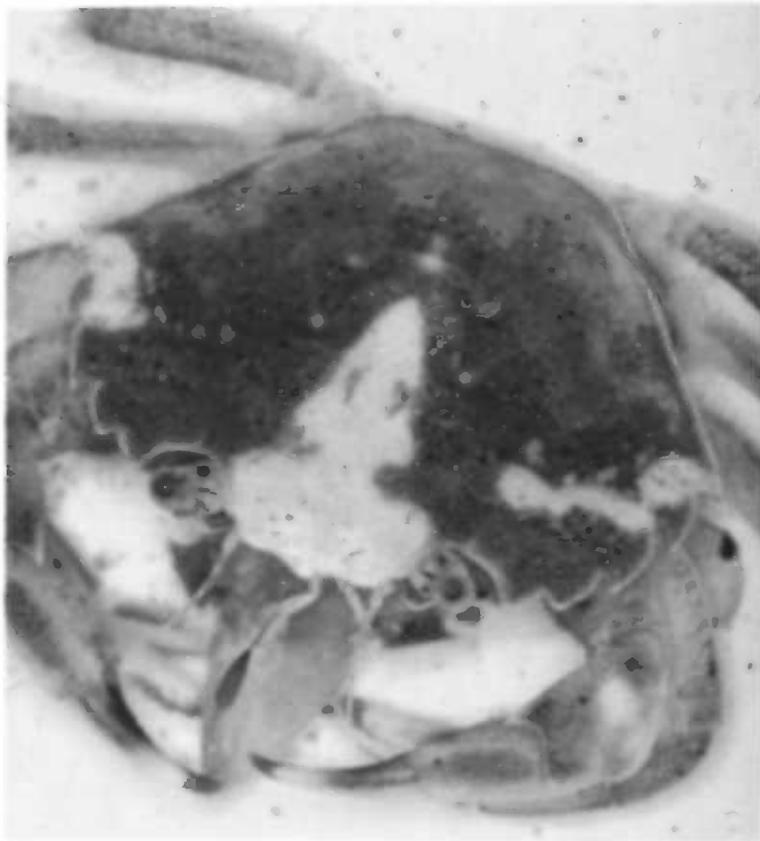


**Size selective predation on the bivalve
Macoma balthica
by juvenile epibenthos**



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December 1998
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The picture on the cover shows a juvenile shore crab (*Carcinus maenas*) with a carapace width of 12 mm preying on 0-group *Macoma balthica*.

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ABSTRACT

The tellinid bivalve *Macoma balthica* passes its juvenile stage in the Wadden Sea in nurseries high in the intertidal zone. The migration to and from these high tidal flats presents various potential dangers to the animals. In order to outweigh the negative influences, the nurseries must offer major beneficial conditions to the youngest stages of *M. balthica*. We hypothesize that the high tidal flats are a more favorable habitat than the lower, because they offer a refuge from predation by juvenile epibenthos. The main epibenthic predators on *M. balthica* potentially are the shore crab (*Carcinus maenas*), brown shrimp (*Crangon crangon*), plaice (*Pleuronectes platessa*), flounder (*Platichthys flesus*) and goby (*Pomatoschistus* sp.). Stomach contents of crabs and shrimp that were caught on the high tidal flats in the eastern Dutch Wadden Sea, were analysed for shell fragments. Only very low numbers of recognizable shell fragments of *M. balthica* were found. On the basis of hinges found in the stomachs, the size of some consumed shells could be estimated. Size selectivity of predation on *M. balthica* by juvenile epibenthos was estimated in an experimental situation. The data show that juvenile epibenthic predators mainly consume the smallest 0-group *M. balthica* when a size range is offered. The electivity index E' shows that the largest size classes are significantly rejected. The fish and shrimp only consumed small amounts of bivalves. The juvenile crabs proved to be fierce predators, consuming relatively large amounts. A significant positive relationship exists between the carapace width of crabs and the mean size of bivalves they consume. Considering the impact juvenile shrimp and crabs in particular could have on the juvenile population of *M. balthica*, this may be a reason for the use of nurseries high in the intertidal zone.

SAMENVATTING

Het nonnetje (*Macoma balthica*), een klein tweekleppig schelpdier behorende tot de familie der Tellinidae, brengt zijn juveniele stadium in de Waddenzee door in zogeheten kinderkamers, gelegen op hoge wadplaten. De migratie naar deze hoog in de getijdzone gelegen wadplaten en weer terug, levert een aantal mogelijke gevaren op voor de jonge nonnetjes. Als tegenwicht voor de risico's die de migratiefasen opleveren, moeten de kinderkamers een zeer groot voordeel voor de juveniele dieren bieden. De hoge wadplaten zouden mogelijk een betere habitat zijn dan lager gelegen platen, omdat ze een vluchtplaats bieden tegen predatie door jonge epibenthos. Potentieel de belangrijkste epibenthische predatoren op het wad zijn de strandkrab, (*Carcinus maenas*), garnaal (*Crangon crangon*), schol (*Pleuronectes platessa*), bot (*Platichthys flesus*) en het grondeltje (*Pomatoschistus* sp.). De maaginhoud van krabben en garnalen die op wadplaten in het oostelijke deel van de Waddenzee zijn gevangen, werd bekeken om te zien of er fragmenten van schelpen in aanwezig waren. Slechts een klein deel van de magen bleek herkenbare fragmenten van nonnetjes te bevatten. Aan de hand van slotjes die in de magen werden aangetroffen kon de grootte van een klein aantal gegeten schelpen bepaald worden. Door middel van een reeks experimenten werd bepaald of predatie op nonnetjes door juveniele epibenthos grootte selectief plaats vindt. De data tonen aan dat de juveniele epibenthische predatoren vooral de kleinste nonnetjes eten wanneer ze een range van grootte klassen aangeboden krijgen. De electivity index E' laat zien dat de grootste nonnetjes significant afgewezen worden door de predatoren. De vissen en garnalen aten alleen kleine hoeveelheden schelpdieren. De juveniele krabben bleken verwoede predatoren te zijn en aten relatief grote hoeveelheden. Er bestaat een significante positieve relatie tussen de carapax lengte en de gemiddelde grootte van de schelpdieren die de krabben consumeren. De grote impact die met name de krabben en garnalen kunnen hebben op de 0-groep nonnetjes, zou een reden kunnen zijn voor het gebruik van kinderkamers hoog in de getijde zone.

1. INTRODUCTION

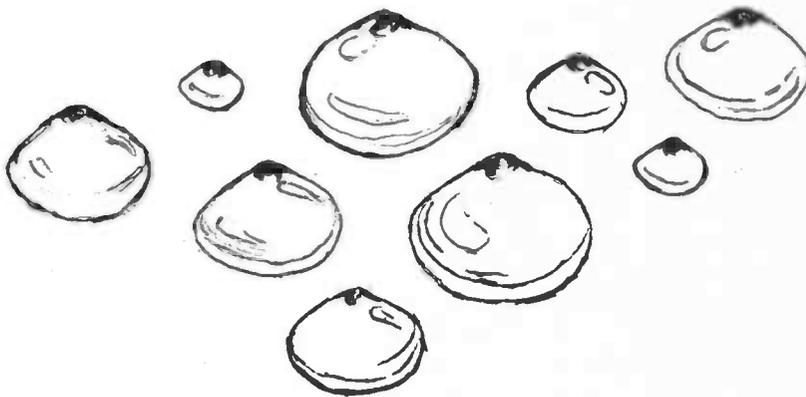
The tellinid bivalve *Macoma balthica* is one of the most widespread and common macrobenthic species in the Wadden Sea. The success of the species is attributed to a strategy of timely shifts to areas that are most suitable to the particular life stage (Beukema, 1993). After spawning of the adults in spring at intermediate tidal levels, eggs and larvae of *M. balthica* are pelagic for a short period. Until May the postlarvae at a size of < 500 µm, initially settle mainly on the low tidal flats (Armonies & Hellwig-Armonies, 1992; Günther, 1991). Subsequently the juvenile bivalves migrate to nurseries high in the intertidal zone, around or above mean tidal level. There, a few months later, 0-group *M. balthica* with a shell length between 1.0 and 10.0 mm occur in maximal numbers. At the onset of winter the young animals leave the high tidal flats and migrate back to lower tidal levels (Beukema, 1993). The transport during the migration phases is facilitated by a long, thin mucus thread that increases the hydrodynamic drag on the bivalves. In this way the juvenile *M. balthica* can be lifted and transported in the water column by tidal currents (Armonies, 1992, 1996; Beukema & de Vlas, 1989). The migration to and from the tidal flats presents various potential dangers to the animals. In the watercolumn they are vulnerable to pelagic predators and run the risk to end up in unfavorable places. To outweigh these risks, the nurseries must offer major beneficial conditions to the youngest stages of *M. balthica*.

One of the advantages of the high intertidal flats is that physical stress due to wave action and tidal currents is less than on the low flats (Beukema, 1993). Also growth rates might be higher due to a higher food supply (Armonies & Hellwig-Armonies, 1992). Furthermore, the nurseries may offer protection against predators (Beukema, 1993). Epibenthic species and wading-birds predate on *M. balthica*. Most of the birds foraging on tidal flats follow the water's edge as the tide falls and rises (Reise, 1985). Research on knots (*Calidris canutus*) has shown that *M. balthica* is their preferred prey (Piersma et al., 1993). Knots mainly select individuals that have a size of around 14 mm. The relative frequency of *M. balthica* smaller than 10 mm in the diet of knots is negligible (Dekinga & Piersma, 1993). Likewise, oystercatchers (*Haematopus ostralegus*) select for the large specimens within a population. They actively select against individuals that are smaller than 11 mm (Hulscher, 1981; Zwarts et al., 1996). The risk for 0-group *M. balthica* of being eaten by waders is therefore small.

Epibenthic species mainly feed on the lower tidal flats during flood tide (Reise, 1985). The tidal flats in the Wadden sea are inhabited by large quantities of brown shrimp (*Crangon crangon*), shore crab (*Carcinus maenas*), plaice (*Pleuronectes platessa*), flounder (*Platichthys flesus*) and goby (*Pomatoschistus* sp.) (Beukema, 1992; Günther, 1990; Janssen & Kuipers, 1980). The diet of these epibenthic species is known to include juvenile bivalves (Aarnio et al, 1996; Evans, 1984; Jensen & Jensen, 1985; Pihl, 1985). Predation on bivalves by epibenthos can be divided in siphon cropping, probably inhibiting growth (Kamermans & Huitema, 1994) and full predation, resulting in death. It is assumed that juvenile epibenthic predators select for the small bivalves (Günther, 1994). Thus, the 0-group is most vulnerable to this type of predation.

