Role of biotic interactions on seasonal migrations of the macrozoobenthos living in the upper tidal-flat of the Mont-Saint-Michel bay, France

Tarik MEZIANE[§]*, Christian RETIÈRE

Laboratoire maritime de Dinard, Muséum national d'histoire naturelle, BP 28, 35801 Dinard, France

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Abstract − On the tidal flat of the western part of the Mont-Saint-Michel bay, the macrozoobenthos of the upper flat is characterised by an assemblage of the *Macoma balthica* community. The dominant species are *M. balthica*, *Nereis diversicolor* and *Corophium volutator*. A field monitoring during a 1-year period along a four-stations transect perpendicularly to the shore showed that biotic interactions affected the local distributions of these species. This was particularly obvious from late spring to late summer while, because of the density increases, competitions for space and/or resources were induced, which stimulated migrations. Intra-specific competition seemed to induce the migration of the 1-year-old *M. balthica*. Consequently, the migration of the young bivalves from the level where this species is dominant to upper levels stimulated the migration of *C. volutator* population. This migration had a negative effect on the abundance of the amphipods. The migration of *N. diversicolor* during the end of the summer population to the lower levels of the tidal flat seemed to prevent the return of the *C. volutator* population to their original before-migration area, even though *M. balthica* density decreased. © 2001 Ifremer/CNRS/IRD/Éditions scientifiques et médicales Elsevier SAS

Résumé − Rôle des interactions biotiques sur les migrations saisonnières du macrozoobenthos de la zone intertidale supérieure de la baie du Mont-Saint-Michel, France. Le haut estran de la zone intertidale de la partie ouest de la baie du Mont-Saint-Michel se caractérise par une faune macrozoobenthique appartenant à la communauté de *Macoma balthica*. Les espèces dominantes sont le bivalve *M. balthica*, l'annélide *Nereis diversicolor* et l'amphipode *Corophium volutator*. Un suivi annuel le long d'un transect de quatre stations perpendiculaire à la côte montre que des interactions biotiques interviennent dans la distribution de ces espèces. Ceci est particulièrement clair durant la période allant de la fin du printemps à la fin de l'été où des compétitions pour les ressources et/ou l'espace sont induites par l'augmentation des densités, stimulant de la sorte les déplacements de populations. Une compétition intra-spécifique semble induire la migration des individus de *M. balthica* âgés d'un an. La migration de ces jeunes bivalves de leur aire de dominance vers des altimétries supérieures stimule le départ de la population de *C. volutator*. Cette émigration a des effets négatifs sur l'abondance de cet amphipode. La migration à la fin de l'été de la population de *N. diversicolor* vers une zone située plus bas sur l'estran prévient le retour de la population de *C. volutator* sur leur aire de distribution

**Correspondence and reprints: fax:* + 81 98 895 8577.

E-mail address: h983001@sci.u-ryukyu.ac.jp (T. Meziane).

[§] Present address: Laboratory of Ecology and Systematics, University of the Ryukyus, Senbaru 1, Nishihara, Okinawa, 903-0213, Japan.

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maximale d'avant la migration et en dépit d'une nette diminution de la densité de *M. balthica*.

***Macoma balthica* / *Nereis diversicolor* / *Corophium volutator* / migration / intertidal flat**

***Macoma balthica* / *Nereis diversicolor* / *Corophium volutator* / migration / zone intertidale**

1. INTRODUCTION

Along the northern European bays and estuaries, population structure and distribution of the species composing the widespread *Macoma balthica* community have been intensively investigated in the last decades (Thorson, 1957; Wolff and de Wolf, 1977; Beukema 1982; Desprez et al., 1986; Beukema and de Vlas, 1989; Beukema et al., 1999). The factors structuring the spatial distribution of these soft bottom invertebrates include environmental characteristics, such as sediment composition (Dankers and Beukema, 1983), anthropic and natural disturbances (see references in Beukema et al., 1999), and biotic interactions. These interactions consist mainly of predation, physical disturbance (e.g. burrowing), food competition and size-class relations (Ólafsson and Persson, 1986; Rönn et al., 1988, and references therein; Vincent et al., 1994). Biotic interactions enhance the mobility of individuals, which mostly decreases the abundances and often contributes to redraw the distribution pattern among species. The scale of dispersal may vary with size and age for a given species (Günther, 1992). In addition, mobility may determine the success of the recruitment-settlement process.

