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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 benthic-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 substratum 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, Thiagarajan 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 benthic-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.

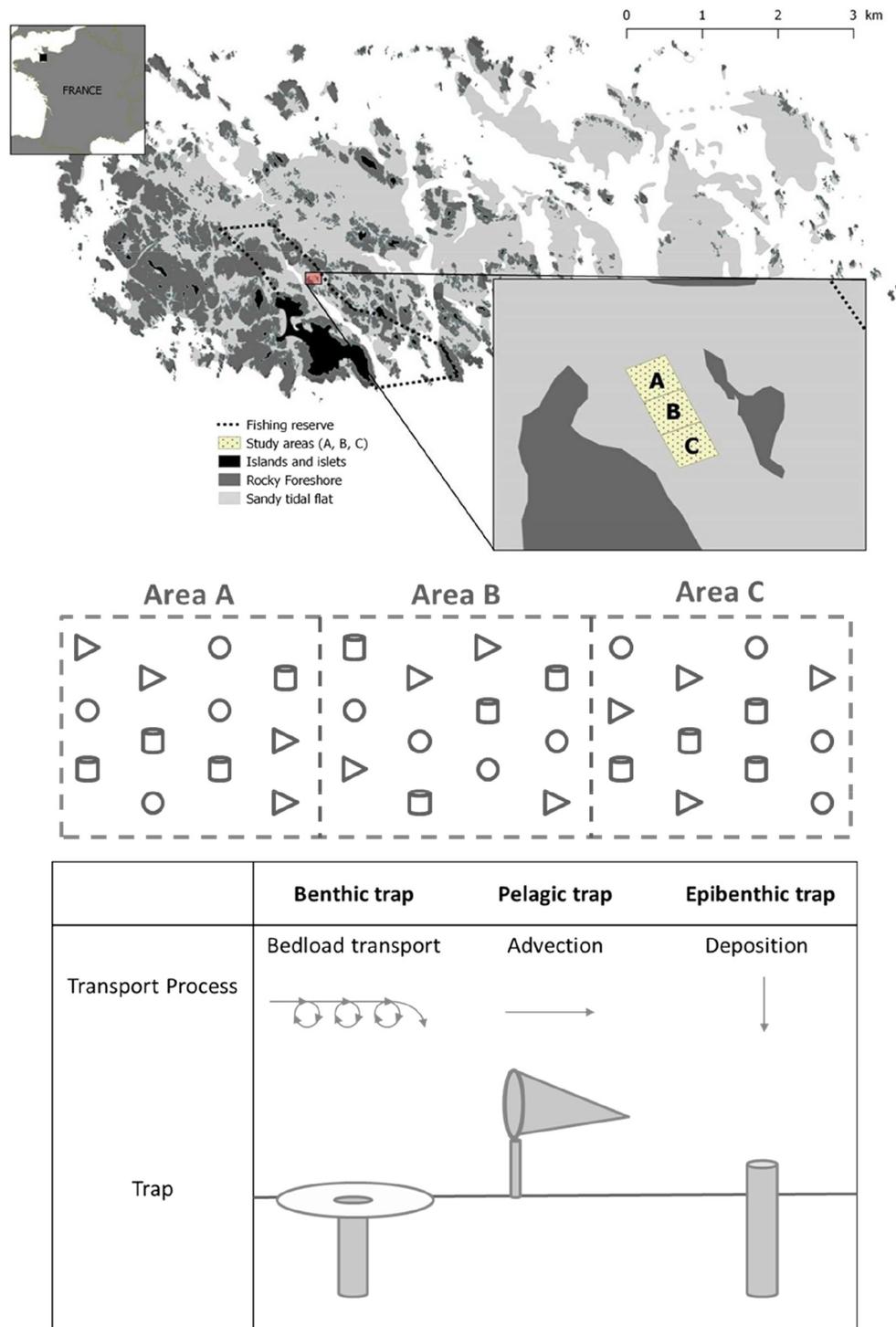


Fig. 1. Top: location and map of the study area on the Chausey archipelago showing the study area and the three experimental plots. Middle: position of recruit traps (triangles, pelagic traps; circles, benthic traps; and cylinders, epibenthic trap). Traps were placed in a regular pattern, but the order 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 \times 1 cm depth; 0.018 m² total surface area) within each of the experimental plots. The resulting material was sieved on 200- μ m-square and 1000- μ m-square meshes to keep only the meiobenthic fraction (between 200 and 1000 μ m) 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 ($^{\circ}$ C), salinity, chlorophyll *a* concentration estimated by fluorescence (μ g/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- μ m mesh to focus on nano- and pico-sized particulate organic matter (Moynihan 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 prefiltered 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 \times 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- μ m 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, post-larvae were considered as settled metamorphosed individuals, characterized by well-visible dissoconch shell and/or gills.

Flow cytometry samples (4.5 mL of prefiltered 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 nanoplankton (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 ($\text{Nb}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$) 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

