



Predation on 0-group and older year classes of the bivalve *Macoma balthica*: interaction of size selection and intertidal distribution of epibenthic predators

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Abstract

The bivalve *Macoma balthica* is a common species in the Wadden Sea and North Sea. Juveniles temporarily use nurseries in the high intertidal. To explain this nursery use, predation pressure was examined for both juvenile and adult *Macoma* at low and high tidal flats. The study was carried out in the eastern Dutch Wadden Sea. Shrimps *Crangon crangon*, adult crabs *Carcinus maenas*, gobies *Pomatoschistus* and juvenile flatfish were more abundant and larger on low than on high tidal flats, but 0-group *Carcinus* was more abundant on the high tidal flats. *Crangon* and 0-group *Carcinus* stomachs frequently contained *Macoma* remains. These predators selectively preyed on small 0-group *Macoma*, both in the field and in laboratory experiments. The effect of predation by epibenthic animals and birds, on the low and high tidal flats, was examined in enclosure experiments (2 mm mesh). There was no effect of epibenthos enclosure on adult *Macoma*. For 0-group *Macoma*, densities were higher in enclosures than in the controls where predators had normal access. The density reduction by epibenthic predators was much larger in the low than in the high intertidal. We found no effect of bird predation on densities of 0- and 1+ group *Macoma*. Thus, 0-group *Macoma* is under high predation pressure by epibenthos in the low intertidal, especially by shrimps, while they are relatively safe in the high intertidal. However, most of the shellfish outgrow their epibenthic predators during their first summer. Therefore, it becomes safe for the bivalves to redistribute to locations where epibenthic predators are abundant, during their first winter. On the other hand, it did not become clear from this study why many of the larger *Macoma* leave the high intertidal. Concluding, the nursery use of *Macoma*-spat in the

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high intertidal is probably, at least partly, an adaptation to avoid epibenthic predation. © 2002 Elsevier Science B.V. All rights reserved.

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1. Introduction

Many intertidal benthic species in the Wadden Sea, a shallow coastal sea in The Netherlands, Germany and Denmark, use nurseries in the high intertidal (Beukema, 1993a; Flach and Beukema, 1994). This holds, for example, for the lugworm *Arenicola marina* (Farke et al., 1979), the shore crab *Carcinus maenas* (Klein Breteler, 1976; Beukema, 1991), the shrimp *Crangon crangon* (Kuipers and Dapper, 1984) and the bivalve *Macoma balthica* (Beukema, 1993a). It is assumed that in these nurseries juveniles of these benthic species are protected against predation by marine organisms such as shrimps, crabs and fish (Beukema, 1993a), that physical disturbance is less (Flach, 1992) and that growth is faster (Armonies and Hellwig-Armonies, 1992). We studied the relation between predation and nursery use of *M. balthica*.

M. balthica is a small bivalve found in coastal areas in temperate regions (Beukema and Meehan, 1985). In the Wadden Sea, juveniles of this species are mainly found on the high intertidal flats. Adults are more widespread and are found in both the low and high intertidal and the subtidal of the Wadden Sea and the adjacent North Sea (Beukema, 1993a). Since the locations where adults and juveniles live are partly spatially separated, *M. balthica* has to undertake migrations between these locations. Juvenile *Macoma* settles in May at a size of 300 μm in the low intertidal. Subsequently, these animals migrate to the high intertidal in June, where they stay until winter. In winter, juvenile *Macoma* migrates again, this time back to the low intertidal and the North Sea (Beukema and De Vlas, 1989; Hiddink and Wolff, in press).

There are three groups of predators on *M. balthica*. Waders and ducks are numerous on tidal flats and exert a high predation pressure on the macrobenthos (Zwarts et al., 1992). Most birds can only forage on the tidal flats when the flats are emerged and therefore their predation pressure is higher on the high tidal flats (Sanchez-Salazar et al., 1987). Shorebirds generally select for relatively large prey. Oystercatchers and Knots for example do not eat *Macoma* smaller than 10 mm (Hulscher, 1982; Zwarts and Blomert, 1992). Densities of shorebirds are usually in the range of 1–5 birds $10,000\text{ m}^{-2}$ (Van de Kam et al., 1999).

Another important group of predators on *Macoma* are epibenthic crustaceans and fish (Van der Veer et al., 1998; Beukema et al., 1998). Being aquatic animals, most epibenthic species are only active when the tidal flats are submerged. Most abundant are the shrimp *C. crangon*, the crab *C. maenas*, gobies *Pomatoschistus minutus* and *P. microps* and juvenile flatfish *Pleuronectes platessa*, *Platichthys flesus* and *Solea solea*. In contrast to the bird predators, the epibenthic species probably select for the smallest individuals. Especially the shrimp *C. crangon* is known to eat large numbers of bivalve spat (Keus, 1986; Van der Veer et al., 1998). *C. maenas* can cause large density reductions of *Macoma*

in enclosure experiments (Fernandez et al., 1999) and *Macoma* is found in their stomach (Scherer and Reise, 1981; Van der Veer et al., 1998; Richards et al., 1999). Stomach content studies showed that bivalves are no important part of the diet of gobies (Fonds, 1973) and no effect of *Pomatoschistus* enclosure on bivalve abundance has been found in enclosure experiments (Berge and Hesthagen, 1981; Jaquet and Raffaelli, 1989; del Norte-Campus and Temming, 1994). We know only one study in which the effect of tidal level on mortality of *Macoma*-spat was examined; Reise (1978) excluded epibenthic predators at four tidal levels: the *Corophium*-zone, seagrass-beds, *Arenicola*-flats and low lying mud flats and found that mortality was only strongly reduced in the low intertidal. The set-up of that study, however, does not allow a conclusion on the effect of tidal level on predation on small bivalves. The third group of predators, which will be considered in a later paper, are infaunal polychaetes and gastropods.

This study tests the hypothesis the migrations of *M. balthica* are an adaptive strategy to avoid epibenthic predation on the juveniles and bird predation on the adults. This hypothesis was formulated by Beukema (1993a), based on descriptive studies in the western Wadden Sea. We looked at the effect of epibenthic and bird predation on density and growth of juvenile and adult *M. balthica*. Because high tidal flats are exposed for a long period, we expect a high predation pressure of birds on *Macoma* on the high flats. On the low tidal flats, we expect a high predation pressure by aquatic epibenthos, as these need water for activity.

This study tests the hypotheses that:

- predation pressure on juvenile *Macoma* is higher on the low than on high tidal flats due to predation by epibenthos, which select for relatively small prey;
- predation pressure on adult *Macoma* is higher on the high tidal flats due to predation by birds, which select for relatively large prey.

Together, these two groups of predators may force *Macoma* to live in the high intertidal as a juvenile and in the low intertidal as an adult.

2. Methods

This study was carried out between March and November in the years 1998, 1999 and 2000. What we call 0-group *Macoma* in this paper are the animals that settled between April and May and were 0–8 months old during the experiments. These animals measure 0.3–5 mm. 1+ group *Macoma* are older animals and were at least 11 months old at the start of the earliest experiments in March.

These animals measure 6–20 mm and can reach an age of 4+ years in the study area.

2.1. Set-up of the study

Predation on *M. balthica* was studied by:

- measuring epibenthic predator densities on low and high tidal flats;

- examining consumption and size selection by epibenthic predators from stomach content analysis;
- examining size selection by epibenthic predators from laboratory predation experiments;
- examining the effect of en- and exclosing epibenthic predators and exclosing birds at low and high tidal flats on density and growth of 0-group and 1+ *Macoma*. The exclosure experiments also included transplantations of 0-group *Macoma* to locations where they did not naturally occur.

2.2. Study site

Our study was carried out at the Groninger Wad in the eastern Dutch Wadden Sea (6°31' E, 53°27' N) (Fig. 1). The average tidal range is 2.4 m. The tidal flat area ranges from –1.4 to +1.0 m NAP (Dutch ordinance level, close to mean tidal level); saltmarshes occur at the higher levels. Mean high water (MHW) is at +1.0 m, mean low water (MLW) at –1.4 m NAP. On the salt marsh side, brushwood groynes of former landreclamation works enclose the tidal flat area above +0.3 m NAP. Sediments range from fine sand to fine silt. We divided the tidal flats into low and high tidal flats, the low flats ranging from –1.4 to +0.2 m NAP and the high one from +0.3 to +1.0 m NAP. The area of the low tidal flats was slightly larger than that of the high tidal flats.

2.3. Density of predators: estimating predation pressure

Densities of epibenthic predators were estimated with a pushnet for the small epibenthos and passively fishing pitfalls for the larger crabs. Because a large fraction of the sampled stations were very shallow (less than 0.5 m of water at high tide), a pushnet was used, because it can fish in these shallow waters and does not disturb the sediment at the locations before fishing. The net was 0.5 m wide and 0.5 m high with a mesh size of 4×4 mm. A person walking on the tidal flats and therefore between knee- and waist-deep in the water, pushed the net over the bottom at an approximate speed of 1 m s^{-1} ; fishing speed was probably lower in deeper waters. Stations were sampled in daytime after high tide, as soon as water depth allowed fishing (less than 1 m, even shallower on the very high flats). The area fished was calculated from the number of steps of 0.7 m (calibrated with a GPS over a large distance) taken by the person with the pushnet. The sampled area was adjusted to predator density and varied from 3.5 m^2 (10 steps) in September 1999 to 17.5 m^2 (50 steps) in November 2000.