The Mont-Saint-Michel bay (English Channel, France) is characterised by a large intertidal domain (240 km^2). Large-scale studies on the intertidal macrofauna have been neglected and only spatially limited data are available. In the western part of the bay, Meziane (1997) showed that the upper part intertidal flat supports a *Macoma balthica* community. More specifically, in the tidal flat of 'Le Vivier-sur-Mer', the bivalve *Macoma balthica* (L.), the annelid *Nereis diversicolor* (O.F. Müller) and the amphipod *Corophium volutator* (Pallas) are found to be the most abundant members of this community. Therefore, this present study aims to explain the spring-summer distributions of these three dominant species in relation to the intra- and inter-species interactions.

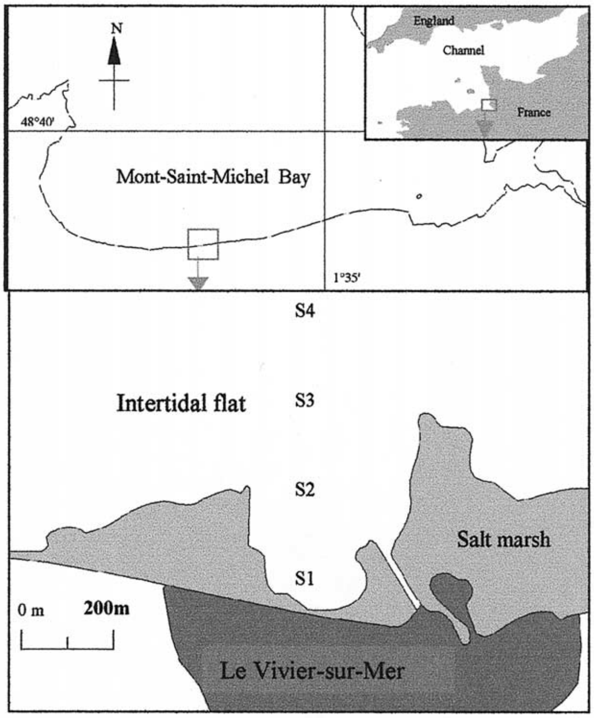

Figure 1. Localisation of the study area and the sampling sites.

2. MATERIALS AND METHODS

The results presented here were part of a monthly survey on an intertidal *Macoma balthica* community during the years 1994–1995 (Meziane, 1997). Population dynamics of the worm *Nereis diversicolor*, the amphipod *Corophium volutator* and the bivalve *Macoma balthica* in addition to other members of the community were investigated in the upper tidal flat of 'Le Vivier-sur-Mer' town situated in the western part of the Mont Saint Michel bay and characterised by the presence of salt marshes (*figure 1*). The flat of 'Le Vivier-sur-Mer' is 4 km large and the tidal amplitude reaches 15 m during spring tides.

The original investigation was conducted at thirteen intertidal stations along a transect perpendicular to the shore. The distance between two stations is 200 m (*figure 1*). Only results from the first four stations (S1 to S4) where maximal abundances were observed for these three species are presented here (Meziane, 1997). The species *N. diversicolor*, *C. volutator* and *M. balthica* contributed from 90 to 99 % of total abundance of the macrozoobenthos on these stations. These species form a sub-assemblage of the *Macoma balthica* community found in muddy to mud-sandy sediment (silt content, fraction < 63 µm, ≈ 10 % and median grain size ≈ 85 mm).