In general it can be said that: 1) In the upper intertidal, large prey is more subject to predation than small prey. 2) Predation pressure on juvenile macrofauna is heavier in the lower than in the higher parts (Reise, 1983). Therefore adult *M. balthica* might avoid a high predation pressure by living on the lower tidal flats, that are exposed for the shortest period of time and less frequently visited by wading birds. The 0-group population on the other hand, may avoid a high predation pressure by spending their juvenile stage on the higher tidal flats, that are less frequently visited by epibenthic predators. This would then give an explanation for the use of nurseries by *M. balthica*.

This study examines whether full predation on *Macoma balthica* by epibenthic species is size selective. The hypothesis that juvenile shore crab (*Carcinus maenas*), brown shrimp (*Crangon crangon*), plaice (*Pleuronectes platessa*), flounder (*Platichthys flesus*) and goby (*Pomatoschistus microps*), select the smallest bivalves will be tested.



2. METHODS

Between June and October 1998, animals were collected from the tidal flats of the Groninger Wad in the eastern Dutch Wadden Sea near Noordpolderzijl (Fig.1, Table 1a-c). Different size classes of *Macoma balthica* were obtained from sediment of 1 to 5 cm deep that was sieved in the field over a 300 or 1000 μm mesh. Juvenile epibenthic predators were caught with a 50 cm broad pushnet or a 20 cm dip net, with a full mesh size of respectively 5.0 and 1.5 mm.

Individuals that were used for an examination of their stomach contents were killed and preserved by placing them in 70% ethanol. Predators and bivalves were maintained in the laboratory in temperature-controlled closed-system aquaria. From June to October the water temperature was kept constant at 15.5 °C. At the end of October the temperature was gradually lowered to 10.0 °C, over a period of three days. Fluctuations of the watertemperature have been measured in November and were + 1.6°C at the most. The salinity of the seawater in the aquaria fluctuated around 31‰. Light was switched on at 7:30 am and switched off at 9:00 pm. The predators were fed artemia nauplia, pollack, dry food and fresh cockles.

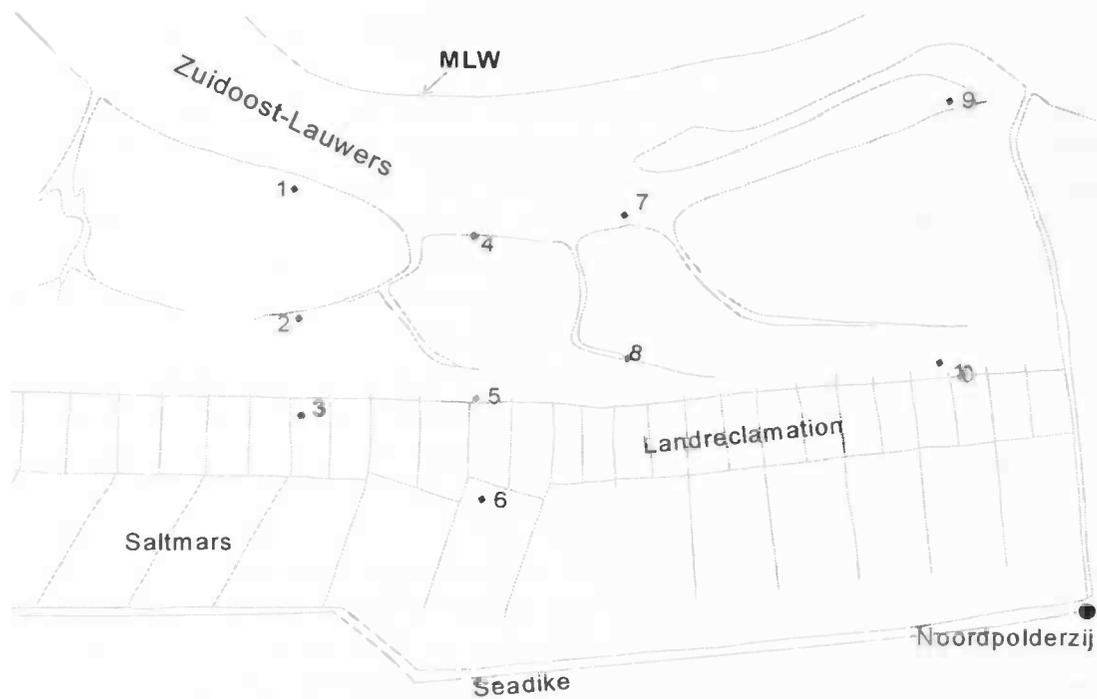


Fig. 1. Location of sampling points on the tidal flats of the Groninger Wad. Locations are represented as numbered squares (see also Table 1a-c). MLW = mean low water level. (From: J.G. Hiddink, unpublished)

A	Date	Location	B	Date	Location
<i>Carcinus maenas</i>	3/6	4 - 8	<i>Macoma balthica</i>	17/6	5
	4/6	1 - 3		4/8	5
	17/6	9 - 10		17/8	5
<i>Crangon crangon</i>	3/6	4 - 8		4/9	5
	4/6	1 - 3		12/9	5
	17/6	9-10			

C	Date	Location
<i>Carcinus maenas</i>	20/7	4 - 8
	17/8	4 - 6
	12/9	4 - 6
<i>Crangon crangon</i>	8/7	1 - 3
	20/7	4 - 8
	17/8	4 - 6
	29/10	4 - 6
<i>Pomatoschistus microps</i>	17/6	9 - 10
	20/7	4 - 8
	17/8	4 - 6

Table 1. Dates and locations on which predators for stomach content analysis (a), experimental predators (b) and *M. balthica* (c) were gathered. For exact locations see also Figure 1.

M. balthica was kept in stock in plastic containers (Appendix, Fig.1), supplied with a layer of native sediment which was first heated and washed with salt water to remove any living organisms. The containers were placed together in a separate aerated aquarium, which was provided twice a week with 1 liter from an algal culture of *Isochrysis galbana*.

This microflagellate alga was chosen for three reasons. 1) *M. balthica* is a facultative deposit feeder, but appears to depend primarily on material present in the water column (Hummel, 1985a). 2) Previous experiments have shown that *M. balthica* is able to use *I. galbana* as a food resource (Hummel, 1985b; Kamermans, 1992; Kamermans & Huitema, 1994). 3) Furthermore the alga is easy to culture in high densities (H. Peletier, pers.comm.). The algae were grown in a batch culture to a dense concentration. An f/2 medium (Admiraal & Werner, 1983) without the addition of silicate (according to Hummel, 1985b), was used to enrich the 0.2 µm filtered seawater (S = 31‰) in which the algae were cultured. Each week the water in the aquarium which held bivalve stock was filtered through a pump for two days, to prevent the accumulation of organic matter.

2.1. Stomach contents

In order to determine whether predation on juvenile *M. balthica* occurs on the tidal flats, the stomach contents of several shore crab and shrimp were analysed for recognizable shell fragments (Table 1a). Prior to the analysis the size of the animals was estimated. Crabs were measured between the tips of the most distal marginal teeth of the carapace. Shrimp were measured stretched out from the tip of the rostrum to the hind margin of the telson (Fig. 3).

The top of each crab's carapace was cut open and pulled away to reveal the stomach sac. This was then removed carefully. The carapace of each shrimp was lifted with a pair of tweezers and cut off. The abdomen was also cut off and the entire cephalothorax was then placed in a small petri dish. Each stomach was opened in a small petri dish and its contents flushed with water for identification under a binocular microscope at 40 x magnification. The occurrence of shell fragments of *M. balthica* in the stomachs was recorded.

Whenever fragments were encountered, a more detailed analysis of the stomach contents was performed in order to find shell tops with hinges. The height of the hinge + top (HTH) was measured under a binocular microscope with an eye piece micrometer (Fig. 2). The length of the consumed bivalve (SL) was then estimated from a predictive equation ($SL=14.071 HTH^{0.734}$), according to Dekinga & Piersma (1993).

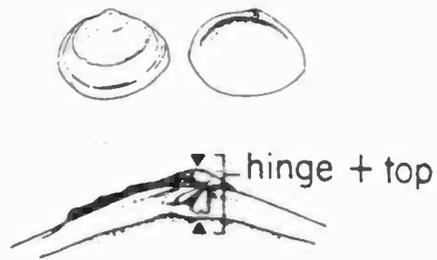


Fig. 2. Exterior and interior of *M. balthica* shell. Lateral teeth and hinge are shown enlarged. (From: Dekinga & Piersma, 1993)

2.2. Laboratory experiments

The experiments were designed to determine if certain size classes of *M. balthica* are more vulnerable to predation by juvenile epibenthos. In order to test whether the predators have a preference, a size range of bivalves was offered. By comparing the number of *M. balthica* that was offered per size class with the number that survived after a fixed period of time, an estimate of selection could be made.

The different sizes of bivalves were sorted in a petri dish filled with sea water. The dish was placed on graph paper under a binocular microscope. The size of the bivalves was estimated at 6.4 x magnification, by measuring the length of the shells to the nearest 0.1 mm. The bivalves were carefully handled with a small spatula or sucked up with a pipette, in order not to damage the shells.

The size range of *M. balthica* that was offered, was subdivided in different size classes (Table 2). Armonies and Hellwig-Armonies (1992), stated that the relative abundance of *M. balthica* < 0.5 mm is smaller than 1% already from mid-June. Indeed, during the collecting of bivalves for the experiments in August and September, specimens < 0.5 mm were rarely found on the tidal flats. Therefore 0.5 mm is the smallest size that was offered during the predation experiments. According to Beukema (1983), juvenile *M. balthica* reach a length of 4 to 10 mm at the end of the first growing season. Thus 10 mm was taken as representative for the largest individuals within the 0-group. It should be noted that around 20% of the 10 mm size class consisted of older (I-group) bivalves. Crabs with a carapace width ≥ 12 mm were furthermore offered *M. balthica* with a length of 12, 14 and 16 mm, consisting entirely of specimens from the I-group and older.

Table 2. Composition of the size range of *M. balthica* that was offered during the experiments.

Length (mm)	Size class	Length (mm)	Size class
0.0 - 0.5	0.5	5.1 - 5.5	5.5
0.6 - 1.0	1.0	5.6 - 6.0	6.0
1.1 - 1.5	1.5	6.1 - 6.5	6.5
1.6 - 2.0	2.0	6.6 - 7.0	7.0
2.1 - 2.5	2.5	7.1 - 7.5	7.5
2.6 - 3.0	3.0	7.6 - 8.0	8.0
3.1 - 3.5	3.5	8.1 - 8.5	8.5
3.6 - 4.0	4.0	8.6 - 9.0	9.0
4.1 - 4.5	4.5	9.1 - 9.5	9.5
4.6 - 5.0	5.0	9.6 - 10.0	10.0

Per size class a sufficient number of bivalves had to be offered to prevent depletion, since this would influence the selection. Pilot experiments were performed to establish this number. On the basis of these pilots it was decided that an amount of 5 bivalves per class should be adequate. This adds up to a maximal number of 115 bivalves in each experimental container, which corresponds to a density of 0.5 specimen cm⁻².

