatory variables, particular attention was paid during the choice of these variables to limit collinearity phenomena (see Appendix S1).

A forward stepwise regression model was computed to reveal variables that best explain variations in migration turnover. Linear regression analyses were performed on trap turnover for dominant species that showed significant variations of turnover migration according to the repeated-measures ANOVA. These analyses were carried out with Minitab v16.2.1 (Minitab; www.minitab.com).

Results

Bivalve recruit migrations

No bivalve recruits were found in the epibenthic traps for either of the experimental periods sampled (17 June and 27 August). Valanko et al. (2010) also noted that the abundance of sinking bivalve recruits is negligible compared to those of bedload and advection transports (e.g., benthic and pelagic traps). Because abundances of sinking recruits were negligible in our experiment, we do not present the results here.

Recruits of 30 bivalve taxa were identified during this survey and five dominant taxa (Fig. 2) accounted for 74% of the total abundances; these included Mytilidae spp. (Mytilus edulis (Linnaeus, 1758), M. galloprovincialis (Lamarck, 1819), and...
their hybrids), *Abra tenuis* (Montagu, 1803), Mac-tridæ spp., Nuculidæ spp., and *Loripes orbiculatis* (Poli, 1791). The identi-
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experimental zones (Table 1), attesting that studied processes affected the whole habitat.

The meiobenthic abundance of Mytilidae spp. is too variable to show significant temporal variability (Fig. 2), but the minimum number of recruits (109 ± 32 ind/m²) was observed in October (Table 1). This low value occurred along with significant increases in benthic ($P < 0.001$) and pelagic ($P < 0.001$) migration turnovers, respectively, that is, by 2.8- and 4.6-fold between September and October (Table 2, Fig. 2).

The abundance of A. tenuis in the meiofauna showed significant temporal variation (Table 1), with the mean passing from 41 ± 18 ind/m² in late August to 200 ± 36 ind/m² in September ($P < 0.001$), followed by a decrease of 55% in October (Fig. 2). The benthic turnover did not vary significantly for this species (Table 2), with an average value of 1.44 d⁻¹. Pelagic turnover showed significant temporal variation (Table 2), with high values in October (Fig. 2). However, as also observed in L. orbiculatus and Mactridae spp., the pelagic turnover values were negligible (less than 10% of benthic turnover).

As was the case for A. tenuis, the meiobenthic abundance of Mactridae spp. peaked significantly in late August and September (Fig. 2), reaching 600 ± 114 ind/m² ($P < 0.001$), then decreased strongly (by 88%). Again, this corresponded to a significant increase in benthic turnover, which grew by 11-fold (from 0.3 d⁻¹ to 3.6 d⁻¹) between September and October (Table 2).

An average abundance of 109 ± 39 ind/m² in meiobenthic recruits of Nuculidae spp. was measured during the entire monitoring season (Fig. 2), with a higher but nonsignificant peak in August (188 ± 48 ind/m²; Table 1). Benthic turnover showed significant temporal variations, with a September maximum of 2.0 d⁻¹, while pelagic turnover significantly increased at the

Table 1. Results of the repeated-measures ANOVA performed on meiofauna recruit abundance.

| Meiofauna recruits and variables | df | MS  | $F$  | $P$  |
|---------------------------------|----|-----|------|------|
| Mytilidae spp.                  |    |     |      |      |
| Date                            | 6  | 51641| 3.60 | 0.028|
| Zone                           | 2  | 48095| 3.36 | 0.070|
| Error                          | 12 | 14333|      |      |
| A. tenuis                      |    |     |      |      |
| Date                            | 6  | 14375| 9.81 | <0.001|
| Zone                           | 2  | 141  | 0.1  | 0.908|
| Error                          | 12 | 1466 |      |      |
| Mactridae spp.                 |    |     |      |      |
| Date                            | 6  | 186905| 18.91| <0.001|
| Zone                           | 2  | 13624| 1.38 | 0.289|
| Error                          | 12 | 9884 |      |      |
| Nuculidae spp.                 |    |     |      |      |
| Date                            | 6  | 4524 | 1.42 | 0.283|
| Zone                           | 2  | 3342 | 1.05 | 0.379|
| Error                          | 12 | 3177 |      |      |
| L. orbiculatus                 |    |     |      |      |
| Date                            | 6  | 4918 | 1.82 | 0.210|
| Zone                           | 2  | 1277 | 0.44 | 0.657|
| Error                          | 12 | 2932 |      |      |

*Note: Significant differences ($P < 0.05$) are indicated in bold.*

Table 2. Results of the repeated-measures ANOVA (A) benthic turnover, and (B) pelagic turnover.

| Turnover and species | Variables | df | MS | $F$  | $P$  |
|----------------------|-----------|----|----|------|------|
| (A) Benthic turnover |           |    |    |      |      |
| Mytilidae spp.       | Date      | 6  | 15.750| 248.52| <0.001|
| Zone                | 2         | 0.094| 1.49 | 0.265|
| Error               | 12        | 0.063|      |      |
| A. tenuis            | Date      | 5  | 3.48 | 0.68 | 0.651|
| Zone                | 2         | 8.187| 1.59 | 0.251|
| Error               | 10        | 5.147|      |      |
| Mactridae spp.       | Date      | 6  | 4.950| 6.82 | 0.002|
| Zone                | 2         | 1.386| 1.91 | 0.190|
| Error               | 12        | 0.725|      |      |
| Nuculidae spp.       | Date      | 6  | 1.186| 4.32 | 0.015|
| Zone                | 2         | 0.283| 1.03 | 0.386|
| Error               | 12        | 0.274|      |      |
| L. orbiculatus       | Date      | 6  | 95.54| 30.79| <0.001|
| Zone                | 2         | 2.984| 0.96 | 0.412|
| Error               | 12        | 3.123|      |      |
| (B) Pelagic turnover |           |    |    |      |      |
| Mytilidae spp.       | Date      | 6  | 0.672| 27.62| <0.001|
| Zone                | 2         | 0.005| 0.20 | 0.825|
| Error               | 12        | 0.024|      |      |
| A. tenuis            | Date      | 5  | 0.043| 3.57 | 0.041|
| Zone                | 2         | 0.011| 1.00 | 0.402|
| Error               | 10        | 0.011|      |      |
| Mactridae spp.       | Date      | 6  | 0.009| 4.00 | 0.020|
| Zone                | 2         | 0.002| 1.00 | 0.397|
| Error               | 12        | 0.022|      |      |
| Nuculidae spp.       | Date      | 6  | 0.406| 6.20 | 0.004|
| Zone                | 2         | 0.184| 2.81 | 0.100|
| Error               | 12        | 0.065|      |      |
| L. orbiculatus       | Date      | 5  | 0.005| 1.00 | 0.465|
| Zone                | 2         | 0.005| 1.00 | 0.402|
| Error               | 10        | 0.005|      |      |

*Note: Significant differences ($P < 0.05$) are indicated in bold.*
end of the season ($P = 0.004$), when the turnover value increased by four (1.2 d$^{-1}$; Table 2).

The meiofaunal abundance of *L. orbiculatus* (maximum $127 \pm 18$ ind/m$^2$) showed no significant temporal variation (Table 1), although there was a gradual decrease through the season with no individuals collected in October samples (Fig. 2). Benthic turnovers were lower than 2.0 d$^{-1}$ until September and increased significantly (by 8.5 times; $P < 0.001$) in October (Fig. 2). This turnover is probably underestimated since September recruit abundance was used to calculate trap turnover instead of the null abundance of *L. orbiculatus* on the sediment in October.

