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Settlement of *Macoma balthica* on an intertidal sandflat in the Wadden Sea

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ABSTRACT· Settlement of *Macoma balthica* was investigated at 4 stations on an intertidal sandflat in the Wadden Sea. The stations were characterized by differences in sediment structure, tidal elevation and macrobenthic community. The supply of planktonic larvae was compared with the abundance of the early benthic stages and their length-frequency distribution. Most of the settlement occurred at the station with the lowest tidal elevation, characterized by mixed sediments. No limiting effects of adult *M. balthica* or a dense assemblage of the filter-feeding bivalve *Mya arenaria* on settlement could be observed. From the temporal course of abundance and the length-frequency distribution of *M. balthica* at the different stations, it was concluded that the higher part of the flat was colonized by post-larvae. Settlement and subsequent post-larval transport are discussed in detail.

INTRODUCTION

The spatial distribution of macrofauna in the intertidal area of the Wadden Sea is determined by the interaction of biotic factors, such as mode of reproduction, settlement, and mobility and mortality of young-of-the-year and older stages, with often extreme abiotic conditions, such as high current speed, instability of the sediment, and strong fluctuations in temperature and salinity. Information about reproductive strategies, temporal occurrence of pelagic and benthic larvae as well as early post-larvae of intertidal macrofauna is available from the basic studies of Jørgensen (1946), Thorson (1946), Smidt (1951) and Heiber (1988). However, investigations of settlement where the abundance of larvae is compared with that of the early benthic stage are rare for the Wadden Sea compared to other marine soft bottom communities (Muus 1973, Rumohr 1980, Luckenbach 1984, Bosselmann 1989).

In this study the settlement of *Macoma balthica*, one of the most common species within the Wadden Sea and the ambient subtidal areas, was investigated by comparing the density of larvae in the water column with the abundance of the early bottom stages. To answer the question whether settlement is spatially restricted, samples were taken at 4 stations with different tidal elevations, macrofauna composition and sediment characteristics.

MATERIAL AND METHODS

The results presented were part of a settlement and recruitment program which ran from spring to autumn 1986. Settlement of *Macoma balthica* was investigated on a transect consisting of 4 stations (B1 to B4) situated on an intertidal sandflat south of the island of Borkum (Ems estuary, German Bight, North Sea; 53° 35′ N, 6° 45′ E). The mean tidal amplitude in this area is about 2.4 m. Fig. 1 shows the positions, water levels and inundation periods of these stations. Information about the macrofauna community from April 1986 at each station is given in Günther (1990a).

For sediment sampling, cores of 25 cm^2 area (30 cm depth) were used (1 per station). Water content, particle size, total and organic carbon were analysed for the upper 10 cm of the sediment separated in 3 horizons. Particle size was determined using the dry sieving and pipette method described by Buchanan (1984). The fraction <63 µm was analysed only for B1 where it constituted more than 10 % of the sediment. To measure the carbon content of the sediment a carbon-sulfur determinator (CS-125, Leco Cooperation, St. Joseph, Michigan, USA) was used.

During the day at high water 3 plankton samples were taken with an Apsteinnet (aperture 10 cm diameter, mesh size 125 µm) between Stns B3 and B4. Due to the shallow water (MHWL about 50 cm) the net was horizontally towed a distance of 10 m.

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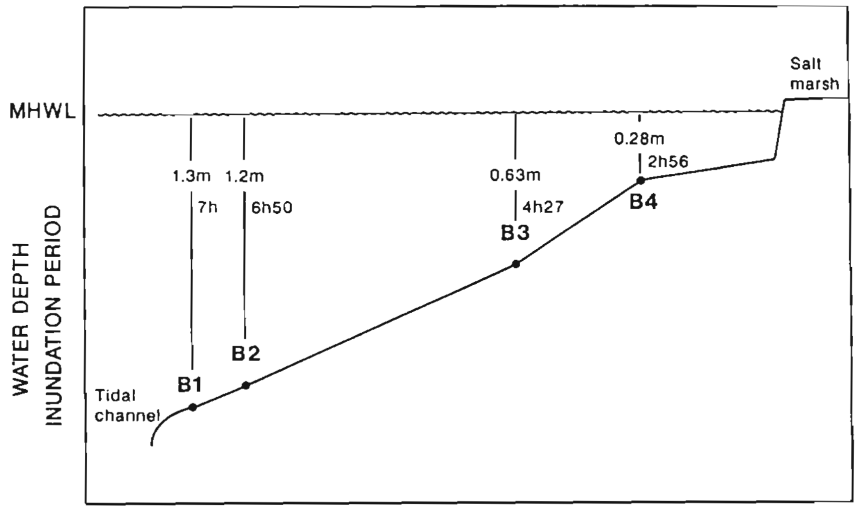