The stations were sampled on 17 September 1999, 8 October 1999, 30 October 1999, 18 April 2000, 18 May 2000, 15 June 2000, 21 July 2000, 17 August 2000, 29 September 2000 and 9 November 2000. No sampling was carried in winter, as predators densities were very low in this period. We sampled 8 to 10 locations (Fig. 1A, series 1999-2, 2000-1 and 2000-2), each within 50 m of the cages of the exclosure experiment (see below).

Adult-crab abundances were estimated with pitfalls of 12.5 cm diameter and 35 cm deep. Pitfalls estimate the product of crab abundance and crab activity (which probably correlates with immersion time and time of stay) and can be used as an estimate of predation pressure. The pitfalls were only used in summer and autumn 1999. They fished

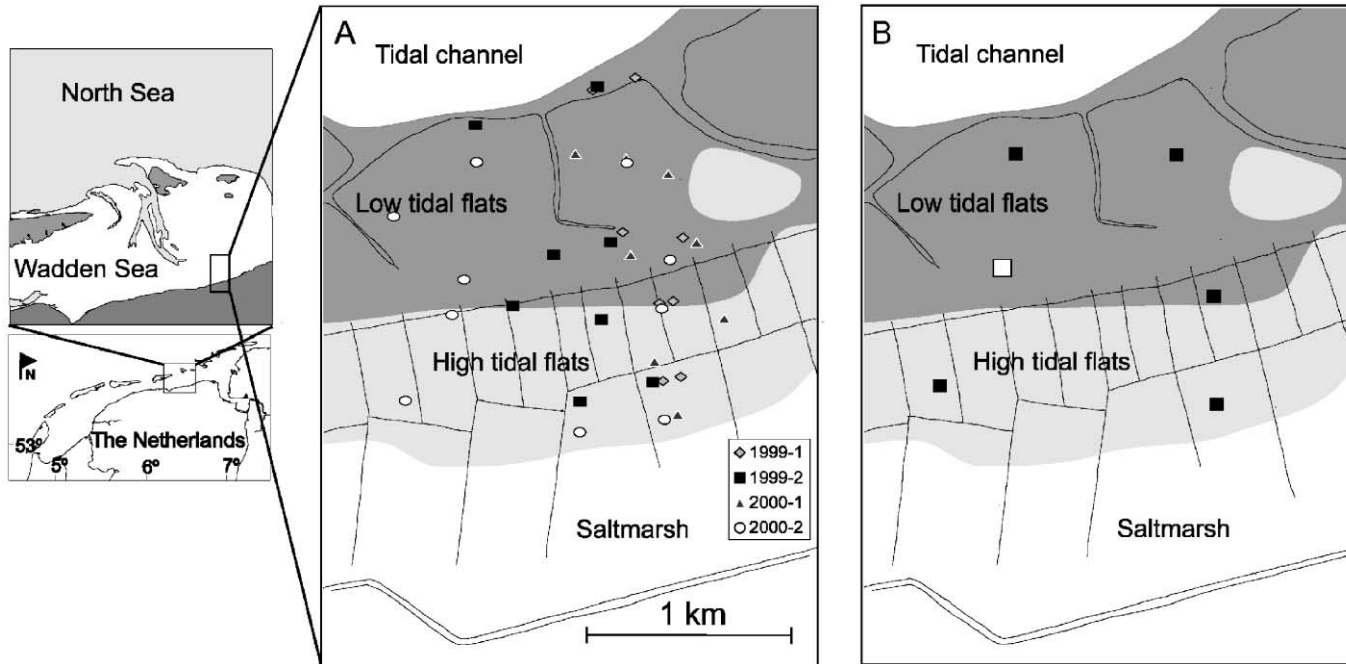


Fig. 1. Map of the study area in the Dutch Wadden Sea. (A) Locations of enclosures in the different series on the Groninger Wad tidal flats. Periods of the different series are presented in Table 2. (B) Locations of the transplantation experiments. Solid squares are the locations where treatments were placed. The open square was the location of the source of the transplanted animals. At this location, a treatment was placed as well.

passively during two high tides in a 24-h period. The traps were used at 6 August, 19 August, 2 September, 8 October, 4 November and 9 November 1999 at the four easterly locations of series 1999-2 (Fig. 1A).

The catch was preserved in the field in 4% formalin and sorted in the laboratory. All predators were measured in the laboratory, except for the pushnet catches in 1999. In shrimps and fish, total lengths were measured. In crabs carapace width was measured and, based on this size, crabs were divided into two groups (the 0-group from 0 to 3 mm in June up to 15 mm in November) and the larger 'adult' group (Klein Breteler, 1976).

The efficiency of the pushnet for *Crangon*, *Carcinus* and gobies entering the net (not those escaping in front of the net) was determined by a 'cod end'-cover experiment on 16 July and 24 August 2001 in gullies. Under the normal mesh (4 × 4 mm), a 2 × 2 mm mesh was attached, leaving 5 cm between the two nets. After fishing, the size of the animals in the two nets was compared. Net efficiency for flatfish was not determined because densities were too low. Because predators' lengths were only measured in 1999, we made no corrections for net efficiency when presenting predator density data. In the calculations of consumption by predators, densities were corrected for net selection.

2.4. Stomach contents of predators

The stomachs of *Carcinus* juveniles and adults, *Crangon*, *P. microps*, *Pleuronectes*, *Platichthys* and *Solea* caught in the field with a pushnet on 15 June 1998 and on 15 June, 21 July, 17 August and 29 September 2000 (method, see above) were selected for stomach content analysis. Predators from all tidal levels were used. Stomachs were opened in a petridish with water and examined under a binocular microscope at 10 × magnification. In each stomach, the number of recognisable *Macoma* shell fragments was counted. As most *Macoma* in stomachs were broken, we developed a method for length estimation of the eaten shell, based on the 'hinge + top' of the shell, which is very durable and rarely broken. Dekinga and Piersma (1993) and Zwarts and Blomert (1992) who used this method for diet analysis of the shorebird Knot *Calidris canutus*, give a calibration line for *Macoma* larger than 4 mm. We made a new calibration line of hinge + top length on shell length with *Macoma* smaller than 7 mm, collected in the field in June 2000. Lengths were measured with a binocular eyepiece micrometer. The length–frequency distribution of *M. balthica* from stomach contents was compared with length–frequency distribution of the field population.

2.5. Size selection by epibenthic predators: laboratory experiments

Size selection by *Carcinus*, *Crangon*, *P. microps*, *Pleuronectes* and *Platichthys* was studied in the laboratory. All experiments were conducted in containers of 15 × 10 × 13 (l × w × h) cm, with a 4-cm sand layer (grain size < 300 µm) on the bottom and a 0.5-mm mesh lid. *Macoma* for the experiments were collected at the Groninger Wad, measured with a binocular eyepiece micrometer and assigned to a size class. For lengths from 0 to 10 mm, size classes of 0.5 mm were used. In pilot experiments, crabs with a carapace width larger than 15 mm did eat *Macoma* larger than 10 mm. Therefore, in experiments with *C. maenas*, three larger size classes were also included: 10–12, 12–14 and 14–16 mm. Size

classes were named after the high end size limit (i.e., the 0–0.5 mm size class is called 0.5 mm in the results). Five *Macoma* were assigned to each size class. The total number of *Macoma* in each experiment was therefore 100 (or 115 in experiments with crabs). The selected *Macoma* were left to bury in the container for 6 h. Animals that did not bury were replaced by animals of the same size class. The whole container (with lid) was placed in an aquarium with running water at 10 °C and a salinity of 30 ‰.

Predators were collected at the Groninger Wad. The duration of the experiment and number of predators were adjusted after several pilot experiments to reach a consumption large enough to examine selection. Before the experiments, predators were starved for 48 h. To examine, for crab and shrimp, the effect of predator size on size selection, experiments were carried out with several sizes of predators (Table 1). Individual crabs and shrimps were never used more than once in an experiment. In experiments with fish, always the same individuals were used, because no other animals were available. Each experiment was replicated five times.

After the experiment, the sediment was sieved over 300 µm. All retrieved *Macoma* were measured and assigned to a size class. The number of consumed shellfish per size class was calculated from the difference between added and retrieved shellfish. In 15 controls without predators, not a single *Macoma* was lost and never more *Macoma* were retrieved than were added.

The selectivity was estimated by the Electivity index, E' . E' is calculated per size class as: $E' = (c_i - o_i)/(c_i + o_i)$ where c_i is number of consumed bivalves per size class and o_i the expected consumption per size class (Ivlev, 1961). The expected consumption o_i was calculated as the average consumption per size class (total number consumed in the experiment divided by the number of size classes). Positive E' values indicate a preference, negative ones rejection. Size classes that were not eaten at all get the E' -value, -1 . The significance of selection was tested with a t -test comparing c_i and o_i per size class, from all five replicas, as in Stamhuis et al. (1998).