### Environmental data

The tidal currents are mainly directed to the northwest during both the flood and ebb tides since the Sound’s channel is oriented along this axis. Currents are toward southeast only when the water level is less than 3 m above the experimental area. Currents were fastest at high water and during spring tides. At the ADV’s position (0.16–0.20 m above the seabed), the highest measured velocity was 0.46 m/s, with high-water peak velocities averaging 0.35 m/s during spring tides and 0.25 m/s during neap tides. Currents are faster higher up in the water column, with surface velocities exceeding 0.70 m/s. Wave heights measured during the recruitment period were moderate, with a maximum wave height value ($H_{m0}$) of 0.50 m; 90% of measured $H_{m0}$ were less than 0.27 m, and $H_{m0}$ was less than 0.10 m 99% of the time. Wave height was strongly modulated by the tidal cycles because of the dissipation of wave energy in shallow water and the largest fetch at high tide, especially during spring tide periods. Waves were almost negligible during shallow-water periods, and no data were available for 12% of the deployment because the AWAC emerged during spring low tides. The study habitat is thus a zone that is weakly impacted by the swell, and hydrodynamic stress is mostly controlled by tidal currents.

Ten environmental variables were selected as proxies of environmental conditions (Table 3) to be used as explanatory variables of secondary migrations. Sea temperature, suspended matter, and turbidity are considered as proxies of physical environmental conditions. Sediment transport rate is related to hydrodynamic conditions in the BBL during the monitoring. We selected six variables to quantitatively and qualitatively characterize the trophic environment, including several components of the planktonic assemblages (bacterial, nanoeukaryote, and picoeukaryote concentrations), proportion of EFA of both benthic (SOM) and pelagic (POM), and chlorophyll $a$ concentration in the water column.

### Environmental trigger of post-settlement migrations

The results of our multiple regression analyses are presented in Table 4. Despite the special

### Table 3. Dynamics of environmental variables.

| Variable               | Type and sampling rate | Description of the indicator | Unit     | Mean        | Standard deviation | Min | Max |
|------------------------|------------------------|------------------------------|----------|-------------|--------------------|-----|-----|
| Environmental data     |                        |                              |          |             |                    |     |     |
| Temperature            | Continuous             | Mean (2 d of data)           | °C       | 18.3        | ± 1.1              | 16.3| 19.9|
| Suspended Matter       | Each sample period ($n = 7$) | Mean ($n = 4$)              | mg/L     | 4.4         | ± 2.2              | 2.1 | 8.3 |
| Turbidity              | Continuous             | Mean (2 d of data)           | NTU      | 1.2         | ± 0.4              | 0.8 | 2.1 |
| Hydrodynamic conditions|                        |                              |          |             |                    |     |     |
| Sediment transport     | Continuous             | Mean (2 d of data)           | g·m$^{-2}$·s$^{-1}$ | 2.5         | ± 1.2              | 1.1 | 4.3 |
| Trophic environment    |                        |                              |          |             |                    |     |     |
| Picoeukaryotes         | Each sample period ($n = 7$) | Mean ($n = 4$)              | nb/mL    | 15078       | ± 4309             | 9964| 20201|
| Nanoeukaryotes         | Each sample period ($n = 7$) | Mean ($n = 4$)              | nb/mL    | 4439        | ± 1028             | 3307| 6264|
| Total bacteria         | Each sample period ($n = 7$) | Mean ($n = 4$)              | nb/mL    | 975262      | ± 248565           | 986296| 1283848|
| POM EFA                | Each sample period ($n = 7$) | Mean ($n = 4$)              | %        | 4.34        | ± 1.87             | 0.72 | 6.82 |
| Benthos EFA            | Each sample period ($n = 7$) | Mean ($n = 4$)              | %        | 11.70       | ± 1.07             | 10.50 | 13.32 |
| Chl $a$                | Continuous             | Mean (2 d of data)           | µg/L     | 3.54        | ± 1.34             | 2.00 | 5.75 |

Notes: For each variable, the type of sampling (continuous recording or periodic sampling), description of the indicator, data unit, mean, standard deviation, and minimum/maximum value measured during the monitoring are indicated. Tendency indicates global data variations. Abbreviations are as follows: POM, particulate organic matter; EFA, essential fatty acid.
Table 4. Results of the forward stepwise multiple regression analyses performed on benthic and pelagic turnover as response variables and all factors as explanatory variables (n = 10).

| Turnover | Taxa | Factors | Regression step | Source of variance | R² | Adjusted R² | P-value | Regression slope |
|----------|------|---------|----------------|--------------------|----|-------------|---------|-----------------|
| Benthic turnover | Mytilidae spp. All (n = 10) | 1 | Nano | 0.548 | 0.458 | 0.057 | 0.00165 |
| | Macridea spp. All (n = 10) | 1 | Nano | 0.620 | 0.543 | 0.036 | 0.00098 |
| | L. orbiculatus All (n = 10) | 1 | Nano | 0.616 | 0.539 | 0.037 | 0.00431 |
| Pelagic turnover | Mytilidae spp. All (n = 10) | 1 | Nano | 0.592 | 0.510 | 0.043 | 0.00035 |
| | Nuculidae spp. All (n = 10) | 1 | Nano | 0.607 | 0.529 | 0.039 | 0.00028 |

Notes: Alpha to enter = 0.15. Highly significant values (P-values <0.05) are in bold.

attention paid to the collinearity of the explanatory variables, two of them (the proportion of EFA in the POM and the seawater temperature) were correlated ($r^2 = -0.81$; see Appendix S1 for more details). Collinearity can be problematic when several or all variable are interrelated (Scherrer 1984), but it was not the case here, suggesting that the statistical model is sufficiently robust. Furthermore, since these two variables were not selected by the stepwise method, it does not have any more effect on the interpretation of the results.

No significant correlations between the abundance of drifters and sediment transport rate were observed. In contrast, benthic and/or pelagic turnover for four out of five dominant taxa (Mytilidae spp., L. orbiculatus, Mactridae spp., and Nuculidae spp.) was strongly positively correlated to the concentration of nanoeukaryotes in the water column (adjusted $R^2 > 0.458$, $P < 0.05$). Benthic and pelagic turnover of Mytilidae spp. was weakly ($P = 0.057$) or significantly ($P = 0.043$) correlated to the nanoeukaryote concentration, respectively. For Mactridae spp. and L. orbiculatus, benthic turnovers were both correlated to nanoeukaryote concentrations ($P < 0.05$, adjusted $R^2 0.543$ and 0.539, respectively), whose variance accounts for more around 55% of that of benthic turnovers. For Nuculidae spp., only pelagic turnover was correlated to nanoeukaryote concentrations (adjusted $R^2 = 0.529$, $P < 0.05$). However, food quality indicators used in this study (EFA and chlorophyll a content) showed no significant correlation with the abundance of drifters.