At the start of each experiment a size range of *M. balthica* was randomly placed in a small plastic container (Appendix, Fig. I), which was supplied with a 4 cm deep layer of fine grained sediment. The depth of the sediment layer in the containers was determined on the basis of the fact that 0-group *M. balthica* on average buries to a depth of around 3 cm (de Goeij, 1993; Steur et al, 1996; Zwarts et al, 1994). The containers were subsequently placed in an aquarium and the bivalves were left to bury themselves in the sediment for at least 6 hours. Individuals that did not bury were replaced by others of the same size class.

The epibenthic predators that were used in the experiments are the shore crab (*Carcinus maenas*), brown shrimp (*Crangon crangon*), plaice (*Pleuronectes platessa*), flounder (*Platichthys flesus*) and goby (*Pomatoschistus microps*). The size of the predators was determined to the nearest 0.1 cm. Crabs were measured between the tips of the most distal marginal teeth of the carapace. Shrimp were measured stretched out from the tip of the rostrum to the hind margin of the telson. The fish species were measured from head to tail (Fig. 3).

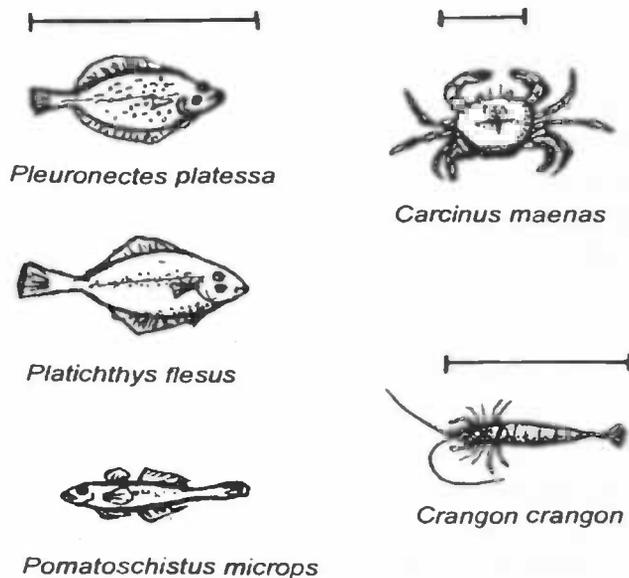


Fig. 3. Size estimation of the different predators. Plaice, flounder and goby were measured from head to tail. Crabs were measured between the most marginal tips of the carapace. Shrimp were measured stretched out, from the tip of the rostrum to the hind margin of the telson.

Crabs with a carapace width of respectively 4, 6, 8, 12, 16 and 20 mm were used for the experiments (Table 3). According to Klein Breteler (1975), these sizes represent different growth stages of 0-group crabs. Newly recruited crabs do not surpass a carapace width of about 20 mm in their first year (Klein Breteler, 1976). At a carapace width of 20 mm maturity is reached (Klein Breteler, 1983). This size limit can therefore be used to distinguish 0-group crabs from the older ones. Prior to the experiments the predators were starved. Crabs were starved for 24 hours (according to Jensen & Jensen, 1985) shrimp and fish were starved for 48 hours (according to J.J. de Wiljes, pers. comm.).

Table 3. Predators that were used for the size selection experiments, the number of individuals that was used per experiment and the duration of the experiments.

Species	Length (mm)	n individuals per experiment	duration of experiment
<i>Pomatoschistus microps</i>	45	1	24h
<i>Pleuronectes platessa</i>	45	1	24h
<i>Platichthys flesus</i>	75	1	24h
<i>Crangon crangon</i>	15, 20, 25	4	24h
<i>Carcinus maenas</i>	4, 6, 8, 12, 16, 20	1	6h

The duration of the experiments was determined on the basis of pilot experiments. Crabs were allowed to feed on the bivalves for 6 hours, representing one tidal period. Shore crabs have two periods of maximum food intake during 24 hours: the first period starts at the beginning of the night, the second about 12 hours later (Afman, 1980). The light in the climate room where the experiments took place was switched off at 9:00 pm. This implicates that theoretically the second consumption peak of the crabs would occur around 9:00 am. To optimise the food intake, the experiments with crabs were always started between 8:30 and 9:30 am. Shrimp and fish were allowed to feed for 24 hours. For each size class of predator the experiment was repeated five times. The experiment with a 25 mm shrimp was repeated three times, due to a depletion of the small bivalve stock at the end of the experiments in November. A fresh predator was used for each experiment, with the exception of the fish. Only one specimen of small plaice and flounder was available for the experiments, so the same individuals were used five times. Only two gobies of 45 mm were caught and therefore these were used for all five repetitions.

At the end of each experiment the predators were removed. The sediment from the containers was sieved over a 300 µm mesh and the number of surviving *M. balthica* from each size class was recorded. By comparing the number of bivalves that was offered per size class with the number that survived, an estimate of selection was made. A number of 15 control experiments without predators was carried out, to determine any possible loss or mortality of bivalves due to the sieving procedure. During the control experiments 100% of the bivalves was retrieved, which demonstrates the accurateness of the method.

2.3. Statistical analysis

The results of the predation experiments were statistically tested with a one-way ANOVA, to compare the mean values of consumed sizeclasses and to see whether there are any significant differences amongst the means. Fisher's least significant difference (LSD) procedure was carried out to determine which means are significantly different from which others (see Appendix III).

In most of the experiments there was more than a 3 to 1 difference between the smallest standard deviation and the largest. This may cause problems since the analysis of variance assumes that the standard deviations at all levels are equal. To test this, two different variance checks were performed: Cochran's C test and Bartlett's test. If the difference amongst the standard deviations proved to be significant, a Kruskal-Wallis test was carried out, which compares medians instead of means. Furthermore, some of the experiments showed a standard skewness and/or kurtosis that is outside the range of -2 to +2, which indicates some significant nonnormality in the data. This violates one of the assumptions of an analysis of variance that the data come from normal distributions. In this case also a Kruskal-Wallis test was carried out.

Selectivity in predation on *M. balthica* was furthermore studied by calculating the Electivity Index E' per size class: $E' = (c_i - o_i) / (c_i + o_i)$. The number of consumed bivalves per size class per experiment is represented as c_i . The offered size classes, converted to the average consumption possibility per size class, are represented as o_i . $E' = 0$ indicates no selectivity, $-1 < E' < 0$ indicates no preference, or rejection and $0 < E' < 1$ indicates preference. If c_i and o_i differ significantly (t-test, $P < 0.05$), preference or rejection is rated significant (adapted from Stamhuis et al, 1998).

To determine which factors (carapace width or bivalve size class) have a statistically significant effect on the size selective predation, a multifactor ANOVA was performed, with the dependent variable being % consumed per size class and the factors being predator length and bivalve size. Fisher's least significant difference (LSD) procedure was carried out to see which crab size class significantly differs from the others in its predation pattern.

3. RESULTS

3.1. Stomach contents

The stomach contents of 13 shorecrabs (carapace width 0.2 - 5.8 mm) and 102 shrimp (length 0.5 - 4.9 mm) were analysed (Table 4). In 46 % of the crabs' stomachs fragments of *M. balthica* were found, whereas only 8% of the shrimps' stomachs contained fragments. A total of 5 hinges was found, two of which were encountered in the stomach of the same shrimp. The estimated size of the shells that were consumed is shown in table 4. The consumed bivalves all belong to the 0-group.

Table 4. Results of stomach content analysis of shore crabs and brown shrimp that were collected at the tidal flats of the Groninger Wad (see also table 1a). The number of predators that were analysed, and the total numbers of recognizable *M. balthica* shell fragments are shown. SL = estimated length of consumed shells on the basis of hinges. PS = size of predators in which stomachs hinges were found.

Species	n	<i>M. balthica</i> shell fragments	SL (mm)	PS (mm)
<i>Carcinus maenas</i>	13	5	3.1	28.0
<i>Crangon crangon</i>	103	8	2.2	3.3
			1.8	3.5
			2.7 + 2.2	4.8

3.2. Laboratory experiments

The six size classes of juvenile shore crabs that were used during the laboratory experiments consumed relatively large quantities of *M. balthica* over a period of 6 hours. Shrimp, goby, plaice and flounder consumed only small quantities over a period of 24 hours (Table 5).

Table 5. Average numbers of *M. balthica* that were consumed per experiment and the potential consumption per individual per day.

Species	Size (mm)	n <i>M. balthica</i> consumed per experiment	Potential consumption per day
<i>Carcinus maenas</i>	4	6.8	27.2
	6	6.6	26.4
	8	10.6	42.4
	12	15.4	61.6
	16	18.2	72.8
	20	27.0	108.0
<i>Crangon crangon</i>	15	3.6	0.9
	20	7.8	2.0
	25	5.2	1.3
<i>Pomatoschistus microps</i>	45	1.8	1.8
<i>Pleuronectes platessa</i>	45	3.6	3.6
<i>Platichthys flesus</i>	75	4.6	4.6

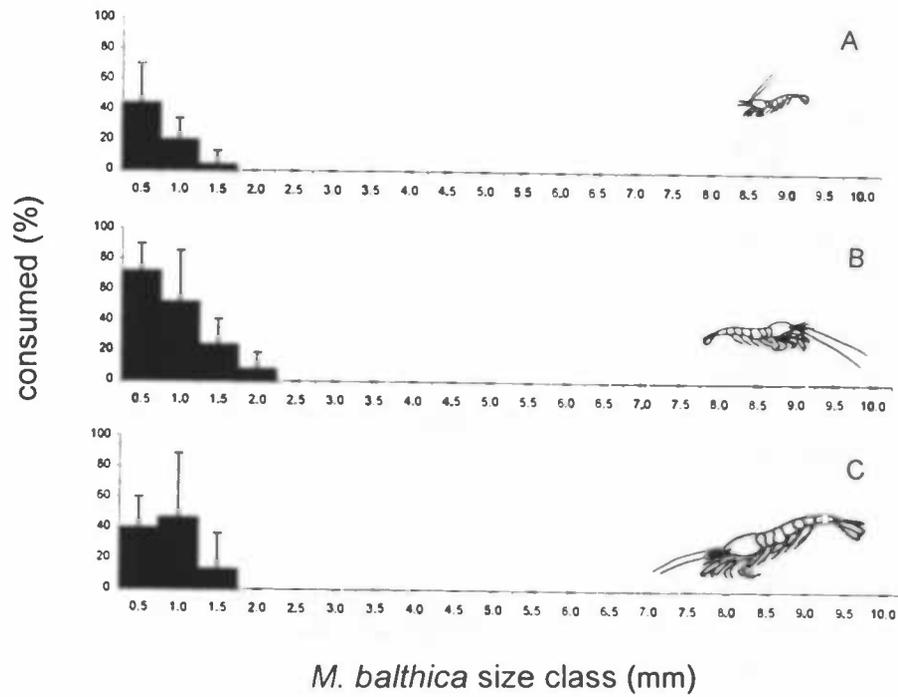


Fig. 4 a-c. Average percentages (+SD) of *M. balthica* consumed by 4 shrimp during a period of 24 hours. Length of the shrimp is respectively 15, 20 and 25 mm.