2.6. Exclosure studies

Exclosure studies intend to exclose predators from a plot and compare abundance of the prey with a control plot where predators have normal access. We examined the effect of predators on the density and growth of *M. balthica* at the low and high tidal flats. The first 'exclosure' experiment examined the effect of epibenthos such as shrimps, crabs and fish

Table 1

Predators in the size selection experiments. Species used, number of predators per experiment, predator sizes, duration and timing of the experiments are given

Species	Predators experiment ⁻¹	Predator sizes (mm)	Duration (h)	Time
<i>Carcinus maenas</i>	1	4, 6, 8, 12, 16, 20	6	9 am to 3 pm
<i>Crangon crangon</i>	4	15, 20, 25	24	9 am to 9 am
<i>Pleuronectes platessa</i>	1	45	24	9 am to 9 am
<i>Platichthys flesus</i>	1	75	24	9 am to 9 am
<i>Pomatoschistus microps</i>	1	45	24	9 am to 9 am

and shorebirds in 1×1 m plots (Fig. 2a). The second ‘transplantation’-experiment aimed at epibenthic predation on 0-group *Macoma* at locations where these small *Macoma* did not occur. To enable study of growth and mortality of 0-group animals on these locations, 100 0-group *Macoma* were transplanted to small cages at these locations (Fig. 2b).

Five different treatments were applied in the enclosure experiment. Epibenthos and birds were excluded from cages with 2-mm mesh size (Ex: enclosure, Fig. 2a). Predators were removed at the start of the experiment with a 1-mm mesh dipnet and by searching visually. The procedural control for this enclosure, allowing epibenthic predator access but otherwise mimicking the condition in a closed cage, was a 2-mm mesh cage with one open side (Co: procedural control). In some cases, epibenthic predators were accidentally en-

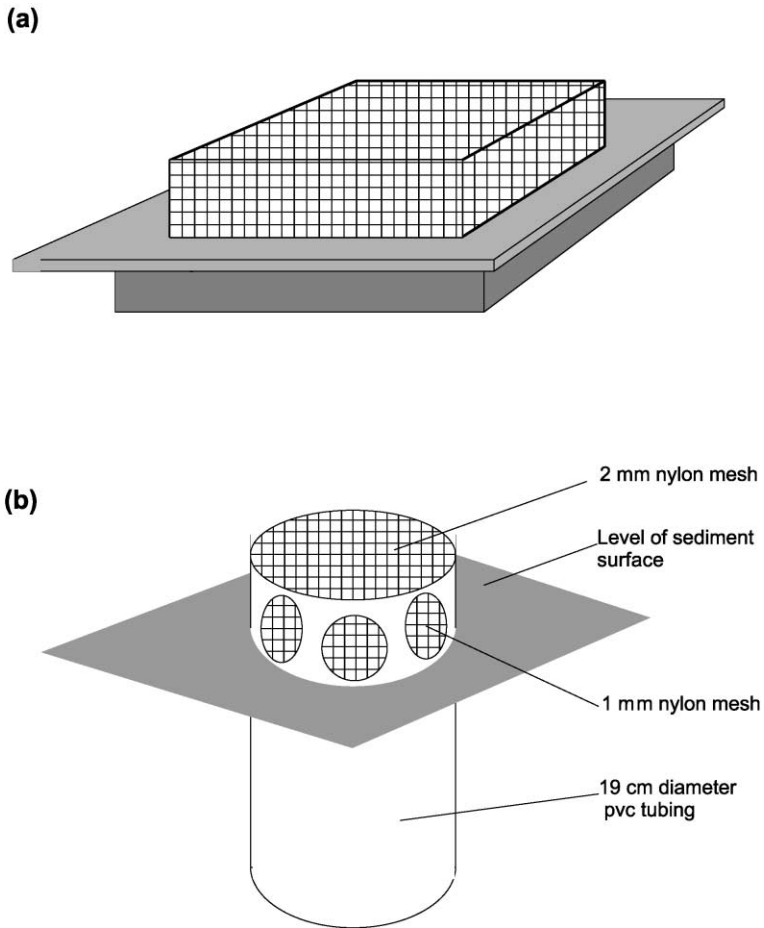


Fig. 2. (a) Construction of an enclosure cage. The grey frame was constructed of PVC-plastic. Mesh width was 2 mm. Ex-cages were completely closed, while in Co-cages, one of the sides was open. (b) Cage (Ex) as used in the transplantation experiment. In the procedural control (Re), all side holes were open (not covered with 1 mm mesh).

closed in the enclosure. In such cases, the cage was analysed as an epibenthic predator enclosure (En: enclosure). Birds, but not epibenthic predators, were excluded with wires at 5 and 15 cm above the sediment surface (Bi: bird enclosure). The control for this plot was an untreated (but marked) plot (Re: reference).

Enclosure (En) of crabs could occur by two means. First, crabs could not have been discovered when placing the cages. Such crabs were locked up during the entire experiment. The second, much more common option, was settlement of larval crabs, in the cages and subsequent growth of the juveniles. These very small crabs were found on almost all plots at the end of series 1999-1 and 2000-1. These crabs, which had only settled 2 weeks before, were very small and probably consumed only small amounts of the large (3–4 mm) *Macoma*-spat (see the results of the size selection experiment). Therefore, we consider low numbers of juvenile crabs (less than the arbitrary 25 crabs with carapace width less than 5 mm) in the Ex-treatment acceptable. Cages with larger crabs were always analysed as En.

As density of *Macoma* was 200–10,000 m⁻² (Hiddink and Wolff, in press) and epibenthic predators reached densities up to 10 m⁻², the size of the plots was chosen as 1 × 1 m. Generally, duration of the experiments was 50–100 days, which should be long enough to see a significant reduction in densities of 0-group *Macoma*. Most experiments were executed between March and October, as in this season epibenthic predators are abundant. Since winter in the Wadden Sea is a period with ice and high wind, making maintenance of cages difficult, only one experiment with the less vulnerable Bi and Re treatment was carried out in winter (series 2000-0).

The ‘enclosure’ experiments were carried out in five consecutive series, four between March and October and one in winter only examining bird predation on 1+*Macoma* (Table 2). Each time, we placed all treatments at 8–10 locations (Fig. 1A). The number of successful replicas per treatment varied between 0 and 10 as some treatments failed due to storms and drifting seaweed (Table 2).

Table 2

Enclosure experiments. Duration, *n* per treatment, distribution of the locations over high and low tidal flats and applied analyses per enclosure study series

Series	1999-1	1999-2	2000-0	2000-1	2000-2	Total
Start date	29-Apr-99	22-Jul-99	27-Jan-00	15-Mar-00	12-Jul-00	
End date	7-Jul-99	22-Sep-99	15-Mar-00	28-Jun-00	25-Oct-00	
Duration (days)	69	62	48	105	105	389
Number of locations	8	8	4	8	10	38
Co	5	6	0	4	8	23
Ex	2	0	0	4	4	10
En	3	5	0	1	3	12
Re	8	8	4	8	10	38
Bi	5	8	4	7	10	34
High tidal flats	16	15	2	12	15	61
Low tidal flats	7	12	6	12	20	57
Length 0-group	yes	yes	not applicable	no	yes	
Length other age groups	yes	yes	yes	yes	yes	
Sediment analysis	no	no	no	yes	yes	

For the 1999-1 series, the locations were chosen in duplicate at four tidal levels (–0.3, 0.0, 0.3 and 0.7 m above MTL). For the 1999-2 series, the locations were chosen at random locations on a 1-km stretch (approximately parallel to the shore) at each of these four tidal levels. The locations for series 2000-1 and 2000-2 were chosen randomly within the map area of Fig. 1A.

All cages were checked weekly. Drifting seaweed was removed and damage was repaired. Accidentally enclosed small crabs found during the first 2 weeks of the experiment in the Ex treatment were removed. Because this period was short compared to the whole experiment, we assumed the predators did not have an effect on *Macoma* densities and these cages were treated as Ex in the analysis.

At the end of each experiment, all treatments were sampled. We took 10 cores of 83 cm² from each plot; these samples were pooled in the field and sieved over 1 mm. For series 1999-1 and 2000-1, one core of 43 cm² was taken to sample spat smaller than 1 mm in the centre of the plot. This sample was sieved in the laboratory over 300 µm. Predator densities in each of the plots were determined by visual inspection at the end of the experiment and from the number of predators in the samples. Samples were stored at –20 °C until sorting in the laboratory. For each *Macoma* in the samples, age was read from the number of year rings on the shell and length was measured with callipers.

In 2000, we examined differences in sediment composition between the treatments. From each plot, a sediment sample was taken to a depth of 10 cm. Samples were dried at 70 °C and weight loss was estimated after incineration at 550 °C for 6 h. After this, samples were grounded in a mortar and grain size distribution was determined by dry sieving. From this, we calculated silt content (<63 µm) and median grain size.