**Discussion**

For the first time in a highly dynamic coarse-sediment habitat, we highlighted the major role of secondary migrations that is controlled mainly by trophic factors rather than passive hydrodynamics. We thus validate the hypothesis that bivalve post-settlement migrations depend on the trophic environment and include several species. However, this trophic trigger does not seem to be related to food quality as estimated by the sum of EFA and/or chlorophyll a content, but mostly to the microalgal composition of the seston. Increases in nanoeukaryote concentrations in the seston stimulated secondary migration behaviors. In oyster larvae (Crassostrea gigas), two picoplankton species (Nannochloris atomus and Stichococcus bacillaris), with mean cell size of about 2 μm, are easily ingested but poorly digested, resulting in poor larval development (Robert 1998). Thus, the less-digestible picoeukaryote species seem not to be an optimal food for young bivalve stages.

The trophic composition changes related to an increase of nanoeukaryote species could be linked to an increase in food quality that is not explained by higher EFA content, but by an increase in the microalga species that are more easily assimilated by bivalve settlers. Pelagic trophic characteristics related to the concentration of nanoeukaryotes in the water column and the secondary migration dynamics were closely related. We therefore propose the concept of a “trophic migration trigger” that is analogous to the “trophic settlement trigger” introduced by Toupoint et al. (2012) for larvae and validated through laboratory experiments by Jolivet et al. (2016): The settlement and recruitment success of M. edulis is promoted by a good quality of the trophic resource in accordance with the match/mismatch theory of Cushing (1990).

Recruitment success of marine invertebrates relies on the synchronization between larval development and food availability (Philippart et al. 2003, Bos et al. 2006, Ouellet et al. 2007). Successful metamorphosis and biological performance of juvenile marine invertebrates are strongly related...
to accumulated energy reserves directly controlled by trophic conditions (Phillips 2002, 2004, Wacker and Elert 2002, Thiagarajan et al. 2005, Pechenik 2006). Thus, both the trophic environment and physiological state strongly influence the survival rates and biological performance of young recruits and hence recruitment success (Gosselin and Qian 1997). We hypothesized that active migration behavior like byssal-pelagic drift, mucus production, and crawling could constitute a significant energetic cost for recently metamorphosed post-larvae. By producing byssus threads (Sigurdsson et al. 1976) or mucus (Nakamura 2015), post-larvae increase their drag and thus increase their drift, allowing an active control of the dispersal via resuspension even under low current conditions (Lundquist et al. 2004). To our knowledge, the energy costs of these behaviors have never been assessed. If drifting threads differ by their single filament structure, they are similar in diameter and structure to attachment threads (Lane et al. 1985, Gosling 2015) and are secreted by a specific gland that disappears during ontogeny. The energy expenditure of byssal thread secretion should be similar to that already estimated for attachment byssal threads, which represents up to 15% of the total energy budget of bivalve adults (Griffiths and King 1979, Hawkins and Bayne 1985). With regard to this expected energy cost, the induction of active behaviors leading to post-settlement migrations should directly relate to the pelagic trophic environment. Nanoeukaryotes can constitute more than 75% of the bivalve diet, as demonstrated by Lindeque et al. (2014) in the Western English Channel. Sonier et al. (2016) also observed retention rates for nanoeukaryotes of up to 60%, and Strohmeier et al. (2012) calculated retention rates up to 90% for particles with a mean size of 20 μm. In addition, the ratio of eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA), two EFA, is an indicator of the relative amount of diatoms and dinoflagellates in the water column (Nelson et al. 2001, Phleger et al. 2002). This ratio remained stable throughout the experimental period (June–October; 1.8 ± 0.4), including the time of the major secondary migration event. Thus, it can be concluded that only a variation in the amount of nanoplanckton in the water column and the group of microalgae will induce migration mechanisms. All these studies show the ability for bivalves to assimilate nanoeukaryotes at the post-larval/juvenile stage to use as fuel for energy-consuming drifting. Recruits thus should migrate when their main food sources are dominant in the environment to limit the energy risk associated with this behavior.

**Massive migration event**

The dominant species associated with the coarse-sediment habitats are able to disperse mostly through bedload transport at the post-larval stage, that is, mussels (Mytilidae spp.), surf clam (Mactridae spp.), nut clam (Nuculidae spp.), and *Loripes orbiculatus*. They show massive migrations during autumn, as attested by the huge increases in benthic and, to a lesser extent, pelagic turnovers, and can thus be considered as migratory species. The maximum turnover values observed here (15.5 d$^{-1}$ or 108.5 week$^{-1}$) are up to 10 times greater than those assessed by Arnornies (1994b) in the fine-mud tidal flats of the Wadden Sea (11 week$^{-1}$). Although it is difficult to compare benthic and pelagic turnover data due to the differences in trap efficiencies, only *Mytilidae* spp. and *Nuculidae* spp. exhibited high pelagic turnover ratios compared to the other dominant species collected. The benthic turnover values were much higher than pelagic values, suggesting that migrations mainly resulted from bedload transport, with the exception of *Mytilidae* spp. and *Nuculidae* spp., which likely also use saltation and resuspension migration strategies.

The massive autumnal migration coincides with a drastic decrease in recruit abundance in the sediment, which could originate from three sources: cohort growth, mortality, and/or emigration. The five dominant migratory species are not associated with the studied habitat (*Glycymeris glycymeris* coarse sands) and are not found in the macrofaunal assemblages at this site (Godet et al. 2010, Toupoint et al. 2016). We can therefore exclude cohort growth as a potential source of the observed meio-benthic abundance decrease, and we thus considered only mortality and migration. In the same habitat, Toupoint et al. (2016) showed great differences in spatiotemporal patterns of meio- and macrofaunal fractions for several taxa by comparing control areas with those disturbed by recreational hand-rake fishing. These authors suggested large recolonization events on disturbed areas through secondary migrations. In addition, because local
dispersal is probably more important than mortality to explain spatial and temporal patterns in bivalve abundance (Norkko et al. 2001), we suggest that most decreases in recruit abundance observed on the seabed should result from emigration out of the study habitat that is not compensated by the new recruit settlement rather than from mortality. Furthermore, 75% of the bivalve species collected in this habitat, representing more than 95% of the total number of benthic recruits, were migrating either by bedload or pelagic transport during the recruitment period, attesting to the almost universal nature of secondary migrations for bivalves belonging to coarse-sediment habitats and their crucial impact on recruitment dynamics.

Adult–recruits interactions can greatly influence local recruitment as shown by Thrush et al. (2000) on the intertidal bivalve *Macomona liliana* due to increased mortality and/or secondary migrations and by Olivier et al. (1996a). Although macrobenthic assemblages associated with our studied site were not characterized during this study, Godet (2008) described finely the associated intertidal *Cerastoderma edule* coarse sands found on the Chausey archipelago. Such low diversified assemblage (species richness = 27, Shannon index = 1.4) is dominated, in terms of abundance, by polychaete species mainly belonging to the Cirratulidae family (*Caulleriella* sp. and *Cirriformia tentaculata*, ≈2000 ind/m²) and by oligochaetes (≈1000 ind/m²), whereas abundances of the dominating bivalve species *C. edule* were low at ≈10 ind/m². As dominant migratory taxa belong to either low (*G. glycymeris* coarse sands) or high (*Abra tenuis* muddy fine sands) intertidal areas, we exclude the impact of intraspecific competition on migration dynamics but consider that interspecific adult–recruits interactions could occur. Flach (1992) and Volkenborn and Reise (2007) have emphasized that bioturbating engineer species such as the lugworm *Arenicola marina* destabilize the sediment with subsequent negative impacts on the recruits’ abundances, so we cannot exclude potential influence of the deposit-feeding Cirratulids or oligochaetes on recruits’ migrations. However, due to the very low abundances of large species as *A. marina* and *C. edule* on this habitat as well as the suddenness of the secondary migration event observed here, we consider that post-settlement migrations should not be primarily attributable to interspecific interactions but to pelagic trophic influence.