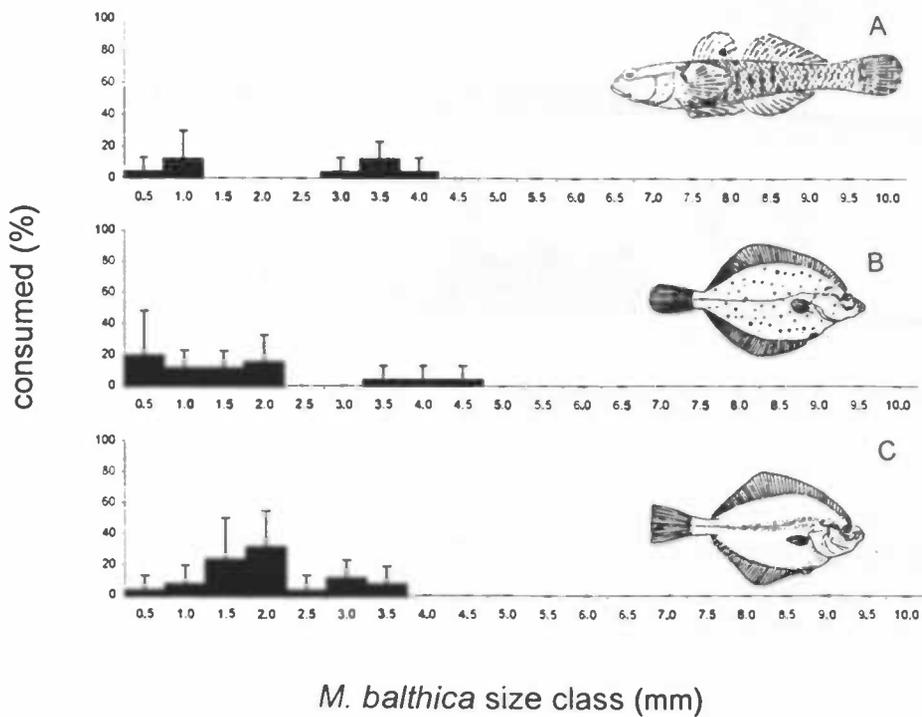


Fig. 5 a-c. Average percentages (+SD) of *M. balthica* consumed by common goby (a), plaice (b) and flounder (c) during a period of 24 hours.

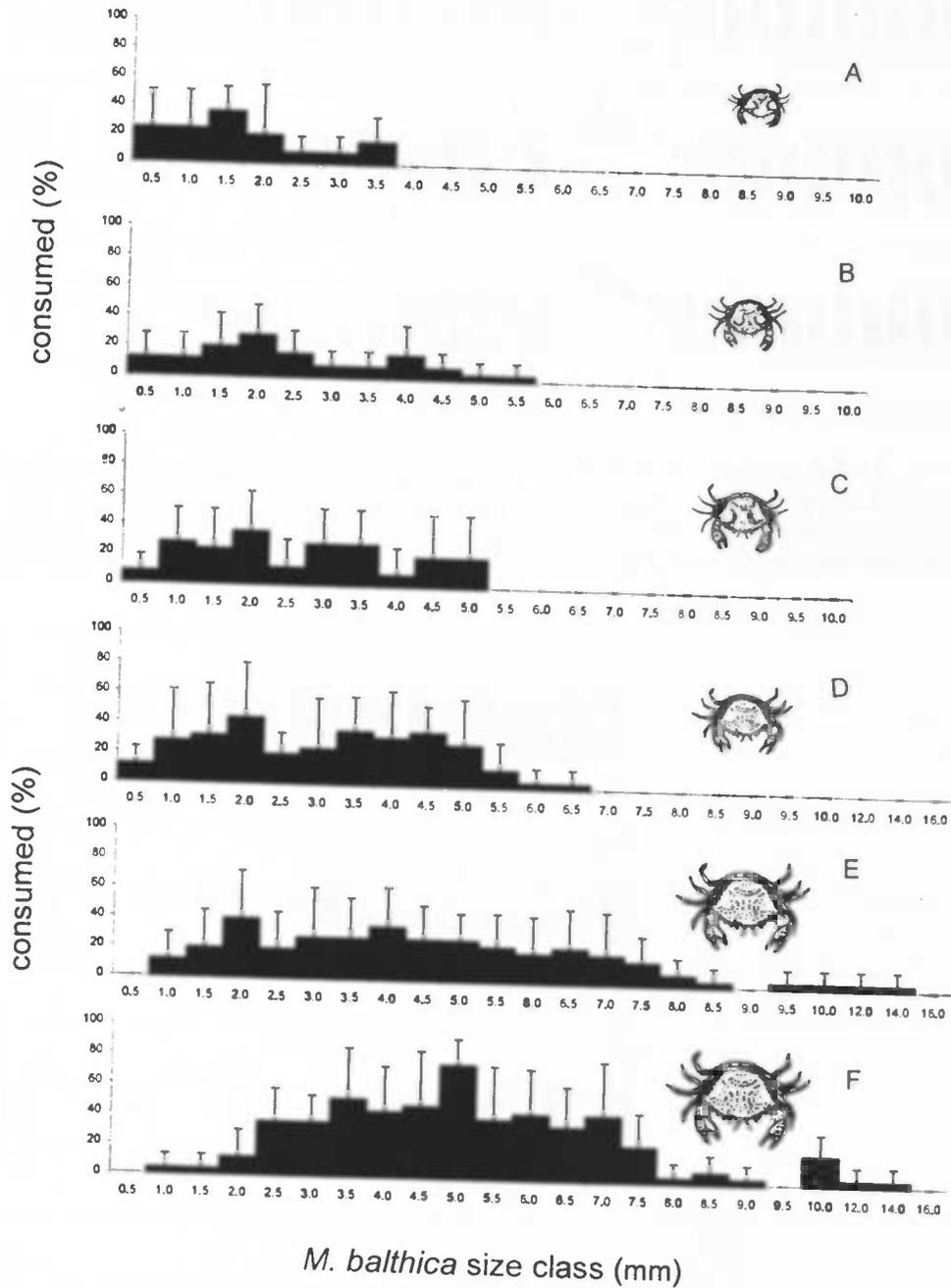


Fig. 6 a-f. Average percentages (+SD) of *M. balthica* consumed by juvenile shore crab over a period of 6 hours. The carapace width of the crabs is respectively (top - down) 4, 6, 8, 12, 16 and 20 mm.

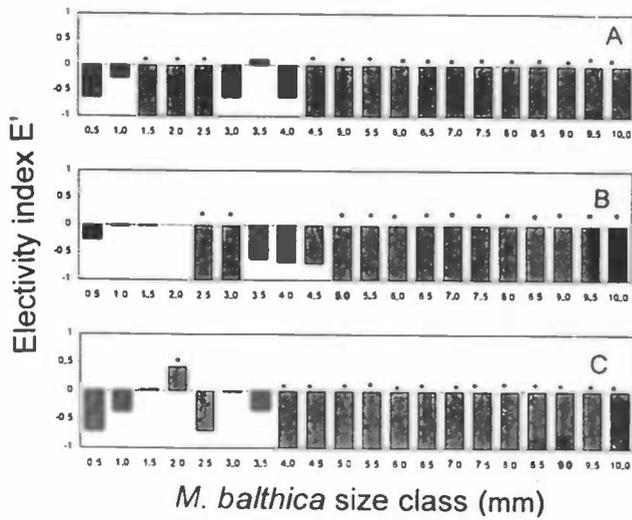


Fig. 7. The electivity index E' , indicating preference or rejectance of respectively goby (a), plaice (b) and flounder (c) per size class of *M. balthica*. An asterisk denotes significant preference or avoidance.

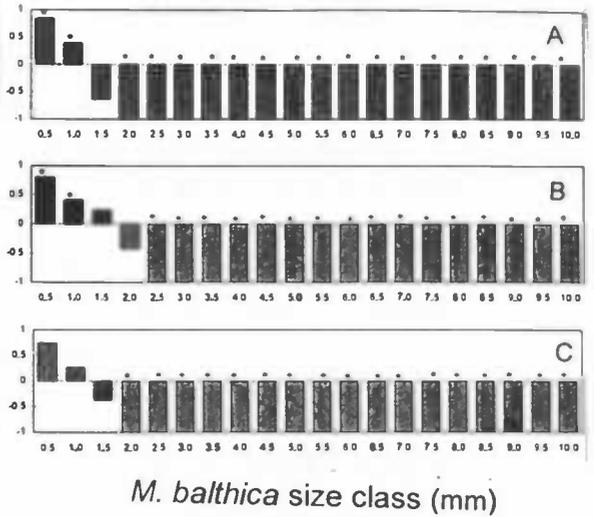


Fig. 8. The electivity index E' , indicating preference or rejectance of shrimp with a length of 15 (a), 20 (b) and 25 (c) mm, per size class of *M. balthica*. An asterisk denotes significant preference or avoidance.

