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Short communication

Observations of a mass occurrence of *Macoma balthica* larvae in midsummer

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Abstract

In 1995 the seasonal development of concentrations of both phytoplankton and larvae of the bivalve *Macoma balthica* was studied in the coastal zone behind the back-barrier island of Spiekeroog (German Wadden Sea). In July/August larvae reached maximum concentrations of about 1000 to 4200 ind. m^{-3} (depending on the sampling site and tidal period), probably in relation to a phytoplankton bloom in July. This observation of an unusually late maximum of *Macoma* larvae is discussed in detail in connection with the recent literature available about spawning of *M. balthica* in the Wadden Sea.

Keywords: *Macoma balthica*; spawning; seasonal development

1. Introduction

Around the North Sea, intertidal populations of *Macoma balthica* (L.) are known to spawn once a year in spring (Caddy, 1967; Lammens, 1967). Subsequent gonadal redevelopment continues into autumn or even the beginning of winter (Caddy, 1967; Lammens, 1967; Chambers and Milne, 1975; Madsen and Jensen, 1987). The rise in water temperature in spring to above 10°C appears to trigger the spawning (Lammens, 1967). Experiments carried out by Honkoop and Van der Meer (1997) suggest that this trigger is pertinent only when the gonads are completely ripe. The process of gonad ripening in *M. balthica* is still not completely understood. In *Mytilus edulis* L. gonad ripening is accelerated by the increase in phytoplankton density (Kautsky, 1982). Comparable studies for *M. balthica* are lacking.

In contrast to those in the North Sea, intertidal *M. balthica* from the southern limit of its distribution (Gironde Estuary, France) are known to spawn twice a year: in late spring/early summer and again from September to November after a rapid redevelopment of the gonads (Bachelet, 1986).

Among the intertidal bivalves of the Wadden Sea, *M. balthica* and possibly *Scrobicularia plana* da Costa are the only species thought to spawn once a year. In contrast, *Cerastoderma edule* (L.) and *Mya*

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arenaria L. and *Mytilus edulis* are reported to have at least the potential of two annual spawning periods (Pfitzenmeyer, 1965; Hummel and Boogards, 1989; Pulfrich, 1997), suggesting that gametogenesis proceeds more rapidly than in *M. balthica*. The spring spawning stimulus in these species is similarly thought to be a rise in water temperature, but the trigger of the autumn spawning is yet unknown.

In the German part of the Wadden Sea after the severe winter of 1985/1986, Günther (1990) observed only one larval peak in *M. balthica*, while in 1982 and 1983, following moderate winters, Heiber (1988) reported a small autumn peak represented in both years by one observation date. Although a similar observation was made by Boysen-Ennen in 1994 (same area of investigation as in the present study, unpublished data), evidence for late spawning in this species was still weak. The present paper describes a case history of a mass occurrence in 1995 of larvae of *M. balthica* as late as July/August, emphazising (1) the need for more information on gonad ripening and spawning stimuli and (2) the high plasticity of temporal patterns in the reproduction of *M. balthica*.

2. Material and methods

2.1. Area of investigation

The area of investigation was the coastal zone behind the barrier island of Spiekeroog, situated on the southern North Sea coast, in the German Bight (Fig. 1). In 1995 meroplankton sampling was carried out at two locations, one situated in the Otzumer Balje tidal inlet (A), and the other in the harbour of Neuharlingersiel (B). At high tide, 70% of the water in the Spiekeroog back-barrier flats is transported via the Otzumer Balje (A), while in the harbour (B) the water exchange by the tides is probably limited. Sampling of phytoplankton was also carried out at the Otzumer Balje station (A), concurrent with the meroplankton sampling. Benthos sampling was carried out at the Gröninger Plate (station C), a mainly sandy intertidal flat situated between the mainland and the island of Spiekeroog. At this sampling site mixed sediments occurred and the benthic fauna was dominated by the polychaetous worms *Heteromastus filiformis* and *Aphelochaeta marioni* (former name: *Tharyx marioni*).