In the transplantation experiment, 100 0-group *Macoma* were added to small Ex and Co-treatments with 1 mm mesh (Fig. 2b) (no En and Bi treatment were applied). Further, 100 *Macoma* were added to a further untreated Ro plot and an untouched plot (Un) was sampled at the end of the experiments. All plots had an area of 283 cm². Before adding the bivalves to the plots, the original 0-group *Macoma* and other shallow living macrofauna were removed with the top layer of the sediment to a depth of 3 cm. The sand was sieved over 500 µm and put back in plots. All *Macoma* that were transplanted into the plots were collected at a common source location at mid tide level, 1 day earlier (Fig. 1B). They were stored overnight in 4 cm of sediment in an aquarium with running water. Two consecutive experiments were conducted. The first experiment started on 11 August 2000 and ended on 27 September 2000 (47 days). The animals were transplanted to six locations (Fig. 1B). The second experiment started on 27 September 2000 and ended on 8 November 2000 (42 days). The animals were transplanted to five different locations (Fig. 1B). At the end of the experiment, all plots were sampled by digging them out to a depth of 5 cm and sieving over 1 mm. The treatment of these samples was similar to the enclosure experiment samples, but only the 0-group and not older shellfish were examined.

2.7. Statistical analysis of caging experiments

Densities and lengths in the enclosure and transplantation experiments were examined in a three-factor ANOVA. We used tidal level (low—<0.2 m above MTL or high—>0.3 m above MTL) and treatment (Co, Ex, En, Re or Bi) as factors. Season (spring or autumn)

was also used as a factor, because differences between the experiments due to differences between seasons were expected. If variances of density data were not homogeneous, a square-root transformation was applied.

3. Results

3.1. Predator density and distribution

The fraction of predators caught by the pushnet, of those entering the net and caught or passing through the mesh, can be described as a function of predator length: $P = 1/(1 + (\exp(-A \times L + B)))$, where P is the proportion caught and L the predators size and A and B are constants (King, 1995). No shrimp smaller than 10 mm were caught, while no shrimps longer than 22 mm passed through the mesh ($A = 0.68$, $B = 11$, $R^2 = 0.89$, $p = 0.000$). No crabs smaller than 2 mm were caught, while no crabs wider than 6 mm passed through the mesh ($A = 1.09$, $B = 5.3$, $R^2 = 0.96$, $p = 0.001$). No gobies smaller than 18 mm were caught by the pushnet, while no gobies longer than 30 mm passed through the mesh ($A = 0.36$, $B = 7.5$, $R^2 = 0.86$, $p = 0.000$). These numbers tell us nothing about predators fleeing in front of the net.

Fig. 3 shows estimates of density for each predator species on the tidal flats from summer 1999 to autumn 2000. *Crangon* and *Carcinus* were the most abundant species, reaching maximal average densities of 12 and 6 ind m^{-2} , respectively. Both crustaceans and the gobies, *P. minutus* and *P. microps*, were most numerous from June to September. Numbers of juvenile flatfish (*Pleuronectes*, *Platichthys* and *Solea*) were low, they were found in May and June only. 0-Group *Carcinus* was more abundant on the high than on low tidal flats (ANOVA, $df = 80$, $F = 7.93$, $p = 0.0061$, Fig. 3). *Crangon* was most numerous on low tidal flats (ANOVA, $df = 80$, $F = 13.01$, $p = 0.0005$). *Pomatoschistus* and flatfish abundance did not differ significantly between low and high tidal flats (ANOVA, *Pomatoschistus*: $df = 66$, $F = 0.93$, $p = 0.33$; flatfish, $df = 21$, $F = 2.34$, $p = 0.14$). In both crabs and shrimps, average sizes in the catches (which were measured only from May to October 2000) were larger on low than on high tidal flats. 0-Group *Carcinus* on the low tidal flats measured 8.0 ± 2.6 mm, and the high flats measured 5.1 ± 2.0 mm (t -test, $p = 0.000$). *Crangon* on the low tidal flats measured 25.2 ± 4.7 mm and the high flats measured 18.8 ± 9.1 mm (t -test, $p = 0.000$).

Adult *Carcinus* were most abundant in both numbers and biomass in the lowest pitfall (-0.3 m above MTL) (Fig. 4, ANOVA on log-transformed numbers: $df = 21$, $F = 8.05$, $p = 0.0013$, ANOVA on log-transformed weight: $df = 21$, $F = 11.11$, $p = 0.0002$). Weight per individual was also highest in this pitfall (ANOVA on log-transformed weight: $df = 16$, $F = 8.93$, $p = 0.0018$). We kept in mind that it is not allowed to draw conclusions on the effect of tidal level on crab abundance from inferential statistics on these pseudoreplicated observations.

Oystercatcher (*Ostralegus haematopus*), Curlew (*Numenius arquata*), Dunlin (*Calidris alpina*), Redshank (*Tringa totanus*), Eider duck (*Somateria mollissima*), Common shelduck (*Tadorna tadorna*) and Mallard (*Anas platyrhynchos*) were common in the research area (De Jong and Koks, 1999). Their spatial distribution was not recorded.

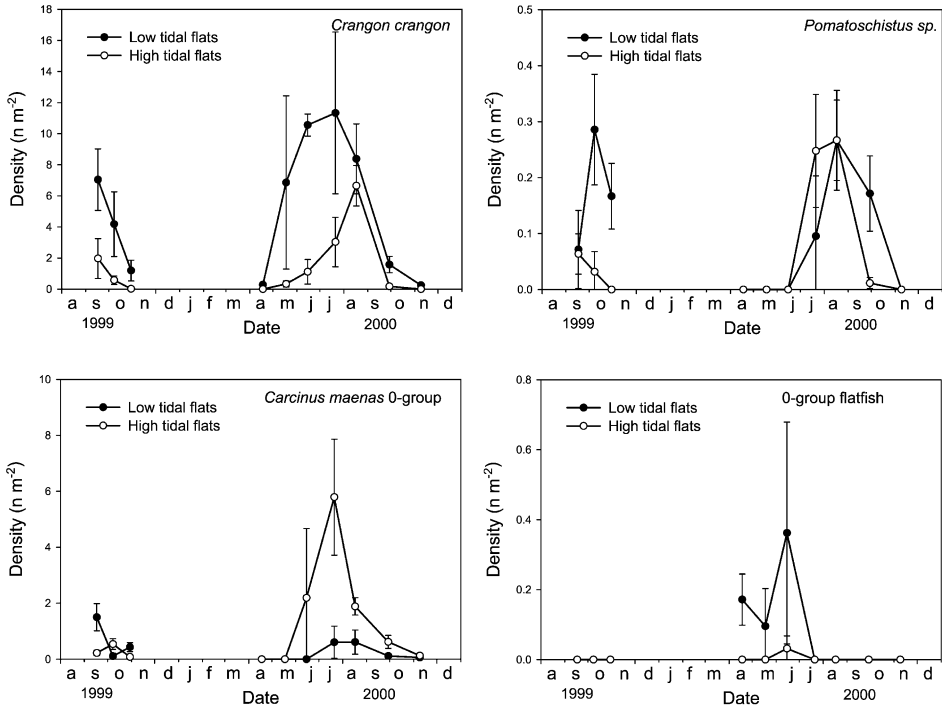


Fig. 3. Estimates of densities of four predators ($\pm 95\%$ confidence intervals) on low and high tidal flats of the Groninger Wad from September 1999 to November 2000. Sampling was carried out at high tide on the tidal flats with a pushnet. Notice the different scalings on the density-axis.

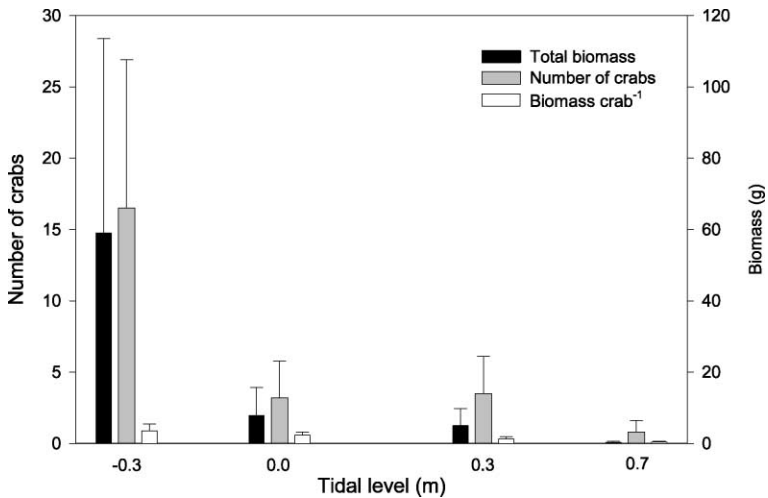


Fig. 4. Number (\pm SD) caught per 24 h (left axis) and weight (\pm SD) (right axis) of *C. maenas* adults in pitfalls at different tidal levels on the tidal flats of the Groninger Wad in late summer and autumn 1999.