Fig. 1. Schematic drawing of the transect. Water depth and the corresponding inundation period are indicated relative to MHWL (Mean High Water Level)

Early benthic stages of *M. balthica* were sampled by taking, at each station, 4 cores of 15 cm^2 area to a depth of 10 cm and preserving the material intact in 5 % buffered formalin. Samples of plankton and benthos were analysed at time intervals of 4 to 14 d. In the laboratory the samples were sieved using a sieve column with 125, 250 and 500 µm mesh size. By this method 3 fractions of animals were obtained: > 500 µm, < 500 but > 250 µm, and < 250 but > 125 µm. Animals of the 125 µm fraction were separated from the sediment using a Boisseau apparatus (McIntyre & Warwick 1984). Bivalves were sorted under a dissecting microscope (×20 to 60 magnification) and the maximum shell length recorded using a computerized image analysing system (×40 magnification).

By applying the same mesh size (125 µm) in the plankton and in the benthos studies a direct comparison in the dynamics of larval and post-larval stages of *Macoma balthica* should be assured. Using Pythagoras Law ($a^2 = b^2 + c^2$) the diagonal of the meshes in both methods was calculated to be about 176 µm. Because of the nearly circular shape of the larvae at this size it can be confidently assumed that slightly larger bivalves (ca 190 µm) were quantitatively retained. Similar mesh sizes were used by Ankar (1980), Luckenbach (1984), Bachelet (1986) and Bosselmann (1989) to study bivalve settlement.

RESULTS

Sediment

Owing to the particle size distribution in the upper 2 to 3 cm of the bottom, Stns B1 to B4 were characterized as follows: B1, sandy (very fine sand) silt; B2 to B4, fine sand (Table 1). While at B1 a change in particle size with depth occurred (from sandy silt to silty very fine sand), the sediment at the other stations was homogeneous with depth.

Content of total and organic carbon was highest at Stn B1, declined to B3 and increased again at B4. This corresponds to the distribution of very fine sand and the <63 µm fraction. At B1 the sediment consisted mainly of faecal pellets.

Settlement

Fig. 2 shows that the density of *M. balthica* larvae in the plankton was highest on 18 May 1986 (2400 ind. m^{-3}). A strong decline in larval densities from 2083 to 163 ind. m^{-3} occurred between 21 May and 28 May. This was the period in which most settlement occurred. On 11 June a second smaller maximum of about 100 ind. m^{-3} was recorded. From 19 June on no larvae of *M. balthica* were found in the plankton, indicating that larval settlement was restricted to the period end of May/beginning of June.

The decline of larval densities in the plankton corresponded best to the increase of bottom stages at Stn B1. Even the small maximum of larvae in June was reflected in the abundance of *M. balthica* at the bottom. On 28 May and 11 June about 50 000 ind. m^{-2} were found at B1.