**Active post-settlement migrations**

Because megatidal conditions generate strong tidal currents, we expected a major role of BBL flows in secondary bivalve migrations. As already emphasized by Bouma et al. (2001) on exposed tidal flats, the initial patterns of recruitment as well as the resuspension of recruits are strongly influenced by the hydrodynamic stress. The number of drifters is related to shear stress kinetics, proving the importance of passive migration processes in such environments (Emerson and Grant 1991, Turner et al. 1997, Olivier and Retière 1998). Because coarser sediments have a higher shear stress level, due to wave exposures and/or to tidal currents, we also expected a greater dominant role of passive vs. active (due to behavior) migrations. Surprisingly, our work shows a strong decoupling between the dynamics of bivalve post-settlement dispersal and those of sediment transport. Commoto et al. (1995) and Turner et al. (1997) also observed a weak correlation between passive sediment transport and *Macomona liliana* dispersal, with higher numbers of migrating recruits than expected according to hydrodynamic stress. According to Norkko et al. (2001), such field results could result from some particular behavior allowing the bivalve recruits to control their own dispersal in a coarse-sediment habitat. However, there is a shear stress threshold above which any behavior has no effect on the control of the migration, especially during windy periods or storms, when all the surficial sediment can be eroded (Emerson and Grant 1991, Hunt and Scheibling 1996). Although swell is the dominant factor in the morphodynamic evolution of soft intertidal sediment areas (Le Hir et al. 2007), our study site was quite protected from waves, and that could explain why passive migration is quite limited.

**Ecological roles of active secondary migrations**

According to Godet et al. (2009), the dominant migratory species in our study originate from areas other than the local *Cerastoderma edule* habitat. In the Chausey islands, mytilids colonize the rocky shores, and sandy mussel beds are rare and restricted to mussel farming zones in the eastern part of the archipelago (Godet et al.
2009), *Nucula nucleus* and *Spisula ovalis* are associated with coarse and heterogeneous sediments of the lower intertidal and shallow subtidal zones (Bensettiti et al. 2004, Godet et al. 2009, 2010). *Loripes orbiculatus* is a typical inhabitant of fine sands colonized by *Zostera marina* seagrass located in the low intertidal and the shallow subtidal zone of the Chausey islands (Bensettiti et al. 2004, Godet 2008). Considering the high rates of benthic turnover observed in situ, we hypothesize that after an initial settlement in the *C. edule* habitat, all these migratory species undergo massive secondary dispersal during autumn to return to habitats preferred by adult populations. Validation of this hypothesis would require the simultaneous monitoring of secondary settlement during autumn on the adult habitats. The coarse sediments of the *C. edule* beds should thus constitute a primary settlement habitat, validating the theory of primary–secondary settlement developed by Bayne (1964): Mussel larvae initially settle on filamentous substrates, and post-larvae would reach the adult mussel beds of the rocky shores by bysso-pelagic drifting. However, we broaden the original theory to include mytilids on soft-bottom habitats as suitable areas for the primary mussel settlement. Settlement on the soft substrate rather than on filamentous or rocky substrate must then represent a significant fitness gain for recruits to justify the cost of active secondary migration and the risk of not finding rocky substrate at the time of secondary settlement. Several advantages can be proposed to explain this primary colonization of soft-bottom by hard-bottom species that are associated with the possibility of burial into the sediment, decreasing the predation risk (Ens et al. 1996, Griffiths and Richardson 2006), and the occurrence of natural biofilms that can act as settlement cues (Bao et al. 2007, Hadfield 2011) or as a source of food (Yeager et al. 1994). Even though secondary settlement on hard substrates was not studied here, the nearby presence of mussel beds (Godet 2008, Fournier et al. 2012) might indicate that mussel post-larvae originating from soft tidal sediments can sustain local mussel populations through secondary dispersal.

*Spisula* spp. and *Nucula nucleus*, which normally inhabit the lower tidal and subtidal areas, colonize a much shallower habitat at the larval stage. Mechanisms for the seasonal dispersal of *Macoma balthica*, especially autumnal and winter migrations, have been well known for three decades (Beukema and de Vlas 1989, Gunther 1991), with the primary settled post-larvae migrating from their nursery zone in shallow levels of the low intertidal flats. According to Beukema and de Vlas (1989) various factors could explain such secondary settlement on the lower zone, including lower growth rates associated with shorter filtration times and immersion stress, higher rates of parasite infection at the upper end of the foreshore, and lower survival at higher levels. Desiccation and heat may also induce recruits to migrate to the lower intertidal zone (Jenewein and Gosselin 2013). Conversely, areas of higher bathymetric levels could constitute preferred primary settlement zones due to lower densities of predators (Reise 1985) and to more suitable hydrodynamic conditions. Larvae would thus initially settle preferentially in calm high tidal flats and redistribute through secondary migrations to more dynamic zones in deeper habitats (Dobretsov and Wahl 2008).

Migrating patterns observed in *A. tenuis* contrast with previously described species: The moderate and highly variable benthic turnovers (1.5 d⁻¹) suggest more diffuse and non-oriented transport processes. In fact, this species is aplanic—it has direct development, that is, a very short or absent primary pelagic dispersal phase (Holmes et al. 2004)—and colonizes high muddy tidal flats located at the interface with the *C. edule* habitat. Resuspension mechanisms of *A. tenuis* recruits would therefore not correspond to a secondary migration but rather to a primary dispersal mechanism to extend the areal distribution. Hence, these migrations would not be necessarily oriented or controlled by any trigger.

While passive secondary migrations result from abiotic disturbance, that is, hydrodynamic stress, especially during sediment erosion conditions, active migrations occur to prevent contact with predators (Frid 1989), desiccation stress (Jenewein and Gosselin 2013), and anthropogenic factors such as the presence of pollutants (Pridmore et al. 1991, 1992) or fishing activity (Toupance et al. 2016). Post-settlement migrations may also provide ecological strategies with no direct response to a disturbance. As described by the desperate larva theory (Knight-Jones 1953, Wilson 1953, Marshall and Keough 2003, Botello and
Krug 2006, Elkin and Marshall 2007) larvae of some species have the ability to delay their metamorphosis by several weeks if conditions are not advantageous to their settlement and may thus re-enter the water column after a first contact with unsuitable substratum. The duration of such a metamorphosis delay is limited by the energy reserves needed for metamorphosis and post-settlement development. According to this theory, after a delay of metamorphosis and an unsuccessful substrate search, a larva can metamorphose and settle on unsuitable substrata to preserve its survival chances during the post-settlement phase. Secondary migrations would then be a way for these larvae recruiting on unsuitable habitats to find more advantageous areas for their further development. This theory contradicts the member/vagrant concept proposed by Sinclair (1988), who considers that if larvae are exported outside a system, it constitutes a loss for the indigenous populations. Thus, the viability of a cohort depends mainly on the number of larvae retained within the system (Iles and Sinclair 1982) and not on the trophic environment.