Samples were collected using 18-cm^2 cores to a depth of 20 cm during the lowest tides that occurred within the last 10 d of each month. In each station, five replicate cores were taken from random locations. After a rapid sift in the field in order to reduce the sediment volume, the core contents were fixed with 10 % buffered formalin and were sized through a 500-µm sieve mesh in the laboratory. After sorting, the animals were identified and counted. In addition, shell lengths of all *M. balthica* individuals were measured along the longest axis to the nearest 0.1 mm. Numbers of individuals are expressed per square meter (ind·m^{-2}). When used in this work, the word recruitment does not refer to the sensus stricto biological meaning (post-larval recruitment) but to the recruitment observed with a 500-µm sieve mesh.

3. RESULTS

3.1. *Macoma balthica*

Throughout the year, *Macoma balthica* individuals were collected from most of the thirteen original stations (Meziane, 1997). However, stations S3 and S4 formed the maximal abundance area. During this study, the highest abundances of *M. balthica* (*figure 2a*) were always measured at S4 (maxima 557 ± 84 ind·m^{-2} in May) except during July where the maximal abundance was recorded at S2 (454 ± 57 ind·m^{-2}). The modal size of 91 % of individuals present in S2 was about 10.5–11.5 mm, which correspond to 1-year-old individuals. This size class was also abundant in S4 (375 ± 117 ind·m^{-2}). However, the dominant class sizes were comprised between 13.0 and 17.5 mm (67 % of total individuals collected, *figure 3*). In August, young individuals represented 53 % of total individuals at S4 where the highest abundance was recorded (386 ± 93 ind·m^{-2}). The young individuals also contributed 80 % of the population collected at S2 (159 ± 109 ind·m^{-2}).

3.2. *Corophium volutator*

Changes of *Corophium volutator* densities at the four stations of this study are presented in *figure 2b*. Throughout the year, the distribution of the population of *C. volutator* was always limited within the area formed by stations S1 to S4 (Meziane, 1997). In May and June, the maximal abundance of *C. volutator* was found at S2 (2 613 ± 1 094 and 7 205 ± 1 070 ind·m^{-2} respectively, *figure 2b*). However, in July, only 5.3 % of total individuals in all samples were found at this station while it was more than 95 % 1 month before (June). Similar distribution patterns were observed during August-September. During these months, most of the individuals were found at S3 (1 113 ± 271 and 3 829 ± 1 102 ind·m^{-2}). In October, the maximal abundance was recorded at S1 (5 056 ± 1 130 ind·m^{-2}).

3.3. *Nereis diversicolor*

During the studied period, the distribution of *Nereis diversicolor* was restricted to the upper part (from S1 to S4) of the intertidal flat (Meziane 1997). From May to July, according to the abundance distribution in the flat (*figure 2c*), the preferred habitat of *N. diversicolor* was situated around station S1. During the second half of summer, the majority of individuals were found at S2 (375 ± 103 ind·m^{-2} in August and 238 ± 93 ind·m^{-2} in September). Conversely, only a few worms were found at S1 in August (46 ± 62 ind·m^{-2}) and no individuals were collected during September. In October, the density distribution along the studied transect returned to the initial pattern with a maximal abundance recorded at S1 (238 ± 90 ind·m^{-2}).

4. DISCUSSION

In May and June, an elevated number of the amphipod *Corophium volutator* at S2 seemed to have a strong negative impact on the presence of the *Nereis diversi*