The abundance of *M. balthica* at Stns B2 and B3 did not clearly correspond to the planktonic larval supply either in the development of the 0-group in total or in the abundance of the smallest stages (125 µm fraction). This was indicated by the lag of the abundance maxima between the stations: Stn B1, 28 May and 11 June; Stn B2, 4 June; Stn B3, 19 June. For B3 there was little suggestion of an association between the maximum number of individuals in the 125 µm fraction (4 June) and the maximum number of the 0-group in total (19 June) At B4 the first 0-group *M. balthica* appeared at

Table 1. Sediment characteristics at the 4 stations

Stn	Sediment depth (cm)	Water content (%)	Particle size distribution (%) >500 µm	>250 µm	>125 µm	>63 µm	<63 µm	Ø31.5µm	Ø15.6µm	Ø7.8µm	Ø3.9µm	Ø<3.9µm	C (total) (%)	C (organic) (%)
B4	0–2	25.16	0.16	1.02	85.52	10.32	3.28						0.3436	0.1704
	2–5	18.85	0.06	0.7	87.18	9.5	2.7						0.2172	0.092
	5–10	18.24	0	1	86.96	8.94	2.98						0.2716	0.0999
B3	0–3	22.05	0.02	2.6	85.42	8.9	2.96						0.2632	0.1084
	3–6	18.71	0.12	3.06	86.88	8.6	2.42						0.1938	0.074
	6–10	17.77	0.12	2.68	85.68	8.88	2.62						0.2092	0.0838
B2	0–3	23.46	0.74	6.34	70.54	15.28	6.94						0.487	0.2077
	3–6	19.02	0.3	3.88	64.4	20.34	6.04						0.4252	0.1534
	6–10	17.82	0.06	1.9	76.2	17.5	4.04						0.2943	0.1253
B1	0–3	43.02	0.12	1.7	34.92	36.24	26.68	5.84	3.78	3.36	2.74	6.24	1.428	0.7667
	3–6	30.2	0.1	1.68	33.48	44.58	19.88	5.54	2.88	2.16	1.96	4.12	1.448	0.5408
	6–10	22.94	0.16	1.7	35.78	48.08	13.9	4.12	1.68	1.2	1.46	2.48	1.1121	0.3189

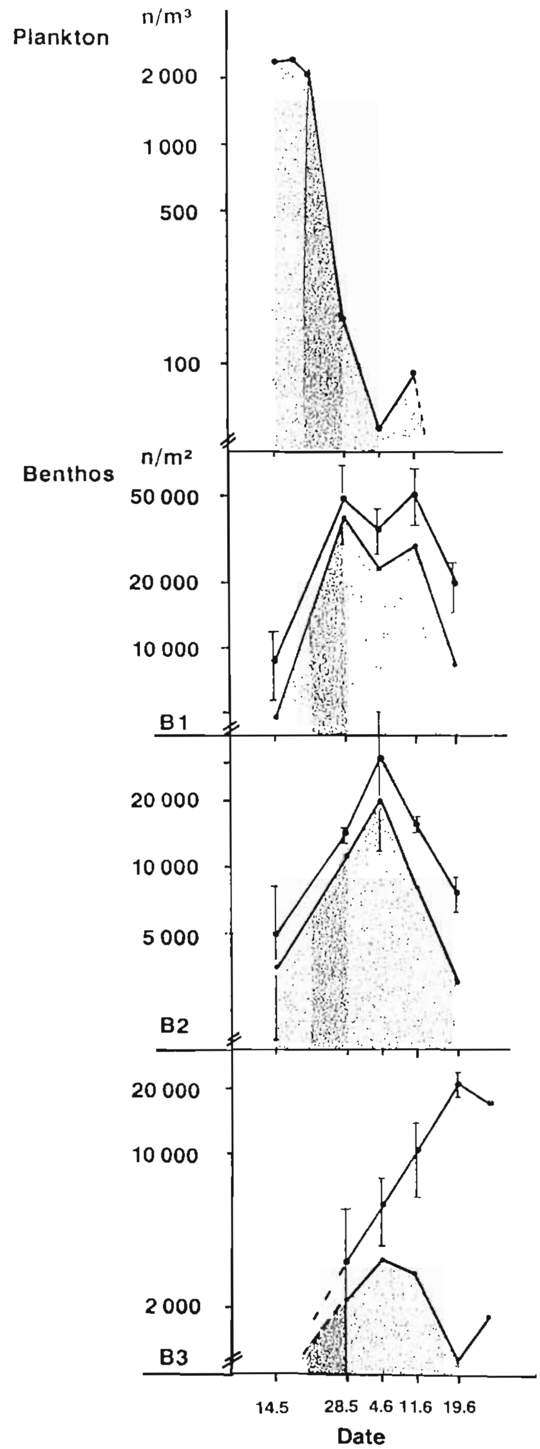

Fig. 2. *Macoma balthica*. Mean density in the plankton (larvae) and in the benthos (Stns B1 to B3). For benthos, symbols with error bars (±SD) give the total number of individuals per m^2. Lighter shading: presence of planktonic larvae and benthic 125 µm fraction. Darker shading: time interval of main settlement