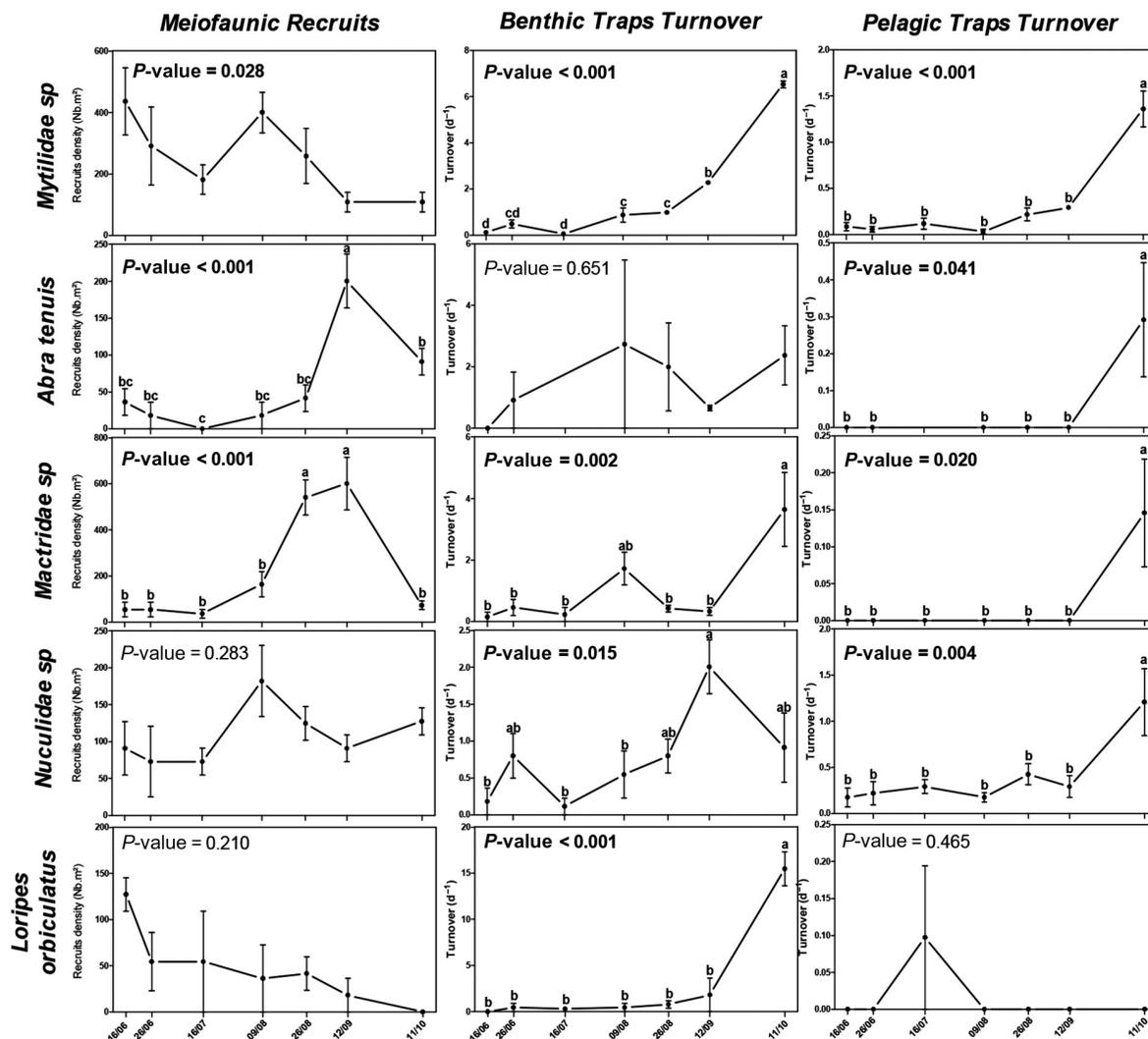


Fig. 2. Secondary migrations of benthic bivalve recruits for the five dominant taxa over the sampling period (June–October 2014). Meiofauna recruit abundances are presented in the left panels, benthic turnover in the middle panels, and pelagic turnover in the right panels. Lines are mean \pm SE; letters indicate significant temporal differences ($P \leq 0.1$).

their hybrids), *Abra tenuis* (Montagu, 1803), Mactridae spp., Nuculidae spp., and *Loripes orbiculatus* (Poli, 1791). The identification of young bivalve recruits based only on taxonomic criteria does not systematically allow identification to the species level. However, based on various macrobenthos inventories made on the Chausey archipelago (Godet et al. 2010), we strongly suspect that Nuculidae spp. are dominated by *Nucula nucleus* (Linnaeus, 1758) and Mactridae spp. by *Spisula ovalis* (J. Sowerby, 1817). During the first part of

the recruitment season, meiofauna recruit assemblages were dominated by *Mytilidae* spp., with a maximum abundance of 437 ± 109 ind/m²; this represented 50% of the total bivalve recruit abundance in the sediment in June. After mid-August, Mactridae spp. dominated bivalve recruit assemblages, with a maximum recruit abundance of 600 ± 114 ind/m² in September, which represents half of the total number of bivalve recruits. Density of meiofaunal recruits and migration turnovers did not differ significantly among the

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).

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		
<i>A. tenuis</i>				
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		
<i>L. orbiculatus</i>				
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.

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 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		
<i>A. tenuis</i>	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		
<i>L. orbiculatus</i>	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		
<i>A. tenuis</i>	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	0.002		
Nuculidae spp.	Date	6	0.406	6.20	0.004
	Zone	2	0.184	2.81	0.100
	Error	12	0.065		
<i>L. orbiculatus</i>	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 $127 \pm 18 \text{ ind/m}^2$) 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)	$\text{g}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$	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 <i>a</i>	Continuous	Mean (2 d of data)	$\mu\text{g/L}$	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	R^2	Adjusted R^2	P -value	Regression slope
Benthic turnover	Mytilidae spp.	All ($n = 10$)	1	Nano	0.548	0.458	0.057	0.00165
	Mactridae spp.	All ($n = 10$)	1	Nano	0.620	0.543	0.036	0.00098
	<i>L. orbiculatus</i>	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 of 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, Thiyagarajan 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 bysso-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 nanoplankton 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 Armonies (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 meiobenthic 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 bed-load 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 negatively 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. Commito 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 (Toupoint 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 bysso-pelagic drift.

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