Our work, focusing on secondary migrations in bivalves, strongly suggests a role of soft-bottom nursery habitats for rocky-shore species. Various factors may justify the role of nursery habitat based on seasonal migrations between high and low intertidal zones and on factors such as predation, hydrodynamics, and parasitism (Beukema and de Vlas 1989). Moreover, the nature of the substratum of particular habitats, such as filamentous substrata (Eyster and Pechenik 1988, Dobretsov and Wahl 2001) or bacterial biofilms (Satuito et al. 1995, Bao et al. 2007), promotes larval settlement by providing more accessible and adapted food resources for young stages. Microphytobenthos are important food sources for bivalves, especially for juveniles, particularly in estuarine intertidal mudflats (Sauriau and Kang 2000). The relationship between individual size and filtration rate of the youngest stages would explain the differences observed in balances between the phytoplankton and microphytobenthos diets (Herman et al. 2000), and therefore, different habitat preferences could explain secondary migrations from nursery areas.

Spatial segregation between young recruits and adults could also originate from intraspecific interactions such as competition or cannibalism. For example, ingestion of bivalve larvae by adults significantly reduces pelagic larva abundances (Borsa and Millet 1992, André et al. 1993, Lehane and Davenport 2004). Nursery recruitment areas distant from adult populations could therefore limit intraspecific competition and increase recruitment. Conversely, cannibalism may be an adult strategy to limit competition by controlling the arrival of new recruits and the expansion of the mussel band (Porri et al. 2008).

**Conclusion**

We highlight here the crucial role of active secondary migrations in coarse-sediment benthic assemblages for several bivalve species. We also show the ability of bivalves to undergo active migrations independently of hydrodynamic stress. We suggest that such migrations result from ontogenic changes in the habitat preference of recruits—switching from initial nursery zones to those of adult populations—and represent a crucial source of connectivity between natural habitats. Moreover, we validated the hypothesis that these active and controlled processes depend on the trophic environment, more specifically on peak abundances of nanoeukaryotes in the water column. Such temporal synchronization between secondary migrations and trophic resource dynamics could originate from energy expenditures associated with active migratory behavior as byssopelagic drift.

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LITERATURE CITED

André, C., P. R. Jonsson, and M. Lindegarth. 1993. Predation on settling bivalve larvae by benthic suspension feeders: the role of hydrodynamics and larval behaviour. Marine Ecology Progress Series 97:183–192.

Armonies, W. 1994a. Drifting meio- and macrobenthic invertebrates on tidal flats in Kônigshafen: a review. Helgoländer Meeresuntersuchungen 48:299–320.

Armonies, W. 1994b. Turnover of postlarval bivalves in sediments of tidal flats in Kônigshafen (German Wadden Sea). Helgoländer Meeresuntersuchungen 48:291–297.

Armonies, W., and M. Hellwig-Armonies. 1992. Passive settlement of Macoma balthica spotted on tidal flats of the Wadden Sea and subsequent migration of juveniles. Netherlands Journal of Sea Research 29:371–378.

Bao, W. Y., J. L. Yang, C. G. Satuito, and H. Kitamura. 2000. Evidence for two chemical cues? Marine Biology: An Annual Review 25:113–165.

Bassim, S., R. W. Chapman, A. Tanguy, D. Moraga, and R. Tremblay. 2015. Predicting growth and mortality of bivalve larvae using gene expression and supervised machine learning. Comparative Biochemistry and Physiology – Part D: Genomics and Proteomics 159:59–72.

Bayne, B. L. 1964. Primary and secondary settlement in Mytilus edulis (Mollusca). Journal of Animal Ecology 33:513–523.

Bayne, B. L. 1971. Some morphological changes that occur at the metamorphosis of the larvae of Mytilus edulis. Pages 259–280 in D. J. Crisp, editor. Proceedings of the Fourth European Marine Biology Symposium. Cambridge University Press, Cambridge, UK.

Bensettiti, F., F. Bioret, J. Roland, and J. P. Lacoste. 2004. “Cahiers d’habitudes” Natura 2000. Connaissance et gestion des habitats et des espèces d’intérêt communautaire. Page La documentation française. La Documen.

Beukema, J., and J. de Vlas. 1989. Tidal-current transport of thread-drifting postlarval juveniles of the bivalve Macoma balthica from the Wadden Sea to the North Sea. Marine Ecology Progress Series 52:193–200.

Beukema, J. J., and R. Dekker. 2005. Decline of recruitment success in cockles and other bivalves in the Wadden Sea: possible role of climate change, predation on postlarvae and fisheries. Marine Ecology Progress Series 287:149–167.

Bishop, C. D., M. J. Huggett, A. Heyland, J. Hodin, and B. P. Brandhorst. 2006. Interspecific variation in metamorphic competence in marine invertebrates: the significance for comparative investigations into the timing of metamorphosis. Integrative and Comparative Biology 46:662–682.

Bligh, E. G., and W. J. Dyer. 1959. A rapid method of total lipid extraction and purification. Canadian Journal of Biochemistry and Physiology 37:911–917.

Blott, S. J., and K. Pye. 2001. Gradistat: a grain size distribution and statistics package for the analysis of unconsolidated sediments. Earth Surface Processes and Landforms 26:1237–1248.

Booth, D. J., and D. M. Brosnan. 1995. The role of recruitment dynamics in rocky shore and coral reef fish communities. Advances in Ecological Research 29:309–385.

Borsa, P., and B. Millet. 1992. Recruitment of the clam Ruditapes decussatus in the Lagoon of Thau, mediterranean. Estuarine, Coastal and Shelf Science 35:289–300.

Bos, O. G., C. J. M. Philippart, G. C. Cadée, and J. Van Der Meer. 2006. Recruitment variation in Macoma balthica: a laboratory examination of the match/mismatch hypothesis. Marine Ecology Progress Series 320:207–214.

Botello, G., and P. J. Krug. 2006. “Desperate larvae” revisited: Age, energy and experience affect sensitivity to settlement cues in larvae of the gastropod Alidria sp. Marine Ecology Progress Series 312:149–159.

Bouma, H., P. P. De Vries, J. M. C. Duiker, P. M. J. Herman, and W. J. Wolff. 2001. Migration of the bivalve Macoma balthica on a highly dynamic tidal flat in the Westerschelde estuary, The Netherlands. Marine Ecology Progress Series 224:157–170.

Buchanan, S., and R. Babcock. 1997. Primary and secondary settlement by the Greenshell mussel Perna canaliculus. Journal of Shellfish Research 16:71–76.

Burgess, R. 2001. An improved protocol for separating meiofauna from sediments using colloidal silica sols. Marine Ecology Progress Series 214:161–165.

Butman, C. A. 1987. Larval settlement of soft-sediment invertebrates—the spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamical processes. Oceanography and Marine Biology: An Annual Review 25:113–165.
Butman, C. A. 1990. Sediment-trap experiments on the importance of hydrodynamical processes in distributing settling invertebrate larvae in near-bottom waters. Journal of Experimental Marine Biology and Ecology 134:37–88.

Caceres Martinez, J., J. A. F. Robledo, and A. Figueras. 1994. Settlement and post-larvae behaviour of Mytilus galloprovincialis: field and laboratory experiments. Marine Ecology Progress Series 112:107–118.

Committ, J. A., S. F. Thrush, R. D. Pridmore, J. E. Hewitt, and V. J. Cummings. 1995. Dispersal dynamics in a wind-driven benthic system. Limnology and Oceanography 40:1513–1518.