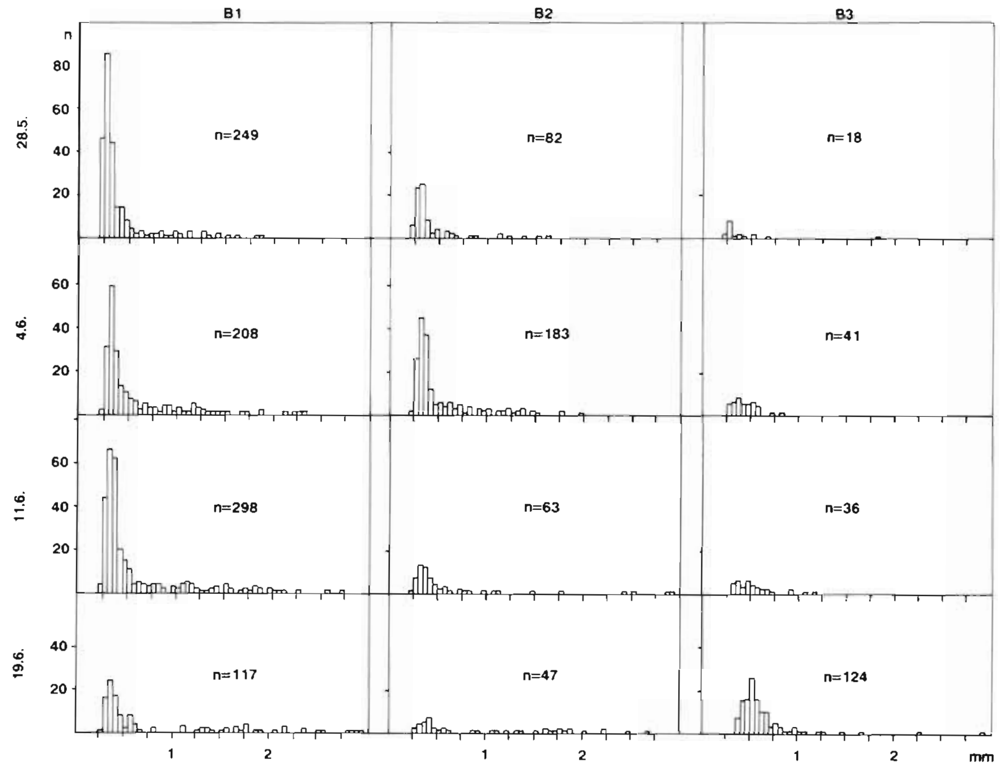

Fig. 3. *Macoma balthica.* Length-frequency distribution at Stns B1 to B3 on 4 dates

the end of May (28 May, 3000 ind. m^{-2}; not included in Fig. 2). The abundance declined at the beginning of June (700 ind. m^{-2}) but increased again up to 19 June (5400 ind. m^{-2}). Though the abundance of bivalves at B4 was generally low, no direct correspondence between larval supply and abundance of early benthic stages was found, as at B3.

Analyses of the length-frequency distribution of *Macoma balthica* at Stns B1 to B3 again showed for B1 a good correspondence with larval abundance (Fig. 3). At the end of May, *M. balthica* with shell lengths in the range 200 to 300 µm dominated. According to Jørgensen (1946) and Olafsson (1988) those are the initial settlers, i.e. this is the lower size at settling. One week later, with only a small supply of settling larvae, the modal size of the length-frequency distribution changed from between 250 and 300 µm (28 May) to between 300 and 350 µm (4 June). On 11 June the number of small individuals (250 to 400 µm) increased again, reflecting a second settlement of larvae. From 28 May until 11 June at B2 the maximum of the length-frequency distribution was between 300 and 350 µm. Although *M. balthica* of 200 to 300 µm occurred, their numbers showed no relation to the plankton dynamics.