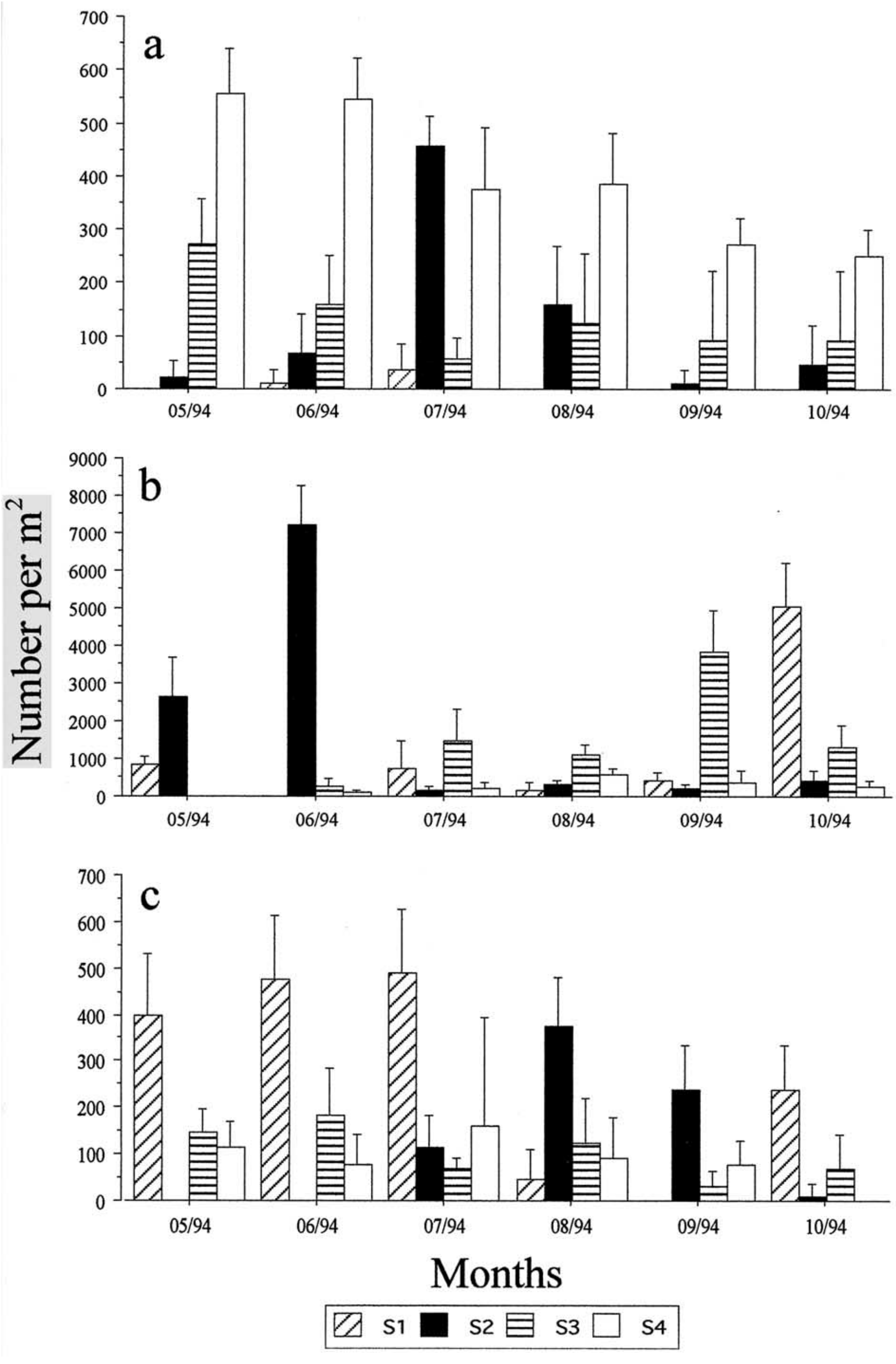

Figure 2. Densities of *Macoma balthica* **(a)**, *Corophium volutator* **(b)** and *Nereis diversicolor* **(c)** at each station expressed as mean ± standard deviation ($n = 5$).

color population. Indeed, no worms were detected at this station during these 2 months while they were present in upper (S1) and deeper (S2) parts of the tidal flat. This observation was in accordance with Ólafsson and Persson's (1986) hypothesis, which assessed that when high abundance of *C. volutator* occurs, recruitment of *N. diversicolor* can be inhibited. At 'Le Vivier-sur-Mer', recruitment of *N. diversicolor* occurred from May to