Delaunay, F., Y. Marty, J. Moal, and J. F. Samain. 1993. The effect of monospecific algal diets on growth and fatty acid composition of Pecten maximus (L.) larvae. Journal of Experimental Marine Biology and Ecology 173:163–179.

Dobretsov, S., and M. Wahl. 2001. Recruitment preferences of blue mussel spat (Mytilus edulis) for different substrata and microhabitats in the White Sea (Russia). Hydrobiologia 445:27–35.

Dobretsov, S., and M. Wahl. 2008. Larval recruitment of the blue mussel Mytilus edulis: the effect of flow and algae. Journal of Experimental Marine Biology and Ecology 355:137–144.

Elkin, C., and D. J. Marshall. 2007. Desperate larvae: influence of deferred costs and habitat requirements on habitat selection. Marine Ecology Progress Series 355:143–153.

Emerson, C. W., and J. Grant. 1991. The control of soft-shell clam (Mya arenaria) recruitment on intertidal sandflats by bedload sediment transport. Limnology and Oceanography 36:1288–1300.

Ens, B. J., E. J. Bunschke, R. Hoenkstra, J. B. Hulscher, M. Kersten, and S. J. De Vlas. 1996. Prey choice and search speed: Why simple optimality fails to explain the prey choice of Oystercatchers Haematoopus ostralegus feeding on Nereis diversicolor and Macoma baltica. Ardea 84A:73–89.

Eyster, L. S., and J. A. Pechenik. 1988. Attachment of Mytilus edulis L. larvae on algal and byssal filaments is enhanced by water agitation. Journal of Experimental Marine Biology and Ecology 114:99–110.

Flach, E. C. 1992. Disturbance of benthic infauna by sediment-rewarming activities of the lugworm Arenicola marina. Netherlands Journal of Sea Research 30:81–89.

Fournier, J., N. Desroy, A. Ehrhold, E. Autret, C. Ordier, and A.-L. Janson. 2012. Cartographic biosédimentaire des fonds subtiliaux de l’archipel de Chausey. Programme HEIMA. Rapport final.

Frid, C. L. J. 1989. The role of recolonization processes in benthic communities, with special reference to the interpretation of predator-induced effects. Journal of Experimental Marine Biology and Ecology 126:163–171.

Godet, L. 2008. L’évaluation des besoins de conservation d’un patrimoine naturel littoral marin: l’exemple des estrangs meubles de l’archipel de Chausey. Museum national d’histoire naturelle – MNHN, Paris, France.

Godet, L., J. Fournier, N. Toupoint, and F. Olivier. 2009. Mapping and monitoring intertidal benthic habitats: a review of techniques and a proposal for a new visual methodology for the European coasts. Progress in Physical Geography 33:378–402.

Godet, L., P. Le Mao, C. Grant, and F. Olivier. 2010. Marine invertebrate fauna of the Chausey archipelago: an annotated checklist of historical data from 1828 to 2008. Cahiers de Biologie Marine 51:147–165.

Gosling, E. 2015. Reproduction, settlement and recruitment. Pages 157–202 in Marine bivalve molluscs. Second edition. Wiley Blackwell, Hoboken, New Jersey, USA.

Gosselin, L. A., and P. Y. Qian. 1997. Juvenile mortality in benthic marine invertebrates. Marine Ecology Progress Series 146:265–282.

Griffiths, C. L., and J. A. King. 1979. Energy expended on growth and gonad output in the ribbed mussel Aulacomya ater. Marine Biology 53:217–222.

Griffiths, C. L., and C. A. Richardson. 2006. Chemically induced predator avoidance behaviour in the burrowing bivalve Macoma balthica. Journal of Experimental Marine Biology and Ecology 331:91–98.

Gunther, C. P. 1991. Settlement of Macoma balthica on an intertidal sandflat in the Wadden Sea. Marine Ecology Progress Series 76:79–79.

Gunther, C. P. 1992a. Dispersal of intertidal invertebrates: A strategy to react to disturbances of different scales? Netherlands Journal of Sea Research 30:45–56.

Gunther, C. P. 1992b. Settlement and recruitment of Mya arenaria L. in the Wadden Sea. Journal of Experimental Marine Biology and Ecology 159:203–215.

Hadfield, M. G. 2011. Biofilms and marine invertebrate larvae: What bacteria produce that larvae use to
choose settlement sites. Annual Review of Marine Science 3:453–470.

Hawkins, A., and B. Bayne. 1985. Seasonal variation in the relative utilization of carbon and nitrogen by the mussel *Mytilus edulis*: budgets, conversion efficiencies and maintenance requirements. Marine Ecology Progress Series 25:181–188.

Herman, P. M. J., J. J. Middelburg, J. Widdows, C. H. Lucas, and C. H. R. Heip. 2000. Stable isotopes as trophic tracers: combining field sampling and manipulative labelling of food resources for macrobenthos. Marine Ecology Progress Series 204:79–92.

Hewitt, J. E., R. D. Pridmore, S. F. Thrush, and V. J. Cummings. 1997. Assessing the short-term stability of spatial patterns of macrobenthos in a dynamic estuarine system. Limnology and Oceanography 42:282–288.

Hiddink, J. G., R. P. Kock, and W. J. Wolff. 2002. Active pelagic migrations of the bivalve *Macoma balthica* are dangerous. Marine Biology 140:1149–1156.

Holmes, S. P., R. Dekker, and I. D. Williams. 2004. Population dynamics and genetic differentiation in the bivalve mollusc *Abra tenuis*: aplanic dispersal. Marine Ecology Progress Series 268:131–140.

Hunt, H. L., and R. E. Scheibling. 1996. Physical and biological factors influencing mussels *Mytilus edulis* settlement on a wave-exposed rocky shore. Marine Ecology Progress Series 142:135–145.

Hunt, H. L., and R. E. Scheibling. 1997. Role of early post-settlement mortality in recruitment of benthic marine invertebrates. Marine Ecology Progress Series 155:269–301.

Huxham, M., and M. Richards. 2003. Can postlarval bivalves select sediment type during settlement? A field test with *Macoma balthica* (L) and *Cerastoderma edule* (L). Journal of Experimental Marine Biology and Ecology 288:279–293.

Iles, T. D., and M. Sinclair. 1982. Atlantic herring: stock discreteness and abundance. Science 215:627–633.

Jenewein, B. T., and L. A. Gosselin. 2013. Ontogenetic shift in stress tolerance thresholds of *Mytilus trossulus*: effects of desiccation and heat on juvenile mortality. Marine Ecology Progress Series 481:147–159.

Jensen, K. T., and J. N. Jensen. 1985. The importance of some epibenthic predators on the density of juvenile benthic macrofauna in the Danish Wadden Sea. Journal of Experimental Marine Biology and Ecology 89:157–174.

Jolivet, A., R. Tremblay, F. Olivier, C. Gervaise, R. Sonier, B. Genard, and L. Chauvaud. 2016. Validation of trophic and anthropic underwater noise as settlement trigger in blue mussels. Scientific Reports 6:33829.

Knight-Jones, E. 1953. Laboratory experiments onregariousness during setting in *Balanus balanoides* and other barnacles. Journal of Experimental Biology 30:584–598.

Lane, D., A. Beaumont, and J. Hunter. 1985. Byssus drifting and the drifting threads of the young postlarval mussel *Mytilus edulis*. Marine Biology 84:301–308.