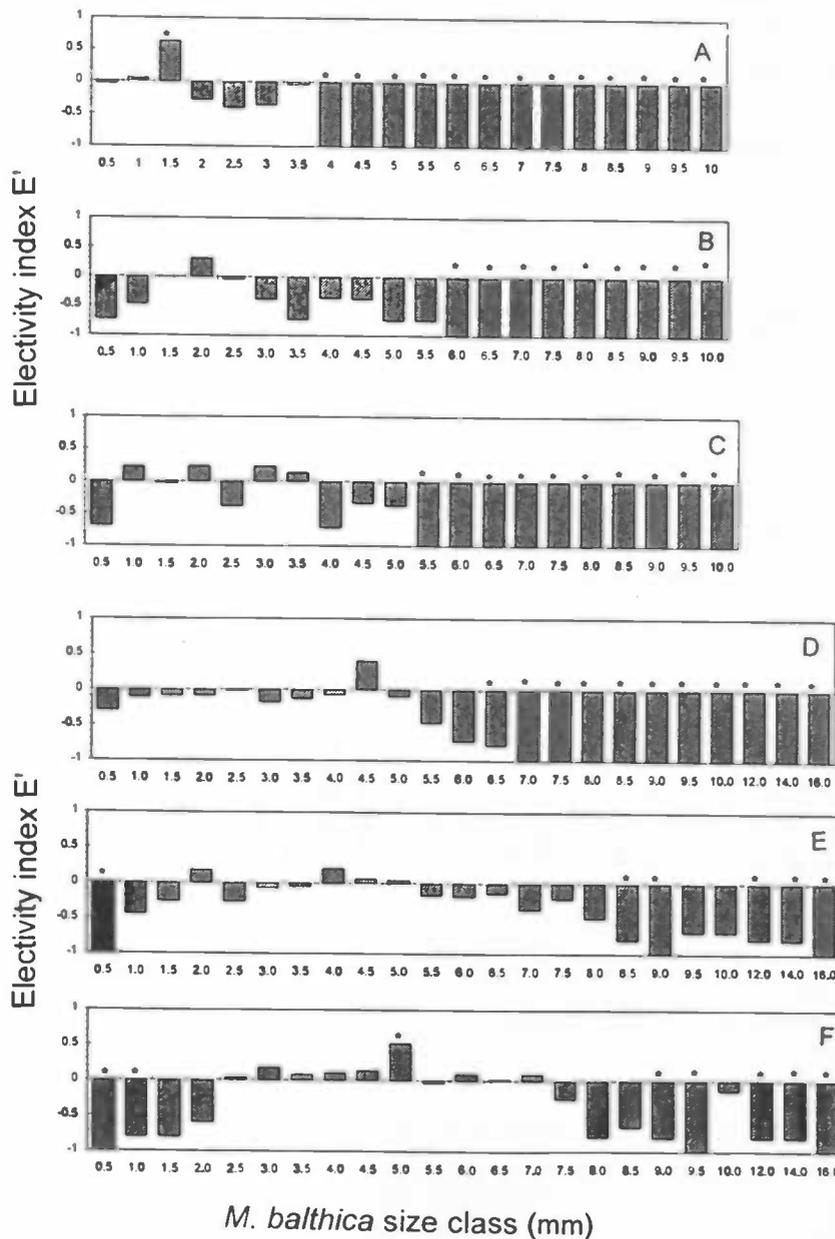


Fig. 9. The electivity index E' , indicating preference or rejectance of crabs per size class of *M. balthica*. Carapace width of the crabs is respectively (top-down) 4, 6, 8, 12, 16 and 20 mm. An asterisk denotes significant preference or avoidance.

Figures 4 - 6 show the average percentages (+SD) of consumed *M. balthica* per size class over a total of 5 experiments each (see also Appendix II and III). Goby, flounder and plaice consumed bivalves that are smaller than 5.0 mm (Fig. 4a-c). The shrimp selected the very smallest specimens that were offered: 0.5 to 2.0 mm (Fig. 5 a-c) Shore crabs consumed bivalves over a much broader range. Juvenile crabs with a carapace width of 4 to 12 mm selected *M. balthica* with a maximum length of 6.5 mm (Fig. 6 a-f). From the same figure it becomes clear that crabs with a carapace of 16 and 20 mm are capable of consuming bivalves > 10 mm.

The electivity index E' indicates that very few size classes are actually preferred (Fig. 7-9). The fish rejected almost all sizes, with the exception of the flounder, which significantly preferred *M. balthica* of 2.0 mm (Fig. 7 a-c). Shrimp with a length of 15 and 20 mm significantly preferred *M. balthica* of 0.5-1.0 mm and rejected bivalves > 1.5 mm. (Fig. 8 a-c). Only shore crabs with a carapace width of 4 and 20 mm showed a significant preference for bivalves of respectively 1.5 and 5.0 mm. All of the juvenile crabs significantly rejected the largest bivalves (Fig. 9 a-h). The larger the crabs become, the larger the bivalves are that they on average select. When the carapace width and the mean size of bivalves that the crabs consumed are plotted against each other, there proves to be a significant positive relationship (Fig. 10). Figure 11 a-b shows the relative contribution of crabs and shrimp to the total amount of bivalves that was consumed. It becomes clear that the heaviest impact of predation is on the smallest sizeclasses of the size range that was offered: for the most part the bivalves from 0.5 to 5.0 are selected.

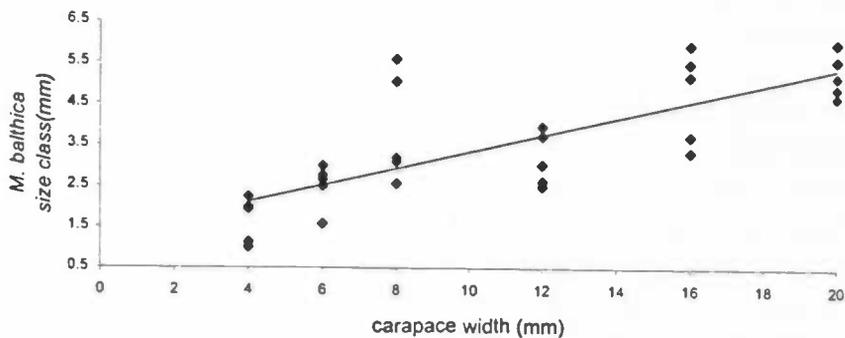


Fig. 10. Carapace width of juvenile crabs plotted against mean consumed *M. balthica* size. Correlation: $r = .87952$

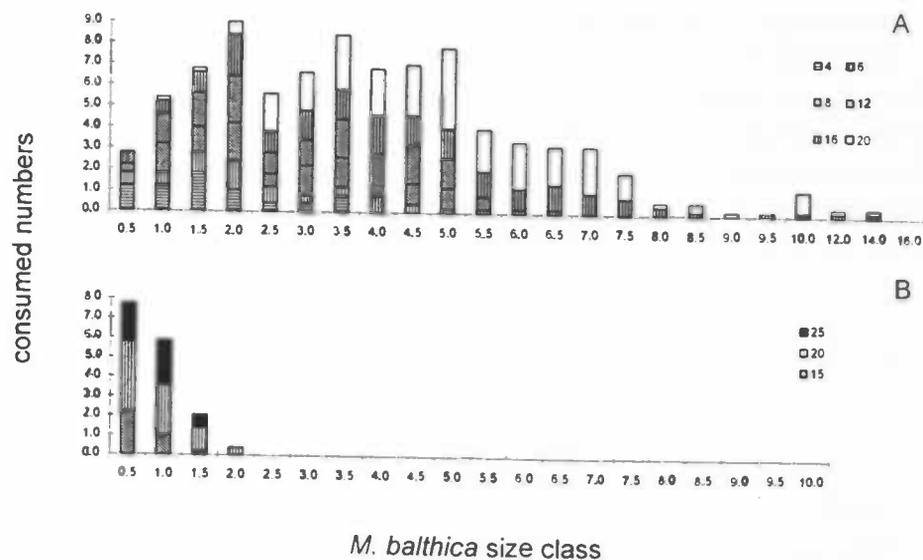


Fig. 11. Total amounts of *M. balthica* consumed by different sizes of crabs (a) and shrimp (b).

4. DISCUSSION

4.1. Stomach contents

The stomach analysis of shore crab and brown shrimp confirm that these predators consume 0-group *Macoma balthica* under natural circumstances. Fragments of *M. balthica* shells were clearly recognisable as such and could be distinguished from fragments of cockles (*Cerastoderma edule*) or mudsnails (*Hydrobia* sp) by their relative thickness and structure. The thin shells of *Scrobicularia* sp. could not be distinguished from that of *M. balthica*. However, their numbers on the tidal flats were so low that they can be neglected.

Nevertheless, the stomach contents might give a misrepresentation of the size classes and quantities of bivalves that are eaten. According to Afman (1980), in summer the main feeding period of shore crabs takes place at night during high tide. A smaller secondary peak in the feeding rate occurs in the afternoon. The predators that were used for stomach contents analysis were caught during low tide, before noon. Therefore the quantity of the food items that was found in the stomachs will always be relatively lower than when the predators are caught during a main feeding period. Afman furthermore mentions that the digestion of food consumed by crabs with a carapace width ≥ 35 mm takes 6 to 7 hours. Smaller crabs have a relatively higher metabolism and their digestion rates will therefore be higher as well. Given the fact that a number of crabs was transported to the laboratory prior to be killed and preserved in ethanol, part of the food in their stomachs might have already been digested. Another factor that gives rise to an underestimation of the food consumption is the way in which crabs consume their bivalve prey. The laboratory experiments show that when crabs devour their food, a substantial part of it is wasted (see also Appendix I, Fig. 2).

According to Pihl and Rosenberg (1984), the main feeding periods of the brown shrimp are comparable to those of the shore crabs. The highest relative number of full stomachs is obtained at night, between 6:00 pm and 6:00 am. In summer, a secondary feeding period occurs around mid-day. The shrimp that were used for stomach contents analysis were caught during low tide before noon, causing an underestimation of the food consumption. Pihl and Rosenberg furthermore noticed that within 2 hours the larger part of the food in the stomachs of shrimp has been digested. The shrimp that were collected for stomach analysis on the 3rd and 4th of June were preserved in ethanol after transportation to the laboratory. The individuals that were caught on the 17th were killed and preserved in the field. This difference in time of preservation is expressed in the relative numbers of unidentifiable stomach contents: around 50% from the first two dates, against 14% of the last date. Most probably the shrimp that were transported to the lab already digested a large part of their food before they were preserved. When analysing stomach contents, these factors can give rise to a considerable underestimation of the food consumption.

4.2. Predation experiments

Carcinus maenas

The data strongly suggest that the shore crab is an important predator of *M. balthica* and is able to seriously reduce the 0-group population. The experiments show that juvenile shore crabs with a carapace width of 4 to 12 mm consume the smallest size classes of *M. balthica*, ranging from 0.5 to 6.5 mm. Bivalves with a shell length ≥ 7.0 mm were not eaten. Juvenile shore crabs with a carapace width of 16 and 20 mm are capable of consuming *M. balthica* over a broader range. However, the larger sized *M. balthica* were not consumed as frequently and in such high amounts as the small sizes of the 0-group. In general, the juvenile shore crabs showed no distinct preference for a specific size class. The crabs rather selected a range of sizes, with a mean size being evidently preferred. The mean size of bivalves that are consumed increases with the size of the crabs. Abbas (1985), also observed this in crabs with a carapace width of 40 to 60 mm that were fed *M. balthica* ranging from 8 to 18mm.

According to the electivity index E' , crabs with a carapace width of 4 and 20 mm significantly preferred bivalves with a shell length of respectively 1.5 and 5.0 mm. This apparent preference of one specific size class is caused by the fact that these size classes were consumed in almost equally high amounts during all five repetitions of the experiments, whereas in the consumption of the other size classes there was much more variation.