3.2. Stomach contents of epibenthic predators

The number of animals of which the stomach content was examined per month and the number of *Macoma* fragments per species is shown in Table 3. Fish are not presented in this table because the number of examined fish was low and no *Macoma*-remains were found in fish stomachs. In total, 38 fragments of *Macoma* shells were found in 338 examined stomachs. In 0-group *Carcinus* on average 0.20 *Macoma* was found. Both *Crangon* and adult *Carcinus* stomachs contained on average 0.10 *Macoma* per stomach.

Calibration showed that there is a significant relation between shell-length and hinge+top length of juvenile *Macoma* (2–7 mm) (Fig. 5): $L = 16.0 \times H^{0.97}$ in which L is the shell length and H is the hinge width ($n = 25$, $R^2 = 0.93$, $p = 0.000$). We found 13 measurable hinges in the stomachs of *Crangon* and only two in 0-group *Carcinus* (both 1.9 mm shell length). All eaten *Macoma* were smaller than 2.5 mm, while length of the whole population on 7 July 1999 ranged from 0.5 to 17 mm (Fig. 6). Stomachs of flatfish and gobies contained no bivalve shells, but did contain up to 50 1-mm pieces of bivalve siphons.

3.3. Size selection by epibenthic predators: laboratory experiments

Carcinus mainly consumed *Macoma* smaller than 5 mm, but eaten *Macoma* ranged from 0.5 to 14 mm in length (Fig. 7A). The size class most consumed in the crab experiments was 2.0 mm. The largest *Macoma* eaten was 14 mm long and opened by a 20-mm crab. The preferred size class depended on the size of the crab; larger *Carcinus* selected for larger prey (Table 4). The relation between the *Macoma*-size class most consumed and the carapace width of the crab was: $\text{Macoma-size} = 0.21 \times \text{carapace width} + 0.95$, $n = 5$ crab size classes, $R^2 = 0.965$, $p = 0.005$.

Carcinus 4-mm crabs significantly positively selected for 1.5-mm *Macoma* and 20 mm crabs positively selected for 5 mm *Macoma* (Table 4). Significantly negative E' -values, indicating rejection, were found for large *Macoma* for all sizes of crabs and for the smallest *Macoma* in 16 and 20 mm wide crabs. *Crangon* only ate *Macoma* smaller than

Table 3

Juvenile *M. balthica* in the stomachs of *C. crangon* and *C. maenas* (juveniles and adults) on the tidal flats of the Groninger Wad. The average number of *M. balthica* per stomach is given

Date	<i>Crangon</i>		<i>Carcinus</i> 0-group		<i>Carcinus</i> adult	
	<i>n</i>	<i>Macoma</i> predator ⁻¹	<i>n</i>	<i>Macoma</i> predator ⁻¹	<i>n</i>	<i>Macoma</i> predator ⁻¹
June-98	101	0.08	7	0.57	6	0.17
June-00	42	0.31	10	0.00	8	0.13
July-00	28	0.04	15	0.07	1	0.00
August-00	20	0.00	20	0.25	0	
September-00	31	0.06	16	0.13	0	
<i>N</i>	222	0.10	68	0.20	15	0.10

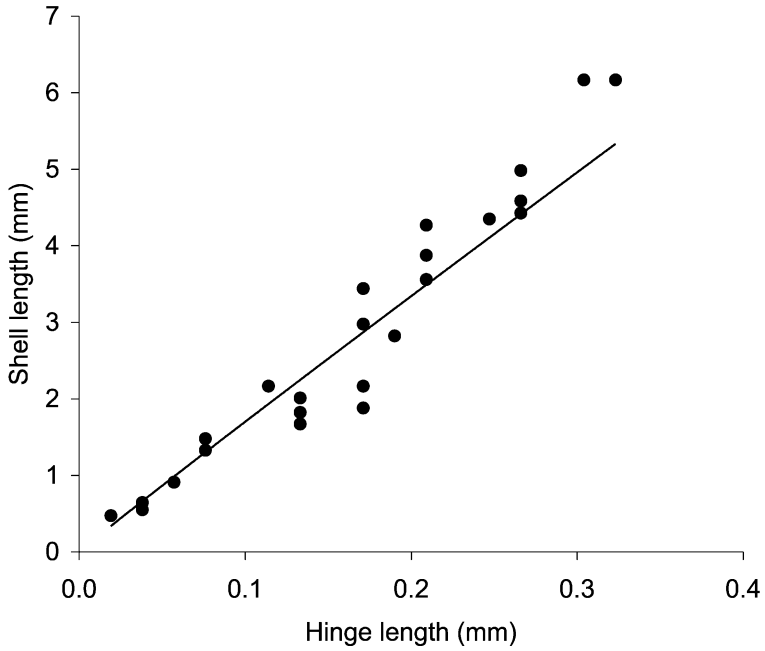


Fig. 5. Calibration of shell length on hinge plus top-width for juvenile *M. balthica*. $n=25$, $R^2=0.93$, $p=0.000$.

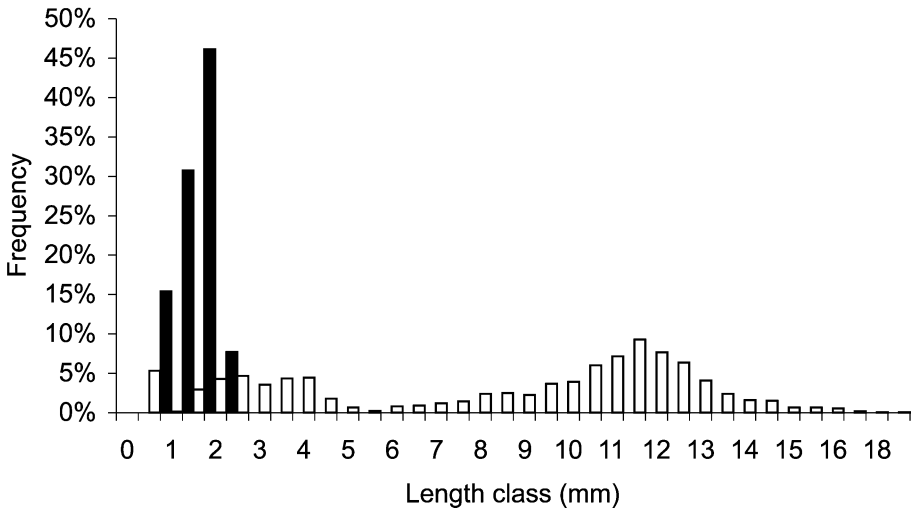


Fig. 6. Length–frequency distribution of *M. balthica* shell length on the tidal flats of the Groninger Wad on 7 July 1999 (white bars) and as found in stomach contents of *C. crangon* (most animals collected on 15 June 2000) (solid bars). Shell length of consumed *M. balthica* was calculated from the size of the hinges as found in the stomachs of *C. crangon*.

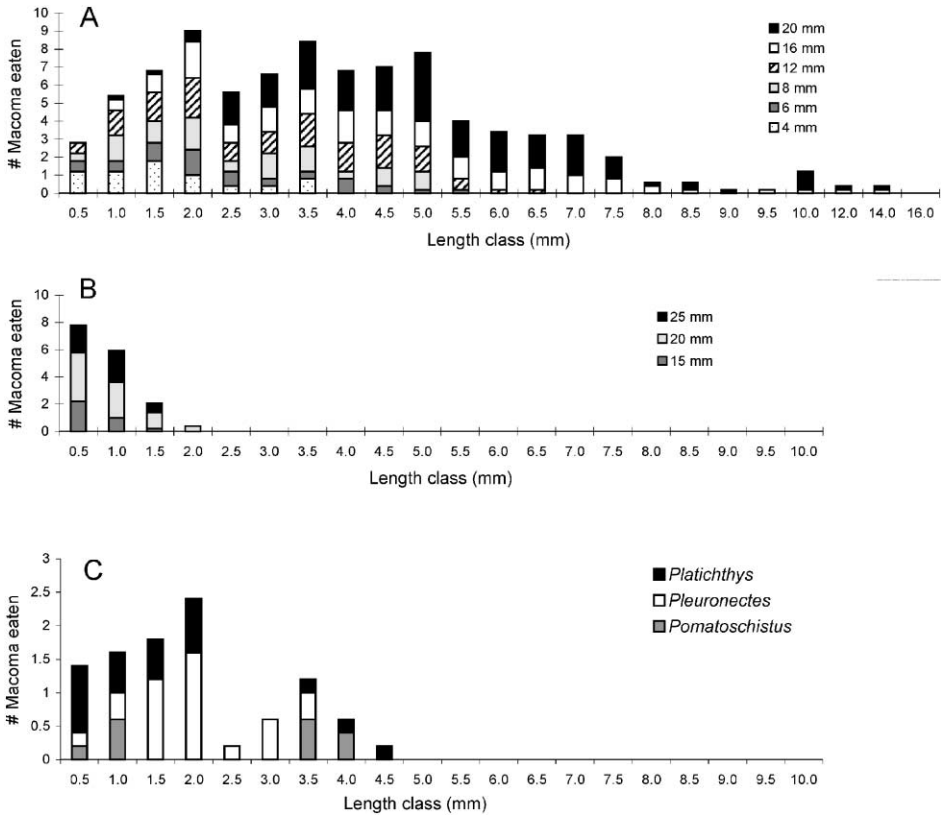


Fig. 7. Length–frequency distribution of the average number of *M. balthica* eaten per experiment by the crab *C. maenas* (A), *C. crangon* (B) and by juvenile flatfish and the goby *P. microps* (C) in laboratory size-selection experiments. Five shellfish were offered per size class, to six size-classes of crabs, three size-classes of shrimps and three fish species (for predator sizes and fish species see legends in graph).