Langdon, C. J., and M. J. Waldock. 1981. The effect of algal and artificial diets on the growth and fatty acid composition of *Crassostrea gigas* spat. Journal of the Marine Biological Association of the United Kingdom 61:431–448.

Lasiak, T. A., and T. C. Barnard. 1995. Recruitment of the brown mussel *Perna perna* onto natural substrata: a refutation of the primary/secondary settlement hypothesis. Marine Ecology Progress Series 120:147–154.

Le Corre, N., A. L. Martel, F. Guichard, and L. E. Johnson. 2013. Variation in recruitment: differentiating the roles of primary and secondary settlement of blue mussels *Mytilus spp*. Marine Ecology Progress Series 481:133–146.

Le Hir, P., Y. Monbet, and F. Orvain. 2007. Sediment erodability in sediment transport modelling: Can we account for biota effects? Continental Shelf Research 27:1116–1142.

Lehane, C., and J. Davenport. 2004. Ingestion of bivalve larvae by *Mytilus edulis*: experimental and field demonstrations of larviphagy in farmed blue mussels. Marine Biology 145:101–107.

Lindeque, P. K., A. Dimond, R. A. Harmer, H. E. Parry, K. L. Pemberton, and E. S. Fileman. 2014. Feeding selectivity of bivalve larvae on natural plankton assemblages in the Western English Channel. Marine Biology 162:291–308.

Lundquist, C. J., C. A. Pilditch, and V. J. Cummings. 2004. Behaviour controls post-settlement dispersal by the juvenile bivalves *Austrovenus stutchburyi* and *Macomona liliana*. Journal of Experimental Marine Biology and Ecology 306:51–74.

Marshall, D. J., and M. J. Keough. 2003. Variation in the dispersal potential of non-feeding invertebrate larvae: the desperate larva hypothesis and larval size. Marine Ecology Progress Series 255:145–153.

Martel, A. L., R. Tremblay, N. Toupoint, F. Olivier, and B. Myrand. 2014. Veliger size at metamorphosis and temporal variability in prodissocochoil II morphometry in the blue mussel (*Mytilus edulis*): potential impact on recruitment. Journal of Shellfish Research 33:443–455.

McGrath, D., P. A. King, and E. M. Gosling. 1988. Evidence for the direct settlement of *Mytilus edulis* larvae on adult mussel beds. Marine Ecology Progress Series 47:103–106.

Meziane, T., F. D’Agata, and S. Y. Lee. 2006. Fate of mangrove organic matter along a subtropical
estuary: small-scale exportation and contribution to the food of crab communities. Marine Ecology Progress Series 312:15–27.

Moynihan, M. A., P. Barbier, F. Olivier, N. Toupoint, and T. Meziane. 2016. Spatial and temporal dynamics of nano- and pico-size particulate organic matter (POM) in a coastal megatidal marine system. Limnology and Oceanography 61: 1087–1100.

Nakamura, Y. 2013. Secretion of a mucous cord for drifting by the clam Meretrix lusoria (Veneridae). Plankton and Benthos Research 8:31–45.

Nakamura, Y. 2015. Mucous-cord secretion for drifting by the clam Meretrix lusoria (Veneridae) under varying light/dark and submergence/exposure conditions. Plankton and Benthos Research 10:18–25.

Navarrete, S. A., B. R. Broitman, and B. A. Menge. 2008. Interhemispheric comparison of recruitment to intertidal communities: pattern persistence and scales of variation. Ecology 89:1308–1322.

Navarrete, S. A., J. L. Largier, G. Vera, F. J. Tapia, M. Parragüé, E. Ramos, J. L. Shinen, C. A. Stuardo, and E. A. Wieters. 2015. Tumbling under the wave: wave-modulated settlement of intertidal mussels and the continuous settlement-relocation model. Marine Ecology Progress Series 520:101–121.

Nelson, M. W., B. D. Mooney, P. D. Nichols, and C. F. Phleger. 2001. Lipids of Antarctic Ocean amphipods: food chain interactions and the occurrence of novel biomarkers. Marine Chemistry 73:53–64.

Neumeier, U., C. Ferrarin, C. L. Amos, G. Umgiesser, and M. Z. Li. 2008. Sedtrans05: an improved sediment-transport model for continental shelves and coastal waters with a new algorithm for cohesive sediments. Computers and Geosciences 34:1223–1242.

Norkko, A., V. J. Cummings, S. F. Thrush, J. E. Hewitt, and T. Hume. 2001. Local dispersal of juvenile bivalves: implications for sandflat ecology. Marine Ecology Progress Series 212:131–144.

Olivier, F., N. Desroy, and C. Retière. 1996a. Habitat selection and adult-recruit interactions in Pectinaria koreni (Malmgren) (Annelida Polychaeta) post-larval populations results of flume experiments. Journal of Sea Research 36:217–226.

Olivier, F., C. Vallet, J. C. Dauvin, and C. Retière. 1996b. Drifting in post-larvae and juveniles in an Abra alba (Wood) community of the eastern part of the Bay of Seine (English Channel). Journal of Experimental Marine Biology and Ecology 199:89–109.

Olivier, F., and C. Retière. 1998. The role of physical-biological coupling in the benthic boundary layer under megatidal conditions: the case of the dominant species of the Abra alba community in the eastern Baie de Seine (English Channel). Estuaries 21:571.

Olivier, F., and C. Retière. 2006. How to leave or stay on the substratum when you can’t swim? Evidence of the role of mucus thread secretion by postlarvae of Pectinaria koreni (Malmgren) in still water and flume experiments. Aquatic Ecology 40:503–519.

Ouellet, P., L. Savard, and P. Larouche. 2007. Spring oceanographic conditions and northern shrimp Pandalus borealis recruitment success in the northwestern Gulf of St. Lawrence. Marine Ecology Progress Series 339:229–241.

Pechenik, J. A. 1990. Delayed metamorphosis by larvae of benthic marine invertebrates: Does it occur? Is there a price to pay? Ophelia 32:63–94.

Pechenik, J. 2006. Larval experience and latent effects—metamorphosis is not a new beginning. Integrative and Comparative Biology 46:323–333.

Pedersen, T. M., J. L. S. Hansen, A. B. Josefson, and B. W. Hansen. 2008. Mortality through ontogeny of soft-bottom marine invertebrates with planktonic larvae. Journal of Marine Systems 73:185–207.

Philippart, C. J. M., H. M. van Aken, J. J. Beukema, O. G. Bos, G. C. Cadée, and R. Dekker. 2003. Climate-related changes in recruitment of the bivalve Maconia balthica. Limnology and Oceanography 48:2171–2185.

Phillips, N. E. 2002. Effects of nutrition-mediated larval condition on juvenile performance in a marine mussel. Ecology 83:2562–2574.

Phillips, N. E. 2004. Variable timing of larval food has consequences for early juvenile performance in a marine mussel. Ecology 85:2341–2346.

Phleger, C. F., M. M. Nelson, B. D. Mooney, and P. D. Nichols. 2002. Interannual and between species comparison of the lipids, fatty acids and sterols of Antarctic krill from the US AMLR Elephant Island survey area. Comparative Biochemistry and Physiology 131:733–747.

Pilditch, C. A., S. Valanko, J. Norkko, and A. Norkko. 2015. Post-settlement dispersal: the neglected link in maintenance of soft-sediment biodiversity. Biological Letters 11:1–6.