The largest size classes that were offered were significantly rejected. For the smallest (≤ 12 mm) crabs this most probably is due to the fact that they do not have enough strength to open bivalves that are larger than a certain critical size. The larger juvenile crabs are capable of opening I-group and older *M. balthica*, with a shell length up to 14 mm. However they rarely consumed these large bivalves. There are two possible explanations for this:

- 1) The larger *M. balthica* are hard to detect for the crabs because they bury deeper than the small ones. Shore crabs search for prey by probing beneath the surface of the sediment with both their chelae and their walking legs (Sanchez-Salazar, 1987). Some general observations were made on the behaviour of the crabs, in a 10 x 10 cm glass aquarium that was supplied with a layer of sediment. Crabs with a carapace width of 20 mm were able to probe the sediment to a depth around 3 cm. Bivalves that buried deeper could have easily been missed by the crabs.
- 2) The crabs reject the largest size classes of *M. balthica*, because they are less profitable in terms of energy acquisition per unit of handling time than the smaller bivalves. It took the largest juvenile crabs on average around 35 seconds to dig up, crush and consume 0-group *M. balthica* of 4 to 6 mm. It was only observed once that a crab dug up a bivalve of 14 mm. The crab spent 2 minutes attempting to crush the umbone area of the shell. Then it left the bivalve on the sediment and started searching for other prey. Within 5 minutes the crab ran into the same 14 mm bivalve again, that was reburying itself in the sediment. By attacking the hinge and chipping the edges of the shell, the crab succeeded in opening it and consuming the flesh after 20 minutes.

This example illustrates that a relatively high amount of time and energy has to be spent by the juvenile crabs in order to open large size classes of *M. balthica*. Laboratory studies on size selection by adult shore crabs on cockles (*Cerastoderma edule*) and mussels (*Mytilus edulis*) show that crabs select prey with the highest energy yield.

Small, easily broken cockles and medium sized mussels appeared to be the most profitable in terms of energy acquisition per unit of handling time, the optimal size of prey increasing with predator (Jubb et al, 1983; Sanchez-Salazar et al, 1987). For juvenile shore crabs it might be the most profitable energetically to consume small bivalves. This goes especially for the 0-group, since their shells are very thin and easier to crush than older year classes.

What are the implications for *M. balthica* in the nurseries in the Wadden Sea? The shore crab is widely distributed on the tidal flats. Adult crabs migrate up-shore with each high tide and back again with the ebb (Naylor, 1962). Juvenile shore crabs stay permanently on the higher parts of the tidal flats, until they reach a carapace width of around 20 mm (Günther, 1990; Klein Breteler, 1976a, 1976b; Naylor, 1962). Densities of juvenile shore crabs on the high tidal flats of Balgzand, in the westernmost part of the Wadden Sea peak around 80 to 200 individuals m^{-2} in mid summer, depending on the temperature of the preceding winter (Beukema, 1991).

The laboratory experiments show that the amount of bivalves that is consumed increases with the size of the crabs. Over a period of 6 hours the crabs consumed an average of 7 to 27 bivalves per individual. Since the juvenile crabs stay on the tidal flats permanently, this gives a potential consumption of around 28 to 108 *M. balthica* per crab per day. Multiplied with the peak densities found by Beukema, this gives an average of respectively 2240 to 5600 bivalves per m^2 per day potentially consumed by the smallest juvenile shore crabs, and a potential consumption of 8640 to 21600 bivalves per m^2 per day for the larger juvenile crabs.

Moreover, Beukema (1991) stated that there is an important influence of winter temperatures on the timing of settlement of juvenile shore crabs. After a mild winter the settlement starts mid June, whereas after a cold winter settlement of juvenile crabs starts in July. This could influence the survival chances of 0-group *M. balthica*. According to Beukema, the first wave of bivalve settlers will escape crab predation after cold winters. He based this statement on the fact that *M. balthica* reaches an average length of 4 mm in August. However, it takes newly settled crabs with a carapace width of ~ 1.5 mm around three weeks to grow a carapace of ~ 6 mm (Klein Breteler, 1975). At this size, the crabs are capable of consuming *M. balthica* of 4 mm. This implies that even after cold winters, the majority of the 0-group population of *M. balthica* is not safe from predation by shore crabs.

Crangon crangon

Juvenile brown shrimp potentially play an important role as predators of 0-group *M. balthica*. The experiments show that shrimp with a length of 15 to 25 mm select the very smallest bivalves of the range that was offered, with a maximum shell length of 2.0 mm. The shrimp rejected bivalves that were larger than that. Shrimp of 15 and 20 mm show a significant preference for *M. balthica* of 0.5 and 1.0 mm. Although shrimp with a length of 25 mm also seem to show a preference for the smallest *M. balthica*, it is not significant according to the electivity index E' . This is probably due to the fact that the experiment was only repeated three times.

Laboratory experiments performed by Keus (1986) show that there is a positive relationship between the length of the shrimp and the size of the bivalves that they can consume. Brown shrimp with a length of 5 to 10 mm consumed prey of maximally 0.8 mm. The largest shrimp, with a length up to 60 mm were able to predate on *M. balthica*

of maximally 6 mm. The ability of shrimp to consume small bivalves indicates a serious risk of predation for 0-group *M. balthica*.

Beukema (1993) stated that the brown shrimp appears to be the most important predator on small tidalflat benthos during the main settlement period of *M. balthica* in the Wadden Sea. Settlement of juvenile shrimp (~ 5 mm) starts in April after mild winters and in May after cold winters, and continues with fluctuating intensity throughout summer and early autumn (Beukema, 1992). The first epibenthic stages of shrimp favour the higher parts of the tidal flats (Günther, 1990). However, at the highest tidal flats (+ 3 dm or higher) in the Wadden Sea shrimp are hardly ever found (Beukema, 1993 and pers. obs.) Nearly all juvenile shrimp stay permanently on the tidal flats around mean tidal level (+2 to -3 dm), hiding in the sediment at low tide. Circa 1 month after settlement the shrimps reach a length of 20 to 25 mm, at which they leave the higher parts of the tidal flats (Beukema, 1992, 1993). Shrimp >30 mm are rarely observed on the high tidal flats (Janssen & Kuipers, 1980).

Maximal densities of ~ 60 juvenile shrimp per m² are observed in June after mild winters and in July after cold winters (Beukema, 1992). Multiplied with the average amount of *M. balthica* that was consumed by shrimp with a length of 15 to 25 mm over a period of 24 hours, this gives a potential consumption of around 120 bivalves per day per m². However, the majority of juvenile *M. balthica* in June already has a length > 1mm and in the beginning of July the average length is ~ 3mm. Furthermore, in summer, the largest amounts of 0-group *M. balthica* can be found above mean tidal level (J.G. Hiddink, pers. comm). This implies that especially after cold winters 0-group *M. balthica* would be relatively safe from predation by juvenile shrimp. After mild winters only the first wave of bivalve settlers and those that settled on the highest tidal flats (above mean tidal level) will be safe from predation by juvenile shrimp.

Pleuronectes platessa

Predation by juvenile plaice most probably does not form a heavy threat for 0-group *M. balthica* on the tidal flats. The experiments can merely give an indication, since the same individual was used for all five repetitions. Assuming that this individual is representative for the entire population of small plaice, the data imply that juvenile plaice consumes only small *M. balthica* and shows no preference for a specific size class.

Plaice spend their juvenile stage on the higher parts of the tidal flats (Creutzberg et al, 1978; Kuipers, 1975). Peak abundance of juvenile plaice on the Balgzand area in the western Wadden Sea are rather low and vary from 0.03 to 0.3 individuals m⁻² (Creutzberg et al, 1978). When this is multiplied with the average amount of *M. balthica* that was consumed during the experiments, this gives a potential consumption of 0.1 to 1 bivalve per m² per day. One of the reasons that the plaice consumed only a small amount of *M. balthica* during the experiments, possibly is that it obtained food by cropping the siphons of the bivalves in the containers. According to Kuipers (1975), the siphons of *M. balthica* form the main food for plaice at the start of their demersal life in the Wadden Sea. The impact of predation by juvenile plaice on 0-group *M. balthica* will therefore be low.

Platichthys flesus

The risk for 0-group *M. balthica* of being eaten by juvenile flounder probably also is rather low. The data imply that flounders with a length of 75 mm consume *M. balthica* from 0.5 to 3.5 mm. According to the electivity index E' , bivalves with a length of 2.0 mm are significantly preferred. However, this might actually only be an individual preference, since all experiments were performed with the same flounder. Therefore, the data can merely give an indication.

The settling period of juvenile flounders on tidal flats in the Wadden Sea coincides with the settling of 0-group *M. balthica* (van der Veer et al, 1991), which is an important food source and easy prey for the juvenile flounders (Aarnio & Bonsdorff, 1997; Matilla & Bonsdorff, 1998). Peak densities of juvenile flounders vary from 0.01 m^{-2} to 0.27 m^{-2} on the tidal flats of Balgzand in the western Wadden Sea (van der Veer et al, 1991). When this number is multiplied with the average amount of bivalves that was consumed per flounder during the experiments, this gives an average consumption of 1.2 *M. balthica* per m^{-2} per day. This implies that the impact of predation by juvenile flounder on 0-group *M. balthica* will be low.

Pomatoschistus microps

The data indicate that predation pressure on 0-group *M. balthica* exerted by juvenile common goby most probably will be very low. However the results of the experiments should be interpreted with care.

All gobies, including the two that were used for the experiments, turned out to be heavily infected with *Gyrodactylus* sp. This parasite was found both externally, attached to the head, body and fins, as well as internally, attached to the gills and oral cavity of the fish. Since this infection will have affected the condition of the gobies, it might also have influenced their feeding behaviour.

The gobies consumed on average only 1.8 bivalve in 24 hours and showed no preference for a specific size class. *M. balthica* > 4.5 mm were significantly rejected according to the electivity index E' . This might approximate the maximum shell size that common gobies with a length of 45 mm can consume. The gobies also significantly rejected the size classes from 1.5 to 2.5 mm. In this case the fish probably did not encounter these size classes which is ascribed to chance rather than actual rejection.

Densities of juvenile common gobies on the tidal flats in the Wadden Sea are not known. In July, maximal numbers of adult common gobies near the island of Sylt, in the northern Wadden Sea are 0.06 individuals per m^2 (del Norte-Campos & Temming, 1994). Multiplied with the average amount of *M. balthica* that was consumed during the experiments, this gives a potential consumption of 0.1 bivalve per m^2 per day. Therefore the impact of predation by gobies on 0-group *M. balthica* will be practically nihil

4.3. Experimental set up

The design of the experiments was adequate to determine whether certain size classes of *M. balthica* are more vulnerable to predation by juvenile epibenthos. However, two marginal notes have to be made.

1) The condition of some *M. balthica* from stock was determined on the basis of their ash free dry weight. Their condition index turned out to be lower than that of *M. balthica* fresh from the tidal flats (J.G. Hiddink, pers. comm.). This implicates that the labdata might give a slight overestimation of the predation pressure, since the yield per bivalve will be lower. In this case the predators have to consume more to gain the same amount of energy. So the condition of the bivalves might have implications for the quantities that are consumed. Nevertheless it is assumed that this has no consequences for the size classes that the predators selected. 2) The density of 0-group *M. balthica* on the tidal flats is higher than in the experimental containers.