2.2. Phytoplankton

Phytoplankton samples were taken from the water surface at station A. Sampling was carried out two hours before high tide. The material was preserved in 4% formalin. Phytoplankton was counted according to the Utermöhl technique (Utermöhl, 1958) in volumes of 3 to 10 cm^3. As bivalve larvae consume phytoplankton cells <30 μm (Balwin and Newell, 1991), only data for this algal fraction are presented here.

2.3. Meroplankton

2.3.1. Otzumer Balje (Station A)

Meroplankton samples were collected from March to November 1995 at intervals of 2 to 8 weeks. Sampling was carried out two hours before high and low tides by filtering 50 dm^3 pumped seawater (water depth 6–7 m) over 125-μm meshes. By using this mesh size, small unidentifiable stages of bivalve larvae were caught as well as larger stages which could be identified from a length of 150 to 175 μm onwards. Thus, in general the maximum larval density of *M. balthica* may have been underestimated. Samples were preserved in a 4% buffered Korsolin seawater mixture. In the laboratory samples were sorted and bivalve larvae were identified to species level.

2.3.2. Neuharlingersiel Harbour (Station B)

Meroplankton samples were collected from April to September 1995 (represented are data from May to the end of August) at intervals of between 6 and 20 days. Sampling was carried out at high tide using an Apstein net (125-μm mesh size, opening diameter 10 cm) hauled vertically through the water column. The water depth at mean high tide was about 4 m. Three repeated hauls were pooled into one sample. The volume filtered was determined via a flow meter and ranged between 75 and 100 dm^3. The samples were fixed with 4% buffered formalin and sorted in the laboratory. Some of them were subdivided using a plankton splitter according to Kott (1953).