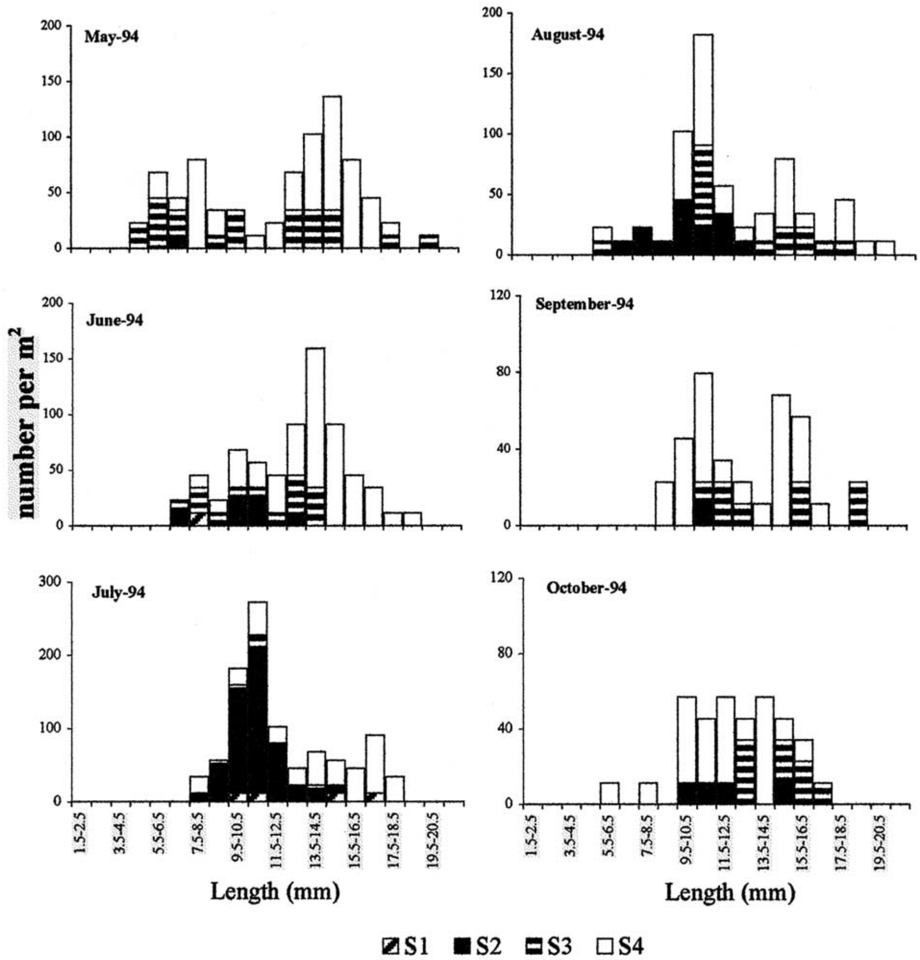

Figure 3. Size-frequency distribution of the bivalve *Macoma balthica* (pool of data from stations S1, S2, S3, and S4).

June (Meziane, 1997). Such interaction between these two species was not confirmed by field experimental study (Jensen and Kristensen, 1990). However, these authors highlighted an effect of the amphipod *C. arenarium* on the migration of *N. diversicolor* juveniles.

Between June and July, the *Corophium volutator* population migrated from S2 to S3, S1 and, probably, to other sites. This redistribution of *C. volutator* was not without consequences on the abundance of this species. Indeed, the total numbers of collected individuals decreased by more than half (*figure 2b*). This intertidal migration probably made these amphipods vulnerable to epibenthic predators (Flach and deBruin, 1994) such as shrimps and gobbies.

Similarly, an increase in *Macoma balthica* abundance was recorded at S2. This high abundance did not correspond to a local recruitment since they were no small individuals at the stations of this study such as those found in winter, but was probably due to a large-scale spatial reorganisation among the adult population. The density increase of 1-year-old recruits of the previous year is certainly due to migration from other area of the tidal flat.