The density of *M. balthica* in the nurseries on the Groninger Wad ranges from > 19000 bivalves per m^2 in May to ~ 5000 per m^2 in October (J.G. Hiddink, pers. comm.). The density in the experimental containers was ~ 500 bivalves per m^2 . This low density might have influenced the feeding behaviour of the predators. This is especially the case when the predation is associated with encounter chance rather than size selectivity.

When they consume bivalves of a certain size class, the chance to encounter more of the same size class declines. The selectivity as shown in the data, might therefore be a result of depletion. This would mean that the preferences shown by the predators might in fact be more pronounced if an unlimited amount of bivalves per size class was offered. For example, in one of the experiments a shore crab with a carapace width of 20 mm consumed 100% of several size classes. As a result of depletion, the crab could not consume more of these and had to turn to other, maybe less preferred sizes classes of *M. balthica*. This gives an underestimation of the selectivity. However it does not make the data less valid, as it is clear that smallest size classes of *M. balthica* are preferred over the larger ones.

4.4. General discussion and conclusion

On the basis of the data it can be concluded that juvenile shore crab, brown shrimp, plaice, flounder and common goby mainly select the smallest 0-group *M. balthica* when a size range of bivalves from 0.5 to 16.0 mm is offered. The impact of predation is dependent on the amounts that are consumed as well as the densities of the predators on the tidal flats. Juvenile shore crab prove to be the most ferocious predators in every respect. Juvenile brown shrimp will only have a significant impact on 0-group *M. balthica* after mild winters and around mean tidal level. Predation by juvenile plaice, flounder and goby will have a negligible effect on 0-group *M. balthica*.

Something that should not be neglected is the fact that the natural diet of the predators does not exist of *M. balthica* solemnly. The shore crab is known to consume a wide variety of prey on the tidal flats. Its diet exists of macrozoöbenthos such as shrimp, polychaetes and bivalves (Abbas, 1985; Afman, 1979; Ropes, 1968). Shrimp are known to feed on all kinds of prey that are available, including microbenthos, meiobenthos and

young stages of macrobenthos (Evans, 1984; Pihl & Rosenberg, 1984; Plagmann, 1939; Wolff & Zijlstra, 1983). Plaice and flounder feed first on meiofauna and later on juvenile and small macrofauna, including juvenile bivalves (Aarnio et al, 1996; Evans, 1984; Kuipers, 1975; Pihl, 1985). The diet of juvenile common gobies includes small macrofauna such as shrimp and polychaete worms. Molluscs are known to make up only a small part of the gobies' diet (Pihl, 1985). The amount of bivalves eaten during the experiments will probably give an overestimation of what the predators consume on the tidal flats, since only one prey species was offered. When given the choice, the predators might prefer a different prey than *M. balthica*. This counts notably for the fish species (Aarnio et al, 1996; Kuipers, 1975; Pihl, 1985).

Although the impact of predation by juvenile fish will thus be small, the predation pressure exerted by juvenile crabs and shrimp could cause 0-group *M. balthica* numbers to decline drastically, unless the bivalves find a refuge in nurseries on the highest tidal flats. Small crabs and shrimp are also prey species of oystercatchers, knut and dunlin, which are amongst the most numerous birds in the Wadden Sea (Hulscher, 1981; Nehls & Tiedemann, 1993; Piersma et al, 1993). It can therefore be argued that predation by birds will regulate the numbers of juvenile epibenthic predators on the high tidal flats. This makes the nurseries relatively the safest place for 0-group *M. balthica*.

5. RECOMMENDATIONS FOR FURTHER RESEARCH

In August something peculiar had happened with the *M. balthica* stock. Several of the bivalves were observed crawling on top of the sediment in the containers. The sediment itself showed many conspicuous tracks. At present, it is still not clear why *M. balthica* exhibits this behaviour. Beukema (1983), stated that the tracks of *M. balthica* moving at the surface will be limited to specimens infected with trematodes. The hypothesis that crawling is induced by parasites has received widespread acceptance, but Mouritsen (1997) invalidated this theory. He argued that crawling specimens represent a group of retarded animals that in order to catch up growth and gonad development optimize deposit feeding at the expense of anti-predator behaviour, and therefore are engaged in frequent relocation to encounter unexploited food resources.

Personal observations support this hypothesis. The bivalves that were crawling in August had been denied of food for two months. After they were supplied with *I. galbana* as a food resource, the numbers of crawlers significantly reduced: within two days of feeding they decreased from 32 to 9. Experiments where *M. balthica* is starved for a long period of time might reveal the answer to the crawling question.

Since the tidal flats also function as nurseries for the epibenthic predators (Janssen & Kuipers, 1980; Reise, 1985), it can be expected that their numbers become very high, unless they are regulated by other predators. It is arguable that birds such as oystercatchers, knut and dunlin, whose diet is known to include shrimp and small crabs (Hulscher, 1981; Nehls and Tiedemann, 1993; Piersma et al, 1993), indirectly protect 0-group bivalves against their main predators. It would be interesting to give this some attention and find out what role wading birds play in the nurseries of *M. balthica*.

Hardly any data are available on the densities of juvenile epibenthos on the highest tidal flats in the eastern Wadden Sea. Literature mainly focuses on adult species or describes densities on sites like the Balgzand area (Beukema, 1991, 1992), the German Bight (Günther, 1990), or even the Danish Wadden Sea (Jensen & Jensen, 1985). This makes it difficult to draw conclusions about the possible effect of predation by juvenile epibenthos on *M. balthica* in the nurseries on the Groninger Wad. It is therefore recommended to determine the densities of juvenile epibenthic predators during the summer months on the high tidal flats of the Groninger Wad.

ACKNOWLEDGEMENTS

I would very much like to thank Jan Geert Hiddink, who kept a supervising eye, thought me the ropes of fieldwork and showed me how to recognize a fish in a fishnet. I really enjoyed those hours on the tidal flats, sieving mud and trying to catch predators. I would also like to thank Wim Wolff, who recommended that I should talk to Jan Geert in the first place, to see if I could do some research for his PhD project. I wish to thank Jos de Wiljes for getting the climate chamber ready in time, Harry Peletier for the algal culture, the men of the workshop for making the experimental containers, Anton Nolle for editing the video and Eize Stamhuis for his useful suggestions. Furthermore, I would like to thank everyone who helped me to gather a supply of “nonnetjes”, shrimp, crabs, fish and several kilo’s of sediment.

5. REFERENCES

- Aarnio, K., Bonsdorf, E and Rosenback, N. (1996). Food and feeding of juvenile flounder *Platichthys flesus* (L.), and turbot *Scophthalmus maximus* L. in the Åland archipelago, northern Baltic Sea. *J. Sea Res.* 36: 311-320.
- Abbas, S.A.M. (1985). Predation of infaunal bivalves by *Carcinus maenas* (L.) in the Burry Inlet, S. Wales. *Ph.D. thesis*. University of Wales, Swansea. pp 1-232.
- Admiraal, W. and Werner, D. (1983). Utilization of limiting concentrations of orthophosphate and production of extracellular organic phosphates in cultures of marine diatoms. *J. Plankton Res.* 5:495-513.
- Afman, B.P. (1980). De voedselopname van de strandkrab *Carcinus maenas* (L.). *Internal Report Netherlands Institute for Sea Research* 4:1-27.
- Armonies, W. (1996) Changes in distribution patterns of 0-group bivalves in the Wadden Sea: byssus-drifting releases juveniles from the constraints of hydrography. *J. Sea Res.* 35: 323-334.
- Armonies, W. and Hellwig-Armonies, M. (1992). Passive settlement of *Macoma balthica* spat on tidal flats of the Wadden Sea and subsequent migration of juveniles. *Neth. J. Sea Res.* 29:371-378.
- Beukema, J.J. (1983). The baltic tellin *Macoma balthica*. In: Wolff, W.J. (ed). *Ecology of the Wadden Sea*. Balkema, Rotterdam. 1: 4/116-117.
- Beukema, J.J. (1991). The abundance of shore crabs *Carcinus maenas* (L.) on a tidal flat in the Wadden Sea after cold and mild winters. *J. Exp. Mar. Biol. Ecol.* 153: 97-113.
- Beukema, J.J. (1992). Dynamics of juvenile shrimp *Crangon crangon* in a tidal-flat nursery of the Wadden Sea after mild and cold winters. *Mar. Ecol. Prog. Ser.* 83: 157-165.
- Beukema, J.J. (1993). Successive changes in distribution patterns an an adaptive strategy in the bivalve *Macoma balthica* (L.) in the Wadden Sea. *Helgol. wiss. Meeresunters.* 47: 287-304.
- Beukema, J.J. and de Vlas, J. (1989). Tidal-current transport of thread-drifting postlarval juveniles of the bivalve *Macoma balthica* from the Wadden Sea to the North Sea. *Mar. Ecol. Prog. Ser.* 52: 193-200.
- Creutzberg, F., Elting, A.T.G.W. and van Noort, J. (1978). The migration of Plaice larvae *Pleuronectes platessa* into the western Wadden Sea. In: McLusky, D.S. & Berry, A.J. (eds). *Proc. 12th Europ. Mar. Biol. Symp.* Pergamon Press, Oxford. pp. 243-251.
- Del Norte-Campos, A.G.C. and Temming, A. (1994). Daily activity, feeding and ratios in gobies and brown shrimp in the northern Wadden Sea. *Mar. Ecol. Prog. Ser.* 115: 41-53.
- Dekinga, A. and Piersma, T. (1993). Reconstructing diet composition on the basis of faeces in a mollusc-eating wader, the Knot *Calidris canutus*. *Bird study.* 40:144-156.
- Elner, R.W. (1978). The mechanisms of predation by the shore crab *Carcinus maenas* (L.), on the edible mussel, *Mytilus edulis* L. *Oecologia* 36: 333-344.
- Evans, S. (1984). Energy budgets and predation impact of dominant epibenthic carnivores on a shallow soft bottom community at the Swedish west coast. *Estuarine, Coastal and Shelf Science.* 18: 651-672.