2.5 mm (Fig. 7B). The smallest size class (<0.5 mm) was most consumed. The 15- and 20-mm shrimp showed a significant positive selection for *Macoma* smaller than 1.5 mm (Table 4). All fish species consumed only few shellfish in the experiments and only ate *Macoma* smaller than 5 mm.

3.4. Growth of epibenthic predators in relation to growth of 0-group *Macoma* in the field

Fig. 8 shows the growth of crabs and *Macoma* in the field from June to November. *Macoma* size was estimated from Re treatments in the enclosure studies and from a survey of 57 stations on the Groninger Wad in 1998 (Hiddink and Wolff, in press). From the actual size of 0-group *Carcinus* from the field and the relation between crab size and preferred *Macoma* size in the laboratory size selection experiment, we calculated the preferred size of *Macoma* for each date for which we knew *Carcinus* size (Fig. 8).

Table 4

Size selection by predators eating *M. balthica* in laboratory experiments. The Electivity index (Ex') per predator species per *M. balthica* length class is given. Positive Ex' -values indicate a preference, negative Ex' -values indicate rejection. Bold Ex' -values are significantly different from zero (t -test, $p < 0.05$)

Species	<i>Carcinus</i>	<i>Carcinus</i>	<i>Carcinus</i>	<i>Carcinus</i>	<i>Carcinus</i>	<i>Carcinus</i>	<i>Crangon</i>	<i>Crangon</i>	<i>Crangon</i>	<i>Pleuronectes</i>	<i>Platichthys</i>	<i>Pomatoschistus</i>
Length class	4	6	8	12	16	20	15	20	25	45	75	45
0.5	-0.04	-0.73	-0.69	-0.30	-1.00	-1.00	0.79	0.80	0.74	-0.27	-0.70	-0.64
1.0	0.06	-0.48	0.23	-0.11	-0.43	-0.80	0.39	0.41	0.22	-0.02	-0.37	-0.26
1.5	0.63	-0.01	-0.03	-0.09	-0.18	-0.80	-0.69	0.24	-0.43	-0.02	0.03	-1.00
2.0	-0.29	0.31	0.24	-0.09	0.21	-0.60	-1.00	-0.42	-1.00	0.00	0.43	-1.00
2.5	-0.40	-0.05	-0.38	-0.02	-0.26	0.04	-1.00	-1.00	-1.00	-1.00	-0.70	-1.00
3.0	-0.36	-0.39	0.23	-0.18	-0.20	0.18	-1.00	-1.00	-1.00	-1.00	-0.02	-1.00
3.5	-0.05	-0.73	0.14	-0.13	-0.16	0.28	-1.00	-1.00	-1.00	-0.62	-0.34	0.11
4.0	-1.00	-0.37	-0.72	-0.08	0.10	0.11	-1.00	-1.00	-1.00	-0.68	-1.00	-0.27
4.5	-1.00	-0.39	-0.34	0.40	0.00	0.09	-1.00	-1.00	-1.00	-0.70	-1.00	-1.00
5.0	-1.00	-0.74	-0.38	-0.10	-0.23	0.53	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
5.5	-1.00	-0.74	-1.00	-0.47	-0.16	0.15	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
6.0	-1.00	-1.00	-1.00	-0.73	-0.18	0.09	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
6.5	-1.00	-1.00	-1.00	-0.79	-0.20	0.02	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
7.0	-1.00	-1.00	-1.00	-1.00	-0.42	0.10	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
7.5	-1.00	-1.00	-1.00	-1.00	-0.22	-0.26	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
8.0	-1.00	-1.00	-1.00	-1.00	-0.58	-0.80	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
8.5	-1.00	-1.00	-1.00	-1.00	-0.69	-0.66	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
9.0	-1.00	-1.00	-1.00	-1.00	-1.00	-0.80	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
9.5	-1.00	-1.00	-1.00	-1.00	-0.80	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
10.0	-1.00	-1.00	-1.00	-1.00	-0.80	-0.14	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
12.0				-1.00	-0.69	-0.81						
14.0				-1.00	-0.78	-0.81						
16.0				-1.00	-1.00	-1.00						

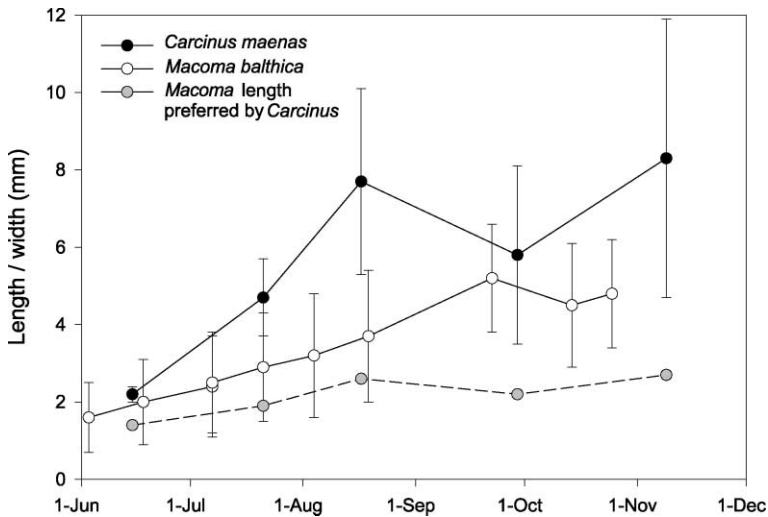


Fig. 8. Size of 0-group *C. maenas* (2000) and 0-group *M. balthica* (1998, 1999 and 2000). The size of *Macoma* preferred by *Carcinus* (in size selection experiments) was calculated from the crab size and plotted in the lowest line. At the start of the growing season, preferred and actual *Macoma* length was approximately equal, while later *Macoma* quickly outgrew the preference of the crabs.

3.5. Exclosure studies

3.5.1. 0-Group *M. balthica*

There was a significant effect of treatment on the density of 0-group *Macoma* (Table 5). Density of the 0-group was very high in the Ex-treatment, while it was low in the Co and En treatment (Fig. 9a). Thus, epibenthic predators consumed a lot of 0-group *Macoma*. Additionally, there was a significant interaction between tidal level and treatment; the differences between treatments Ex and Co were larger in the low than in the high intertidal. This means that epibenthic predators ate more 0-group *Macoma* in the low intertidal than in the high intertidal. 0-group *Macoma* was significantly larger in the high intertidal, there was no effect of treatment (Fig. 9b, Table 5).

3.5.2. 1+Group *M. balthica*

Density of older *Macoma* was not affected by the treatments (Fig. 9c and Table 5). There was however a significant interaction between tidal level and treatment, as the density of 1+ *Macoma* was higher in En and Co than in Ex in the low intertidal, while this effect was absent in the high intertidal. The 1-group was significantly larger in experiment in autumn than in spring, there was no significant effect of tidal level or treatment on 1-group length (Fig. 9d, Table 5).

The average number (\pm SE) of large crabs *C. maenas* in the treatments, at low tide, was 0 (\pm 0) in Ex (by definition), 1.4 (\pm 0.5) in En, 0.2 (\pm 0.1) in Co, 0 (\pm 0) in Re and 0.2 (\pm 0.2) in Bi at the end of the experiment. The average number of 0-group crabs *C.*

Table 5

Exclosure experiments, Three-factor ANOVA-tables. Density and length for 0-group and 1+group *Macoma balthica*

Source	df	Mean square	F-ratio	P-value
<i>Density 0-group Macoma balthica (SQRT-transformation)</i>				
Season	1	30,719	33.64	0.0000
Tidal level	1	11,625	12.69	0.0006
Treatment	4	5224	4.61	0.0019
Tidal level × treatment	4	59,992	6.54	0.0001
Residual	96	916		
Total (corrected)	106			
<i>Length 0-group Macoma balthica</i>				
Season	1	125.72	138.36	0.0000
Tidal level	1	5.96	6.56	0.0129
Treatment	4	0.94	1.04	0.3959
Tidal level × treatment	4	0.67	0.74	0.5677
Residual	62	0.90		
Total (corrected)	72			
<i>Density 1+ group Macoma balthica (SQRT-transformation)</i>				
Season	2	191.5	6.28	0.0027
Tidal level	1	139.0	1.28	0.2608
Treatment	4	19.5	0.64	0.6363
Tidal level × treatment	4	130.6	4.28	0.0030
Residual	105	30.5		
Total (corrected)	116			
<i>Length 1-group Macoma balthica</i>				
Season	1	20.36	40.5	0.0000
Tidal level	1	1.6	3.25	0.0747
Treatment	4	0.8	1.55	0.1926
Tidal level × treatment	4	0.4	0.85	0.4963
Residual	97	0.5		
Total (corrected)	107			

maenas was 5.7 (\pm 2.8) in Ex, 6.3 (\pm 3.1) in En, 4.6 (\pm 3.2) in Co, 1.6 (\pm 0.6) in Re and 1.6 (\pm 0.7) in Bi at the end of the experiment.