For identification, comparison material analysed

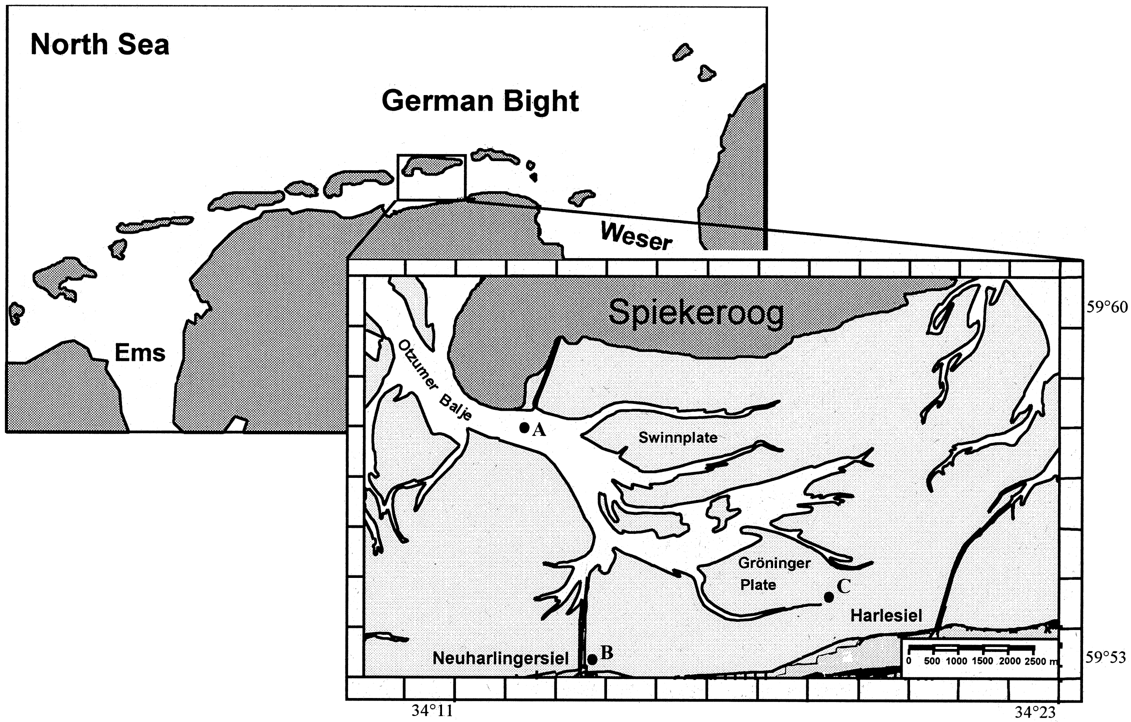

Fig. 1. The area of investigation. (A) The station in the Otzumer Balje; (B) the Neuharlingersiel harbour station; (C) the benthos sampling station at the Gröninger Plate.

by K.W. Ockelmann was used. Cross checking of the bivalve larvae from the Otzumer Balje and Neuharlingersiel Harbour was also done. Because we recognised the larvae of *Tellina* sp. in the Otzumer Balje, it is not likely that the two species were confused.

2.3.3. Gröninger Plate (Station C)

Benthos sampling was carried out at the southern border of the Gröninger Plate. Here mixed sediments occur, in which settlement of bivalves regularly takes place (Günther, 1990; Jaklin et al., in prep.). Samples were collected from April to August in time intervals of 1 to 3 weeks. One additional sampling was carried out on 18 December 1995.

Five parallel samples were taken with a corer of 33 cm^2 area and preserved intact in 5% buffered formalin. Sorting and identification of postlarvae was carried out in the laboratory after sieving of the sediment on a sieve column of 500, 250 and 125 μm. To demonstrate settlement of larvae, only the mean abundance of postlarvae $<$500 μm will be presented.

3. Results and discussion

Fig. 2a presents the density of algae $<$30 μm potentially contributing to the diet of bivalve larvae. With less than 6×10^9 cells m^{-3}, the spring phytoplankton bloom in 1995 was extraordinarily small while later peaks in summer reached the magnitude of a 'normal' spring bloom. In the North Frisian Wadden Sea a delay of the 1995 spring bloom was observed with increasing phytoplankton densities occurring as late as May. This irregular seasonal development was assumed to be related to a shortage in light available for the algae due to the high turbidity of the water column in spring 1995 (Tillmann and Hesse, pers. comm., 1998).

The density of *M. balthica* larvae in the meroplankton was similarly low during the spring spawning period (Fig. 2b), although larval abundances usually peak at this time of year (Heiber, 1988; Günther, 1990, 1991). Due to the lack of data it cannot completely be excluded that *M. balthica* had spawned