On 28 May the length-frequency distribution of the bivalves at Stn B3 may have reflected initial settlement of larvae. But on 11 June initial settlers (200 to 300 µm shell length) did not occur. The increase in abundance of *M. balthica* between 11 and 19 June was characterized by an input of bivalves with a modal size of 500 to 550 µm, which does not correspond to the larval supply and to the size at settlement. At the end of the investigation period, the length-frequency distribution at B1, B2 and B3 differed significantly (Kolmogoroff-Smirnoff test, $p < 0.05$).

If the abundance of *Macoma balthica* post-larvae at the 4 stations is compared, on 28 May and 11 June the abundance at Stn B1 was significantly higher than at the other stations (Fig. 4). On 19 June the abundance at both B1 and B3 was significantly higher than at B2 and B4.

DISCUSSION

The spatial distribution of the smallest benthic stages of *Macoma balthica* suggested that initial settlement occurred mainly in the deeper part of the flat (Stns B1 and B2). The mixed sediments at B1, indicating low current velocities, were preferred to the sandy sediments at B2 to B4. Investigations on *M. balthica* which included the early benthic stages were carried out by Smidt (1951) and Bachelet (1987) in intertidal areas and by Ankar (1980), Mölsä et al. (1986) and Olafsson (1988) in subtidal areas. From the occurrence of spat on sandy and muddy sediments, Smidt (1951) and Olafsson (1988), as well as Muus (1973) for the related species *Macoma calcarea*, concluded that settlement was non-selective with respect to substrate. Differences between the results presented here, which indicate a strong preference for mixed sediments, and these earlier investigations may be because of differences in the factors determining the settlement process. Settlement can be determined by active selection of the habitat by competent larvae due to negative or positive settlement cues as well as by the passive deposition of larvae comparable to sediment particles (Eckman 1983, Hannan 1984, Nowell & Jumars 1984, Luckenbach 1987). According to the reviews of Woodin (1986) and Butman (1987) both processes can occur simultaneously in different strengths and scales.

Whether settlement of *Macoma balthica* was determined more by active substrate selection or by passive deposition cannot be stated unequivocally. However 'gregarious' settlement induced by a positive chemical cue originating from adults of the same species, as observed in *Ostrea edulis* (Bayne 1969), seems unlikely. In this case, the density of settlers should have been highest at Stn B2 with the highest abundance of adults (Günther 1990a). On the other hand, no limiting effect on larval settlement was observed due to the presence of adults or of a dense bed of *Mya arenaria* at B1 (patches of 500 to 1000 ind. m^{-2}; Günther 1990a, b). Although suspension feeders are able to ingest planktonic larvae (e.g. Kristensen 1957) it does not necessarily follow that there will be a limiting effect on settlement (Maurer 1983, Ertman & Jumars 1988).

The effect of mortality on the spatial distribution can only be estimated. According to Watzin (1983, 1986), mortality induced by predatory meiofauna does not influence the settlement patterns of bivalves but does affect post-settlement survival. The higher correspondence of larval supply to number of settlers and size of benthic stages at Stn B1 compared to the other stations indicated that the differences in abundance reflected a settlement pattern and were not a result of recruitment-affecting processes. Recruitment of the 1986 *Macoma balthica* 0-group was limited by epibenthic predators at the end of July/August when the post-larvae had reached a mean length of 0.8 to 1 mm at Stn B3 and 2.5 to 3 mm at B1 (Günther 1990b).