These numbers may be a good measure for the predation pressure in the closed En- and Ex-treatment, but they are no good measure for predation pressure in the other treatments, because the larger crabs (that have a biomass that is about 30 times higher than that of 0-group crabs) show tidal migration and are not found on the tidal flats at low tide. Therefore, the above presented crab densities in the open treatments underestimate predation pressure. It is better to examine the densities in Figs. 3 and 4 as a measure of predation pressure.

At the end of the experiment, in some of the Ex and Co cages there were several centimeters of erosion or sedimentation of the sediment. However, there existed no significant differences in the sediment composition (silt content, median grain size and organic content) between treatments.

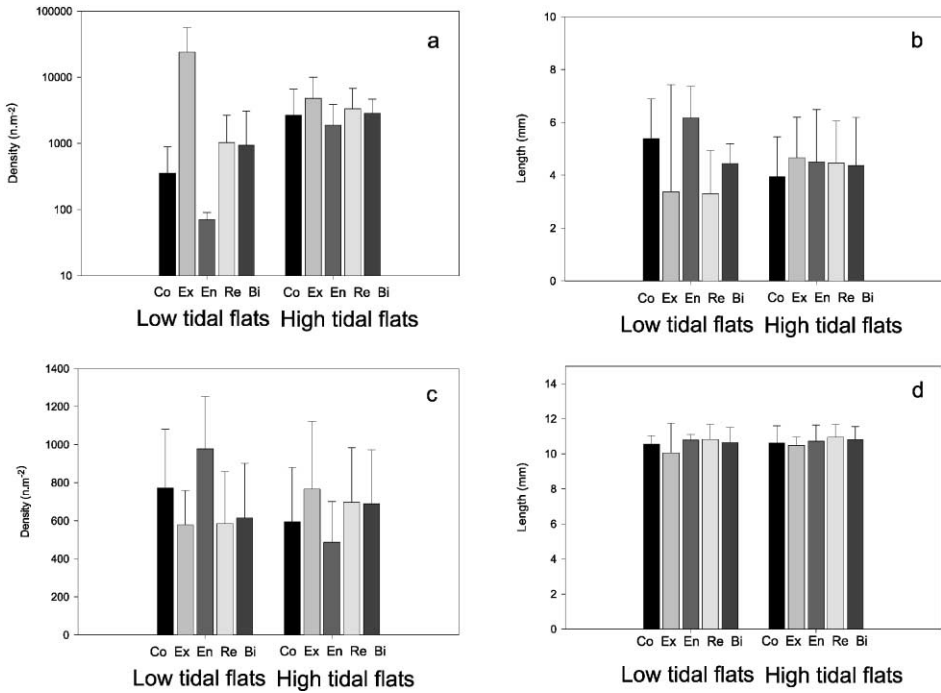


Fig. 9. Enclosure experiment. Density (a), length (b) of 0-group and density (c) and length (d) 1+ group *M. balthica* (+SD) in the five different treatments at two tidal levels in the enclosure experiment. Re: Procedural control epibenthos enclosure, Ex: Enclosure epibenthos, En: Enclosure epibenthos, Re: marked but otherwise untreated, Bi: Birds enclosure. Low tidal flats: below 0.2 m above MTL, High tidal flats: above 0.3 m above MTL.

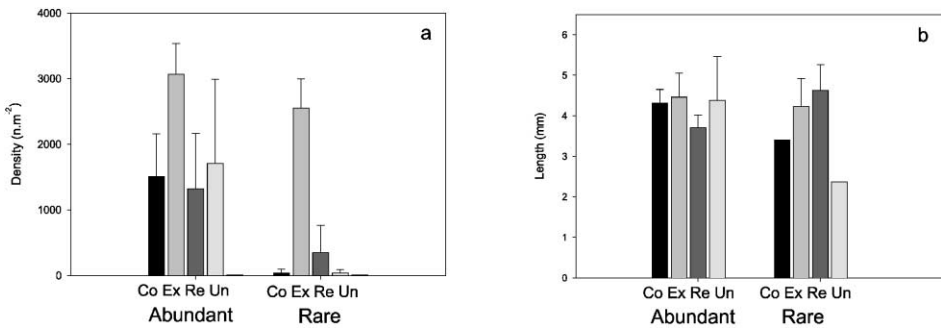


Fig. 10. Transplantation experiment. Density (a) and length (b) of 0-group *M. balthica* (+SD) in the four different treatments at locations where 0-group *Macoma* was originally abundant and rare, respectively. Re: procedural control, with open sides 100 *Macoma* added, Ex: enclosure of predators, 100 *Macoma* added, Re: only marked with bamboo sticks 100 *Macoma* added, Un: untreated, ambient density sample, no *Macoma* added or removed.

Table 6

Two-factor ANOVA tables of the transplantation experiment. Density and length for 0-group *Macoma balthica*

Source	df	Mean square	F-ratio	P-value
<i>Density 0-group Macoma balthica (SQRT-transformation)</i>				
Abundance	1	4854.76	45.59	0.0000
Treatment	3	2025.3	18.89	0.0000
Tidal level × abundance	3	436.356	4.09	0.0140
Residual	34	106,712		
Total (corrected)	41			
<i>Length 0-group Macoma balthica</i>				
Abundance	1	1.5	4.4	0.0469
Treatment	3	0.8	2.3	0.0979
Tidal level × abundance	3	2.1	5.9	0.0033
Residual	26	0.3		
Total (corrected)	33			

3.6. Transplantation experiment

At all high intertidal locations, 0-group *Macoma* were abundant. At two low intertidal locations, the 0-group was absent, while at one low intertidal location the 0-group was abundant. The density of 0-group *Macoma* was strongly affected by both the treatment and the original abundance (Fig. 10a, Table 6). The density in Ex was much higher than in Co and Re, thus predation pressure on 0-group *Macoma* outside Ex was high. The significant interaction between treatment and abundance shows that the difference in density between treatments was much larger on locations where the 0-group was rare. The 0-group was significantly larger on places where it was abundant (Table 6 and Fig. 10b), this was caused by animals from the Un-treatment (not transplanted, originally present animals, therefore only few on the 'rare'-locations) that were small on 'rare' locations. There was a significant interaction between abundance and treatment that was not caused by these few animals, but because animals from the Ex were larger than animals from Re on places where *Macoma* was abundant, while the effect was the other way round on locations where *Macoma* was rare.

4. Discussion

This study evaluates the effect of interaction between predation and tidal level on the abundance of *M. balthica*. The epibenthic predators *C. crangon*, adult *C. maenas* and juvenile flatfish were most abundant and largest on low tidal flats, as was already shown by Beukema (1993a). Only 0-group *Carcinus* was most abundant, but also smaller, on the high tidal flats. *Crangon* and 0-group *Carcinus* were the most abundant predators and their stomachs contained many *Macoma* remains. All epibenthic predators selected for small (generally smaller than 5 mm), 0-group *Macoma*. Summarising, epibenthic predation pressure must be higher in the low than in the high intertidal.

The efficiency of the pushnet (escape through meshes) was, based on predator length as recorded in the field, 55% for *Crangon*. If a third power relation between length and biomass is assumed, the catch efficiency in terms of biomass was 97%. For 0-group *Carcinus*, the average catch efficiency was only 6%, due to the very low efficiency for crabs smaller than 4 mm, which were abundant in July. The catch efficiency in terms of biomass was much higher at 56%. For gobies, the average catch efficiency was 80% in numbers and 88% in terms of biomass. Further, predation pressure was underestimated because shrimps and gobies could escape in front of the net. Because these predators were larger in the low intertidal, the predation pressure on the low tidal flats probably was larger, also relative to high-tidal flat predation. As predator densities were underestimated, predation is even more important in practice.

Both crabs and *Macoma* grow during the summer. From a comparison of growth rates of crabs and shellfish in the field, we can conclude that most *Macoma* outgrow predation by *Carcinus* 0-group within their first summer. Although *Carcinus* grew faster than *Macoma*, it did not grow fast enough to keep its preferred size up with actual *Macoma* size. Shrimps did not eat any *Macoma* larger than 2.5 mm in the laboratory experiments and larger than 3.0 mm in the field. As mean *Macoma* length reached 3 mm in August (Fig. 8), shrimp predation becomes probably less important after August, although there were still smaller *Macoma* after August and *Macoma* was found in *Crangon* stomachs in September (Table 4).

Our conclusions on the enclosure experiments are somewhat hampered by the problems with enclosing crabs and the loss of some cages. We made a somewhat arbitrary distinction between successful enclosures and accidental enclosures of crabs. Based on the results of size selection experiments and stomach content analysis, it seems justified to assume that the just settled 0-group *Carcinus* eat only few 3–4 mm long *Macoma* in a short time span. Therefore, we believe that our treatments indeed represent different predation pressures and that it is justified to draw conclusions on the predation at different tidal levels.