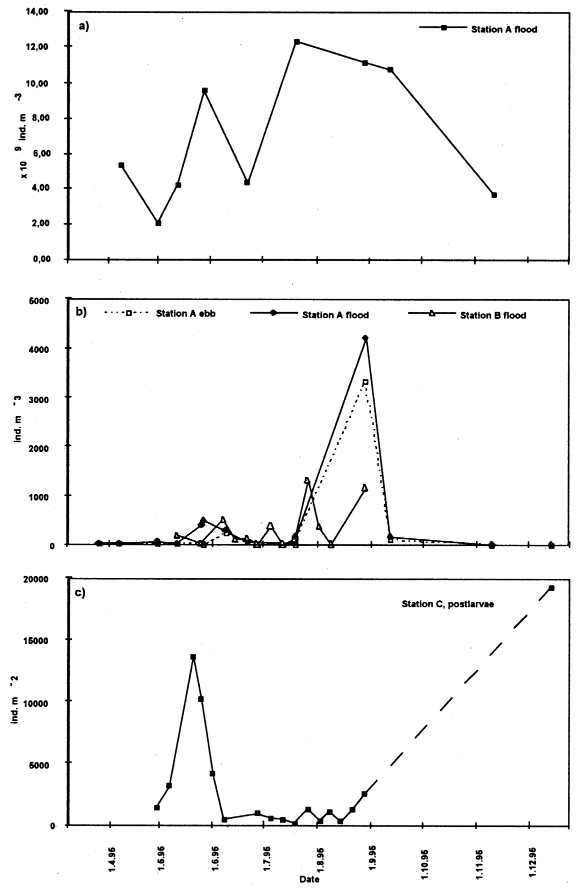

Fig. 2. Density of (a) small phytoplankton (<30 μm), of (b) *M. balthica* larvae, and (c) of *M. balthica* postlarvae in 1995. For the larvae, results from two sampling locations (Station A: Otzumer Balje; Station B: Neuharlingersiel harbour) are presented.

already before April. But the trigger water temperature of 10°C was reached only in the second half of April 1995 (data: Deutscher Wetterdienst), implying that no spawning will have taken place before that date.

In contrast to data found in 1994 and 1996 (Jaklin et al., in prep.), larval densities increased again at both sampling locations in July (Station B) and August 1995 (29 August; Stations A and B), indicating summer spawning of *M. balthica* in the Wadden Sea. This contradicts the results of Lammens (1967), who concluded from studies on gonad development of intertidal *M. balthica* that they spawn only once a year in spring. Also the results of Honkoop and Van der Meer (1997) imply a single spring spawning in intertidal populations, suggesting that spawning intensity is related to preceding winter temperature regimes and food availability during gametogenesis.

Though the larval densities in spring were low, a clear settlement peak was observed in May in the benthos of the Gröninger Plate (Fig. 2c). The second period of occurrence of *M. balthica* larvae in 1995 was reflected in an increase of postlarval abundance in August and particularly in an extraordinarily high density of postlarvae (mostly smaller than 800 μm) as late as December 1995.

The observations reported here point to the occurrence in certain years of repeated spawning events in *M. balthica* in the Wadden Sea, a phenomenon previously reported for populations close to the southern limit of the geographical distribution of this species (Bachelet, 1986). Which part of the population (subtidal or intertidal) generally contributes to such a late spawning in the Wadden Sea can only be determined by studying the seasonal gonad development of both tidal and subtidal *M. balthica*. However, the high larval density of *M. balthica* observed in summer in the present study (the highest reported to date) suggests that a considerable part of the population had spawned.

The late spawning event observed in the present study raises questions as to the causative factors. The possibilities are: (1) In 1995 the abiotic as well as food conditions in the Wadden Sea were similar to those in the Gironde Estuary, thus allowing two spawning periods. The winter 1994/95 was extremely mild and the water temperature during summer was extraordinarily high. In June–August a positive temperature anomaly was observed with values up to 3 standard deviations higher than the 25-y average (Umweltbundesamt, 1996). Simultaneously the seasonal development of the phytoplankton was unusual, with a heavy bloom occurring as late as July–September. Such late blooms are assumed to play a key role in the occurrence of two growing periods of *M. balthica* in the Seine estuary (Beukema and Deprez, 1986) and are most likely to be the cause of two spawning periods in this region as well. (2) This unusually heavy and late phytoplankton bloom may have triggered a second spawning in *M. balthica* as well as in other dominant bivalves of the Wadden Sea (Jaklin et al., in prep.). That phytoplankton blooms may induce spawning events was described by Himmelmann (1975) and Starr et al. (1991), viz. for sea urchins and mytilid bivalves. As such intense and delayed phytoplankton blooms occur on rare occasions only, their effect on the reproductive behaviour of bivalves has not yet been determined.

Future research on *M. balthica* should thus focus on: (1) what drives/accelerates gonad development, (2) when does the subtidal part of the *M. balthica* population in the Wadden Sea spawn, and finally (3) what triggers summer/autumn spawning in *M. balthica* or in other bivalve species.

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