To interpret the strong increase of *Macoma balthica* at Stn B3 on 19 June the following has to be considered: (1) In accordance with the abundance of planktonic larvae, main settlement took place between 21 and 28 May and the larval supply had ceased between 11 and 19 June. At B3 the main settlement resulted in quite low abundances of *M. balthica*; the strong increase in benthic stages occurred with 3 wk delay. (2) The length-frequency analysis from 19 June (B3) showed a modal length of 500 to 550 µm although settlement occurs at 200 to 300 µm (Jørgensen 1946, Olafsson 1988). The mesh size applied allowed quantitative sampling of all bottom stages (see 'Material and Methods'). Thus the increase in abundance in combination with the observed length-frequency distribution cannot be due to sieve recruitment. From these points it only can be deduced that in the upper part of the flat (B3), the 0-group of the bivalve consisted mainly of immigrating post-larvae. For this reason the small stages found here in May may be individuals that settled in the deeper part of the flat and were subsequently redistributed by tidal currents. Thus, the differences in the patterns of abundance over time between Stns B1 and B2 were due to an initial settlement on which was superimposed a redistribution of the early benthic stages. This is supported by the differences in the length-frequency distributions at these stations.

In contrast to the results of Smidt (1951) and Bachelet (1987), where post-larvae apparently stayed at the place of settlement, in this study settlement and post-larval transport broadly overlapped. For the intertidal areas of the Wadden Sea, Baggerman (1953) described post-larval transport mainly for *Cerastoderma edule* but to a smaller degree for *Macoma balthica* and *Mya arenaria*. Transport of *M. balthica* by currents was recorded by catches of post-larval stages in plankton hauls and sediment traps (Beukema 1973, Heiber 1988, Olafsson 1988, Beukema & deVlas 1989, Günther 1990b) as well as in laboratory experiments (Bonsdorff

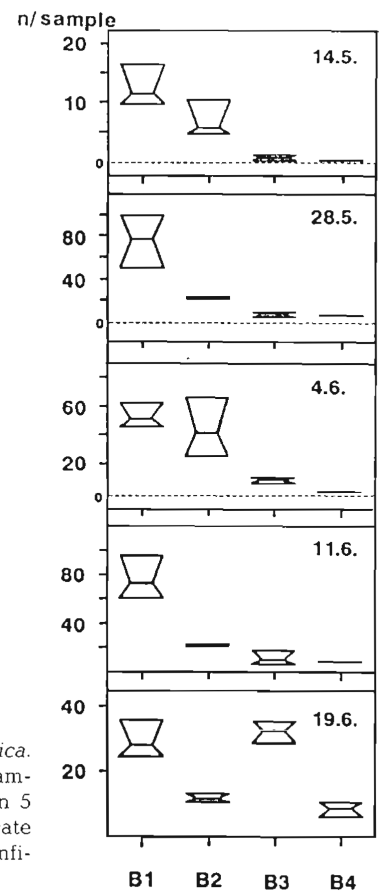

Fig. 4. *Macoma balthica*. Abundance (nos. per sample) at Stns B1 to B4 on 5 dates. Box plots indicate medians with 95 % confidence limits

1984, Beukema & deVlas 1989). This transport has been observed in winter (Beukema 1973, Beukema & deVlas 1989) as well as after stormy weather (Olafsson 1988). Transport has also been recorded in summer and winter for different age-classes of the bivalve (Heiber 1988). In some investigations post-larval transport was concluded to be occurring from changes in the spatial distribution of *M. balthica* and from the ability of this species to colonize defaunated areas (Boyden & Little 1973, Myren & Pella 1977, Wolff & deWolf 1977, Ratcliffe et al. 1981, McLusky et al. 1983).

In summarizing settlement and transport of *Macoma balthica* in the Wadden Sea a distinction must be made between summer migrations, which are directed to the higher parts of the tidal flats, and winter migrations, directed towards sublittoral areas. Because of the temporal sequence of spatfall, transport of early post-larvae to the upper parts of the flats in summer and the transport of juveniles and adults into the sublittoral in winter, the terminology of Beukema (1973) and Beukema & deVlas (1989) who called the winter transport 'secondary spatfall' should be revised. Differences in the direction of the transport as well as the byssus thread mechanism of drifting (Beukema & deVlas 1989) may indicate that active behaviour of the bivalves is involved in these processes.

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