Therefore, it was questioned whether the spatial reorganisation of one of the two species, *C. volutator* and *M. balthica*, had an impact on the migration of the other. It was probably not the arrival of the *C. volutator* population in S3 which induced the departure of the young bivalves. This selective migration of *M. balthica* was probably the result of an intra-specific competition for space and food resulting from a density increase as suggested by Vincent et al. (1989, 1994). An increase of density was precisely what occurred just before the summer migration. Therefore, it was highly probable that the settlement of young *M. balthica* at S2 between June and July was responsible for reducing the number of *C. volutator*. Such a negative effect of *M. balthica* on the recruitment of the amphipods has been demonstrated experimentally (Jensen and Kristensen, 1990). These authors suggested that this impact is mainly from physical disturbance. This was what probably happened at 'Le Vivier-sur-Mer' since the young bivalves colonised the same sediment layer as these amphipods (top 5 cm, Meziane and Retière, pers. obs.). Consequently, the success of the settlement of *C. volutator* at S3 from July to September (*figure 2b*), where *M. balthica* were numerous, was made possible because the amphipods occupied a different sediment layer than the bivalves, mostly adults, more deeply buried than the youngest bivalves. The absence of spatial competition between adults of these two species has been suggested in both field and experimental studies (Bonsdorff et al., 1986; Flach, 1992).

Between July and August, *Nereis diversicolor* individuals moved from S1, where they are numerous during the other months, towards S2. Horizontal migration of *Nereis* population within the tidal flat has been previously reported for adults in the Baltic sea (Armonies, 1994). The reason that initiated this migration in 'Le Vivier-sur-Mer' is still not clear but summer dessication associated with very low tides during this season may induce the worms to migrate to better habitats. As a consequence of this migration event, the universal summer recruitment of this species (Bachelet, 1987) was unsuccessful and did not replace older cohorts (Meziane, 1997). This was probably due to the predation pressure and to the tidal currents, which may have displaced the youngest worms while they were out of their burrows to a deeper level where sediments were unsuitable for settlement. In this part of the Mont-Saint-Michel bay, current speeds are about $0.3\ m \cdot s^{-1}$ on average and therefore have high transport capacities.

Similarly, by settling at S2 between July and August, the *Nereis diversicolor* population may have prevented the return of the *Corophium volutator* population who earlier migrated to other areas. Indeed, negative impact on the abundance of *C. volutator* population, while these amphipods were placed with high densities of *N. diversicolor*, were observed during in situ experiments by Ólafsson and Persson (1986) and Rönn et al. (1988). Ólafsson and Persson (1986) initiated their experiments when they realised that abundances of *C. volutator* and *N. diversicolor* were inversely related along the Swedish littoral. They indicated that the negative effect of *N. diversicolor* on *C. volutator* was essentially due to a physical disturbance such as burrowing activity, which may decrease the feeding time of amphipods and destroy their tubes. In addition, *N. diversicolor* can also reduce the density of the amphipod by direct predation (Rönn et al., 1988).

Between September and October at S1, populations of *Nereis diversicolor* and *Corophium volutator*, in contrast to what was observed in spring-summer, were cohabitating. The autumnal increase of *N. diversicolor* and *C. volutator* densities at this station were essentially due to new recruitments (Meziane, 1997). The presence of small individuals of one species seems not to promote the migration of the other species. This may have been due to the fact that burrowing activities of these annelids did not attain a level that could initiate the migration of the small amphipods and the density reached by *C. volutator* could not inhibit the recruitment of young *N. diversicolor*.

To conclude, in relation to the seasonal increase of abundance due to recruitment events, the dominant species of the upper part of the intertidal flat of 'Le Vivier-sur-Mer', *Macoma balthica*, *Corophium volutator* and *Nereis diversicolor* exhibited from the end of the spring to the end of summer a modification of their spatial distribution patterns. The increase of densities induced migration of the population as a result of intra- and inter-specific competitions.

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