In our enclosure and transplantation studies, only densities of 0-group, and not the older, *Macoma* were reduced by epibenthic predators. Epibenthic predation reduced densities stronger in the low than in the high intertidal. We did not find a significant effect on length by treatment in the enclosure experiments.

We found no effect of bird predation on densities of 0- and 1+ group *Macoma*. However, from many studies it is obvious that shorebirds eat large *Macoma* (Hulscher, 1982; Zwarts and Blomert, 1992; Piersma et al., 1993; Beukema, 1993b). Therefore, it is possible that the power of our experiment was too weak to detect (a small?) predation by shorebirds, a problem which is often encountered in shorebird enclosure studies (Sewell, 1996) or that the experiments had a too small spatial and temporal scale (Van der Meer et al., 2001). In the study area and period, the oystercatcher, *O. haematopus*, was the most abundant shorebird, with on average 2500 birds roosting in the area at high tide during the whole year (De Jong and Koks, 1999). This would result in about 1.2 foraging birds ha^{-1} at low tide. Hulscher (1982) calculated that an oystercatcher foraging on *Macoma* only, eats 499 *Macoma* low tide $^{-1}$, thus almost 1000 day $^{-1}$, in our case this equals 0.12 *Macoma* m^{-2} day $^{-1}$. Hence, in our longest experiments (105 days) a difference of about 13.5 *Macoma* m^{-2} can be expected between controls and bird enclosures (if oystercatchers eat *Macoma* only and if no other species takes *Macoma*). As the standard

deviation within treatments was many times this value (Fig. 9), it is not surprising that no significant differences in densities between bird exclosures and controls were found. The power of our experiment to find this small difference was less than 10%.

The significant interaction between tidal level and treatment in the exclosure experiment (Table 5, Fig. 9) suggests increased survival of adult *Macoma* in the low intertidal and reduced survival in the high intertidal under epibenthic predation, which is unexpected and cannot be explained.

4.1. Consumption by predators

Table 7 gives an order-of-magnitude calculation of the consumption and the resulting mortality of 0-group *Macoma* by *Crangon* and 0-group *Carcinus*. This calculation was based on predator and prey densities and stomach contents found in our study. We used average densities from April to November. Densities were corrected for net efficiency according to biomass (see start of discussion), because biomass probably gives a better estimate of predation pressure than corrected densities, which count very small and large predators equally. To recalculate stomach contents to a daily consumption, we used evacuation time of stomach contents for *Crangon* and *Carcinus* from the literature (Afman, 1980; Pihl and Rosenberg, 1984; del Norte-Campus and Temming, 1994). The estimated mortality values (Z) are 0.0091 day^{-1} for low tidal flats and 0.0008 day^{-1} for high tidal flats (Table 7). Total field mortality values that were calculated from the average from Re treatments in the exclosure experiment in 1999 and 2000 and values from 57 stations on the Groninger Wad in 1998 (Hiddink and Wolff, in press) for low and high tidal flats were 0.0107 and 0.0017, respectively. *Crangon* and 0-group *Carcinus* predation can

Table 7

Order of magnitude calculation of the consumption of 0-group *Macoma* by the epibenthic predators *C. crangon* and 0-group *C. maenas* ($\pm 95\%$ confidence intervals). The calculations were based on average densities from sediment cores and pushnets (corrected for net efficiency) and stomach contents for the period April to November. Evacuation times were obtained from Afman (1980) for *Carcinus* and the average of del Norte-Campus and Temming (1994) and Pihl and Rosenberg (1984) for *Crangon*. Confidence intervals were calculated from the confidence limits of the observations

		Low tidal flats	High tidal flats
Density ($n \text{ m}^{-2}$)	<i>Macoma balthica</i>	1022 \pm 168	3329 \pm 449
	<i>Crangon crangon</i>	4.9 \pm 1.5	1.7 \pm 0.9
	<i>Carcinus maenas</i>	0.6 \pm 0.4	2.4 \pm 1.7
Stomach content (<i>Macoma</i> stomach $^{-1}$)	<i>Crangon crangon</i>	0.12 \pm 0.01	0.08 \pm 0.01
	<i>Carcinus maenas</i>	0.28 \pm 0.03	0.08 \pm 0.01
Evacuation time (h)	<i>Crangon crangon</i>	1.7	1.7
	<i>Carcinus maenas</i>	6.5	6.5
Consumption (<i>Macoma</i> $\text{m}^{-2} \text{ day}^{-1}$)	<i>Crangon crangon</i>	8.70 \pm 3.05	2.04 \pm 1.19
	<i>Carcinus maenas</i>	0.60 \pm 0.45	0.70 \pm 0.63
Calculated Z (day^{-1})	due to <i>Crangon crangon</i>	0.0085 \pm 0.0016	0.0006 \pm 0.0003
	due to <i>Carcinus maenas</i>	0.0006 \pm 0.0003	0.0002 \pm 0.0002
Total calculated Z		0.0091 \pm 0.0020	0.0008 \pm 0.0004
Average observed Z field 1998–2000		0.0107 \pm 0.0042	0.0017 \pm 0.0048
% Z explained by predation <i>Crangon</i> and 0-group <i>Carcinus</i>		85%	49%

explain 85% of the Z on the low tidal flats and 49% on the high tidal flats can be explained.

Because densities of *Macoma* were lower in the low intertidal (due to migration to the high intertidal; Hiddink and Wolff, in press), equal predation rates will result in a higher mortality in the low intertidal. However, predatory consumption (in *Macoma* $\text{m}^{-2} \text{day}^{-1}$) was higher in the low intertidal, while densities of *Macoma* were lower (Table 7). Therefore, not only the relative but also the absolute predation pressure was higher in the low intertidal.

Thus, 49–85% of the observed mortality can be explained from the observed stomach contents and densities of *Crangon* and 0-group *Carcinus*. The remaining mortality may be explained by the following.

- Underestimating predator density due to (large) predators fleeing in front of our net.
- Predation by adult *Carcinus* (on average 0.1 *Macoma* stomach⁻¹, but no reliable density data available). From the pitfall data (Fig. 4), a substantial predation pressure by large crabs is expected.
- Predation by *Crangon* and *Carcinus* without ingestion of hard shell parts. As *Macoma* without shell cannot be recognised visually, this will result in an underestimation of predatory consumption. This problem can be solved by using immunological techniques (Van der Veer et al., 1998). Unfortunately, this method does not distinguish between siphon cropping (and survival) and predation on the complete animal (and thus death) and will therefore result in overestimation of predation.

- Predation by infaunal polychaetes; this will be considered in a later paper.

Evacuation times are probably temperature and size dependent but literature values for crab evacuation times are probably quite accurate for our study, as this was studied in crabs from the Dutch Wadden Sea at 18 °C (Afman, 1980). Evacuation times for shrimps were studied in Sweden at 14 °C (Pihl and Rosenberg, 1984) and in the northern German Wadden Sea at unknown temperatures (del Norte-Campus and Temming, 1994). The presumably lower temperatures at these higher latitudes may cause longer evacuation times and an underestimation of predation pressure in our study. Migration was not important in the studied period (Hiddink and Wolff, in press).

4.2. General conclusions

We conclude that small *Macoma* are under high predation pressure in the low intertidal, especially by shrimps, while they are relatively safe in the high intertidal. During their first year, the shellfish outgrow their small epibenthic predators. Therefore, it becomes safe for the bivalves to redistribute to locations where epibenthic predators are abundant, during the bivalves' first winter. Therefore, the migration of newly settled *Macoma*-spat from the low to the high intertidal and their stay in the high intertidal might be seen as an adaptation to avoid epibenthic predation. The absence of 0-group *Macoma* in tidal channels and the North Sea (Hiddink and Wolff, in press) where aquatic predators are abundant, confirms this idea.

This study explains why juvenile *Macoma* temporarily live in the high intertidal. It does not clarify why they leave these nurseries again in their first winter. Lengths from the unmanipulated Re-treatment in the enclosure experiment at low and high tidal flats give an indication of growing conditions at low and high tidal flats. For the 0-group, length of

animals was highest in the high intertidal, a phenomenon also observed by Armonies and Hellwig-Armonies (1992), but 1 + group *Macoma* were larger and had a better condition in the high intertidal too. This observation is surprising because the time available for feeding is longer in the low intertidal. However, it has been observed in other studies (Green, 1973; Bachelet, 1980) and may be caused by growth increase due to parasite infestation (Zwarts, 1991; Lim and Green, 1991). However, adult growth is usually fastest in the low intertidal (Harvey and Vincent, 1990, 1991; Beukema, 1993a; Vincent et al., 1994). As we found no significant epibenthic or bird predation on 1 + *Macoma* and growth was better, the high intertidal seems to remain the best location for *Macoma* as they grow older. Nevertheless, Beukema (1993a) found higher mortality-values for adults living in the high than in the low intertidal.

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