Pineda, J., F. Porri, V. Starczak, and J. Blythe. 2010. Causes of decoupling between larval supply and settlement and consequences for understanding recruitment and population connectivity. Journal of Experimental Marine Biology and Ecology 392:9–21.

Pineda, J., N. B. Reynolds, and V. R. Starczak. 2009. Complexity and simplification in understanding recruitment in benthic populations. Population Ecology 51:17–32.

Porri, F., T. Jordaan, and C. D. McQuaid. 2008. Does cannibalism of larvae by adults affect settlement
and connectivity of mussel populations? Estuarine, Coastal and Shelf Science 79:687–693.

Pridmore, R. D., S. F. Thrush, V. J. Cummings, and J. E. Hewitt. 1992. Effect of the organochlorine pesticide technical chlordane on intertidal macrofauna. Marine Pollution Bulletin 24:98–102.

Pridmore, R. D., S. F. Thrush, R. J. Wilcock, T. J. Smith, J. E. Hewitt, and V. J. Cummings. 1991. Effect of the organochlorine pesticide technical chlordane on the population structure of suspension and deposit feeding bivalves. Marine Ecology Progress Series 76:261–271.

Raby, D., M. Mingelbier, J. J. Dodson, B. Klein, Y. Lague-deuc, and L. Legendre. 1997. Food-particle size and selection by bivalve larvae in a temperate embayment. Marine Biology 127:665–672.

Reise, K. 1985. Tidal flat ecology: an experimental approach to species interactions. Springer, Berlin Heidelberg, Germany.

Richards, M., F. Edwards, and M. Huxham. 2002. The effects of the adult density of Macoma balthica on the recruitment of juvenile bivalves: a field experiment. Journal of Sea Research 47:41–54.

Robert, R. 1998. Nutritional inadequacy of Nannochloris atomus and Stichococcus bacillaris for the oyster Crassostrea gigas (Thunberg) larvae. Haliotis 27:29–34.

Saito, G., K. Natoyama, M. Yamazaki, and N. Fusentani. 1995. Induction of attachment and metamorphosis of laboratory cultured mussel Mytilus edulis galloprovincialis larvae by microbial film. Fisheries Science 61:223–227.

Sauriau, P., and C. Kang. 2000. Stable isotope evidence of benthic microalga-based growth and secondary production in the suspension feeder Cerastoderma edule (Mollusca, Bivalvia) in the Marennes-Oleron Bay. Hydrobiologia 440:317–329.

Scherr, B. 1984. Biostatistique. G. Morin, Montréal, Québec, Canada.

Sigurdsson, J. B., C. W. Titman, and P. A. Davies. 1976. The dispersal of young post-larval bivalve molluscs by byssus threads. Nature 262:386–387.

Sinclair, M. 1988. Marine populations: an essay on population regulation and speciation. University of Washington, Seattle, Washington, USA.

Sonier, R., R. Filgueira, T. Guyondet, R. Tremblay, F. Olivier, T. Meziane, M. Starr, A. R. LeBlanc, and L. A. Comeau. 2016. Picophytoplankton contribution to Mytilus edulis growth in an intensive culture environment. Marine Biology 163:73.

Strohmeier, T., Ø. Strand, M. Alunno-Bruscia, A. Duniker, and P. J. Cranford. 2012. Variability in particle retention efficiency by the mussel Mytilus edulis. Journal of Experimental Marine Biology and Ecology 412:96–102.

Thiyagarajan, V. 2010. A review on the role of chemical cues in habitat selection by barnacles: new insights from larval proteomics. Journal of Experimental Marine Biology and Ecology 392:22–36.

Thiyagarajan, V., O. S. Hung, J. M. Y. Chiu, R. S. S. Wu, and P. Y. Qian. 2005. Growth and survival of juvenile barnacle Balanus amphitrite: interactive effects of cyprid energy reserve and habitat. Marine Ecology Progress Series 299:229–237.

Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. Biological Reviews 25:1–45.

Thrush, S. F., J. E. Hewitt, V. J. Cummings, M. O. Green, A. Greig, and M. R. Wilkinson. 2000. The generality of field experiments: interactions between local and broad-scale processes. Ecological Society of America 81:399–415.

Todd, C. D., P. J. C. Phelan, B. E. Weismann, A. R. Gude, C. Andrews, D. M. Paterson, M. E. Loneran, and G. Miron. 2006. Improvements to a passive trap for quantifying barnacle larval supply to semi-exposed rocky shores. Journal of Experimental Marine Biology and Ecology 332:135–150.

Toupoint, N., P. Barbier, R. Tremblay, P. Archambault, C. W. McKindsey, G. Winkler, T. Meziane, and F. Olivier. 2016. Influence of intertidal recreational fisheries and “bouchot” mussel culture on bivalve recruitment. Marine Environmental Research 117:1–12.

Toupoint, N., L. Gilmore-Solomon, F. Bourque, B. Myr-and, F. Pernet, F. Olivier, and R. Tremblay. 2012. Match/mismatch between the Mytilus edulis larval supply and seston quality: effect on recruitment. Ecology 93:1922–1934.

Tremblay, G., C. Belzile, M. Gosselin, M. Poulin, S. Roy, and J.-E. Tremblay. 2009. Late summer phytoplankton distribution along a 3500 km transect in Canadian Arctic waters: strong numerical dominance by picoeukaryotes. Aquatic Microbial Ecology 54:55–70.

Tremblay, R., F. Olivier, E. Bourget, and D. Rittschof. 2007. Physiological condition of Balanus amphitrite cyprid larvae determines habitat selection success. Marine Ecology Progress Series 340:1–8.

Turner, S. J., J. Grant, R. D. Pridmore, J. E. Hewitt, M. R. Wilkinson, T. M. Hume, and D. J. Morrisey. 1997. Bedload and water-column transport and colonization processes by post-settlement benthic macrofauna: Does infaunal density matter? Journal of Experimental Marine Biology and Ecology 216:51–75.

Valanko, S., A. Norkko, and J. Norkko. 2010. Strategies of post-larval dispersal in non-tidal soft-sediment communities. Journal of Experimental Marine Biology and Ecology 384:51–60.
Volkenborn, N., and K. Reise. 2007. Effects of Arenicola marina on polychaete functional diversity revealed by large-scale experimental lugworm exclusion. Journal of Sea Research 57:78–88.

Wacker, A., and E. V. Elert. 2002. Strong influences of larval diet history on subsequent post-settlement growth in the freshwater mollusc Dreissena polymorpha. Proceedings of the Royal Society B: Biological Sciences 269:2113–2119.

Webb, K. L., and L. E. Chu. 1983. Phytoplankton as a food source for bivalve larvae. Pages 272–291 in G. D. Pruder, et al. editors. Proceedings of the Second International Conference on Aquaculture Nutrition. Louisiana State University, Baton Rouge, Louisiana, USA.

Wilson, D. P. 1953. The settlement of ophelia bicornis savigny larvae. Journal of the Marine Biological Association of the United Kingdom 32:209–233.

Yeager, M. M., D. S. Cherry, and R. J. Neves. 1994. Feeding and burrowing behaviors of juvenile rainbow mussels, Villosa iris (Bivalvia: Unionidae). Journal of the North American Benthological Society 13:217–222.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2510/full