- Günther, C.P. (1990). Distribution patterns of juvenile macrofauna on an intertidal sandflat: an approach to the variability of predator/prey interactions. In: Barnes, M. & Gibson, R.N. (eds). *Trophic relationships in the marine environment. Proc. 24th Europ. Mar. Biol. Symp.* Aberdeen University Press. pp 77-88.
- Günther, C.P. (1991). Settlement of *Macoma balthica* on an intertidal sandflat in the Wadden Sea. *Mar. Ecol. Progr. Ser.* 76: 73-79.
- Günther, C.P. (1994). Recruitment of *Macoma balthica* (L.) on an intertidal sandflat in the Wadden Sea. *Senckenbergiana Maritima* 25: 11-20.
- Janssen, G.M. and Kuipers, B.R. (1980). On tidal migration in the shrimp *Crangon crangon*. *Neth. J. Sea Res.* 14: 339-348.
- Jubb, C.A., Hughes, R.N. and Rheinhardt, T. ap. (1983). Behavioural mechanisms of size-selection by crabs, *Carcinus maenas*, feeding on mussels, *Mytilus edulis* L. *J. Exp. Mar. Biol. Ecol.* 66: 81-87.
- Hulscher, J.B. (1981). The Oystercatcher *Haematopus ostralegus* as a predator of the bivalve *Macoma balthica* in the Dutch Wadden Sea. *Ardea.* 70: 89-152.
- Hummel, H. (1985a). Food intake of *Macoma balthica* (Mollusca) in relation to seasonal changes in its potential food on a tidal flat in the Dutch Wadden Sea. *Neth. J. Sea Res.* 19:52-76.
- Hummel, H. (1985b). Food intake and growth in *Macoma balthica* (Mollusca) in the laboratory. *Neth. J. Sea Res.* 19: 77-83.
- Janssen, G.M. and Kuipers, B.R. (1980). On tidal migration in the shrimp *Crangon crangon*. *Neth. J. Sea Res.* 14: 339-348.
- Jensen, K.T. and Jensen, J.N. (1985). The importance of some epibenthic predators on the density of juvenile benthic macrofauna in the Danish Wadden Sea. *J. Exp. Mar. Biol. Ecol.* 89: 157-174.
- Kamermans, P. (1992). Nutritional value of solitary cells and colonies of *Phaeocystis* sp. for the bivalve *Macoma balthica* (L.). In: Growth limitation in intertidal bivalves of the Dutch Wadden Sea. *Ph.D. thesis*, State University of Groningen. pp. 103-112.
- Kamermans, P. and Huitema, H.J. (1994). Shrimp (*Crangon crangon* L.) browsing upon siphon tips inhibits feeding and growth in the bivalve *Macoma balthica* (L.). *J. Exp. Mar. Biol. Ecol.* 175: 59-75.
- Keus, B. (1986). De predatie van de garnaal (*Crangon crangon*) op het broed van het nonnetje (*Macoma balthica*). *Internal Report Netherlands Instituut for Sea Research.* 5: 1-43.
- Klein Breteler, W.C.M. (1975). Laboratory experiments on the influence of environmental factors on the frequency of moulting and the increase in size at moulting of juvenile shore crabs, *Carcinus maenas*. *Neth. J. Sea Res.* 9:100-120.
- Klein Breteler, W.C.M. (1976a). Migration of the shore crab *Carcinus maenas*, in the Dutch Wadden Sea. *Neth. J. Sea Res.* 10: 338-353.
- Klein Breteler, W.C.M. (1976b). Settlement, growth and production of the shore crab, *Carcinus maenas*, on tidal flats in the Dutch Wadden Sea. *Neth. J. Sea Res.* 10: 354-376.
- Klein Breteler, W.C.M. (1983). The shore crab *Carcinus maenas*. In: Wolff, W.J. (ed). *Ecology of the Wadden Sea.* Balkema, Rotterdam. 1: 119-121.

- Kuipers, B. (1975). Experiments and field observations on the daily food intake of juvenile plaice, *Pleuronectes platessa* L. In: Barnes, H. (ed). *Proc. 9th Europ. mar. biol. Symp.* Aberdeen University Press. pp 1-12.
- Matilla, J. and Bonsdorff, E. (1998). Predation by juvenile flounder (*Platichthys flesus* L.): a test of prey vulnerability, predator preference, switching behaviour and functional response. *J. Exp. Mar. Biol. Ecol.* 227: 221-236.
- Mattila, J., Olafsson, E.B. and Johansson, A. (1990). Predation effects of *Crangon crangon* (Fabricius) on benthic meio- and macrofauna on shallow sandy bottoms - an experimental study from southern Sweden. In: Barnes, M. & Gibson, R.N. (Eds). *Trophic relationships in the marine environment. Proc. 24th Europ. Mar. Biol. Symp.* Aberdeen University Press. pp. 503-516.
- Naylor, E. (1962). Seasonal changes in a population of *Carcinus maenas* (L.) in the littoral zone. *J. Anim. Ecol.* 31: 601-609.
- Nehls, G. and Tiedemann, R. (1993). What determines the densities of feeding birds on tidal flats? A case study on dunlin, *Calidris alpina*, in the Wadden Sea. *Neth. J. Sea Res.* 31: 375-384.
- Piersma, T., Hoekstra, R., Dekinga, A., Koolhaas, A., Wolf, P., Battley, P. and Wiersma, P. (1993). Scale and intensity of intertidal habitat use by knots *Calidris canutus* in the western Wadden Sea in relation to food, friends and foes. *Neth. J. Sea Res.* 31: 331-357.
- Pihl, L. (1985). Food selection and consumption of mobile epibenthic fauna in shallow marine areas. *Mar. Ecol. Progr. Ser.* 22: 169-179.
- Pihl, L. & Rosenberg, R. (1984). Food selection and consumption of the shrimp *Crangon crangon* in some shallow marine areas in western Sweden. *Mar. Ecol. Progr. Ser.* 15: 159-168.
- Plagmann, J. (1939). Ernährungsbiologie der Garnele (*Crangon vulgaris* Fabr.). *Helgol. Wiss. Meeresunters.* 2: 113-162.
- Reise, K. (1985). Tidal flat ecology - An experimental approach to species interactions. Springer-Verlag Berlin Heidelberg. pp. 26-28.
- Ropes, J.W. (1968). The feeding habits of the green crab, *Carcinus maenas* (L.). *Fish. Bull.* 67: 183-202.
- Sanchez-Salazar, M.E., Griffiths, C.L. and Seed, R. (1987). The effect of size and temperature on the predation of cockles *Cerastoderma edule* (L.) by the shore crab *Carcinus maenas* (L.). *J. Exp. Mar. Biol. Ecol.* 111:181-193.
- Stamhuis, E.J., Videler, J.J. and de Wilde, P.A.W.J. (1998). Optimal foraging in the thalassinidean shrimp *Callinectes subterranea* - Improving food quality by grain size selection. *J. Exp. Mar. Biol. Ecol.* 228:197-208.
- Steur, C., Seys, J. and Eppinga, J. (1996). Ecologisch profiel van het Nonnetje (*Macoma balthica*). *RIKZ rapport* 96.002.
- Van der veer, H., Bergman, M.J.N., Dapper, R. and Witte, J.IJ. (1991). Population dynamics of an intertidal 0-group flounder *Platichthys flesus* population in the western Dutch Wadden Sea. *Mar. Ecol. Progr. Ser.* 73: 141-148.
- Wolff, W.J. and Zijlstra, J.J. (1983). The common shrimp *Crangon crangon*. In: Wolff, W.J. (ed). *Ecology of the Wadden Sea*. Balkema, Rotterdam. 1: 122-123.
- Zwarts, L. (1996). Waders and their estuarine food supplies. *Ph. D. thesis*, State University of Groningen. pp. 155-172.

Zwarts, L., Blomert, A.M., Spaak, B. and de Vries, B. (1994) Feeding radius, burying depth and siphon size of *Macoma balthica* and *Scrobicularia plana*. *J. Exp. Mar. Biol. Ecol.* 183:193-212.

APPENDIX I

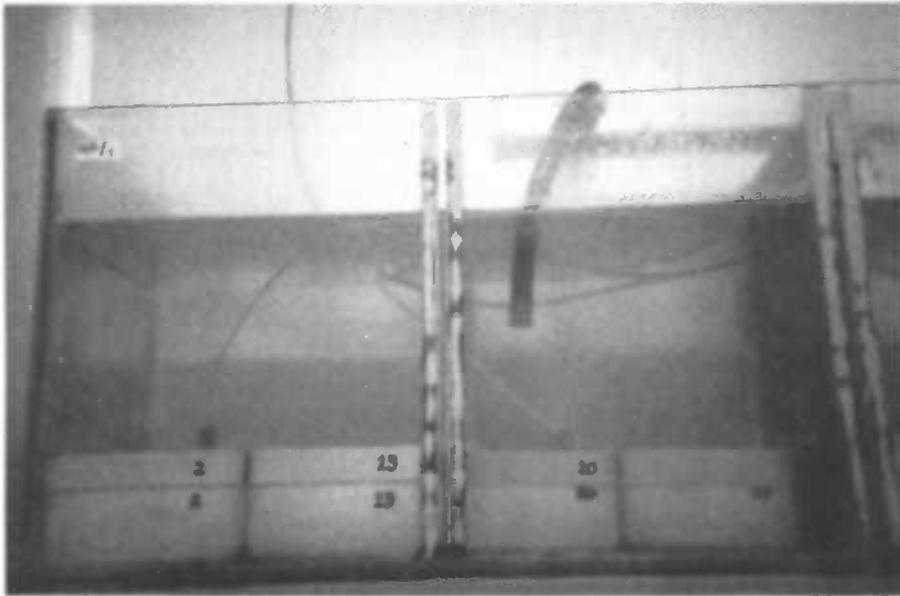


Fig. I. Experimental containers (15 x 10 x 13 cm), covered with 1 mm mesh lids, in an aerated aquarium.

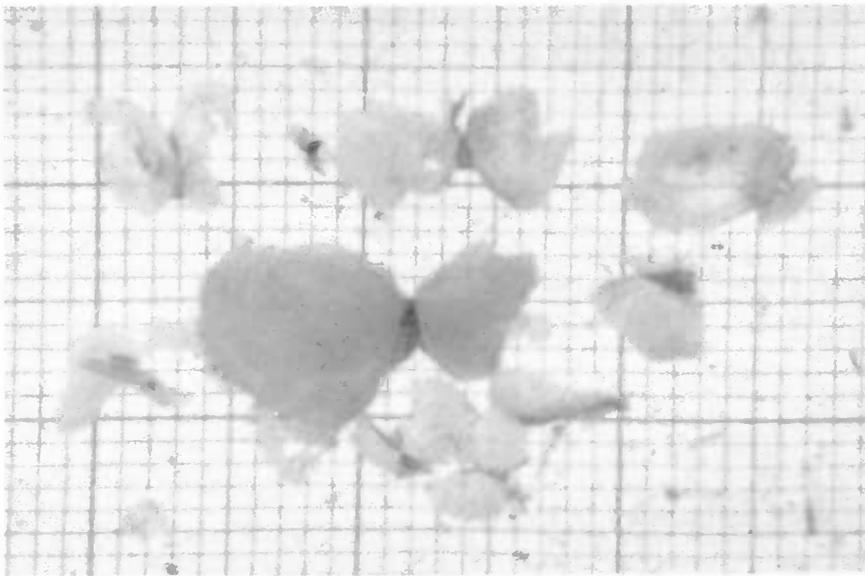


Fig. II. Fragments of different size classes of *M. balthica* after 6 hours of predation by a juvenile shore crab with a carapace width of 20 mm.

APPENDIX II

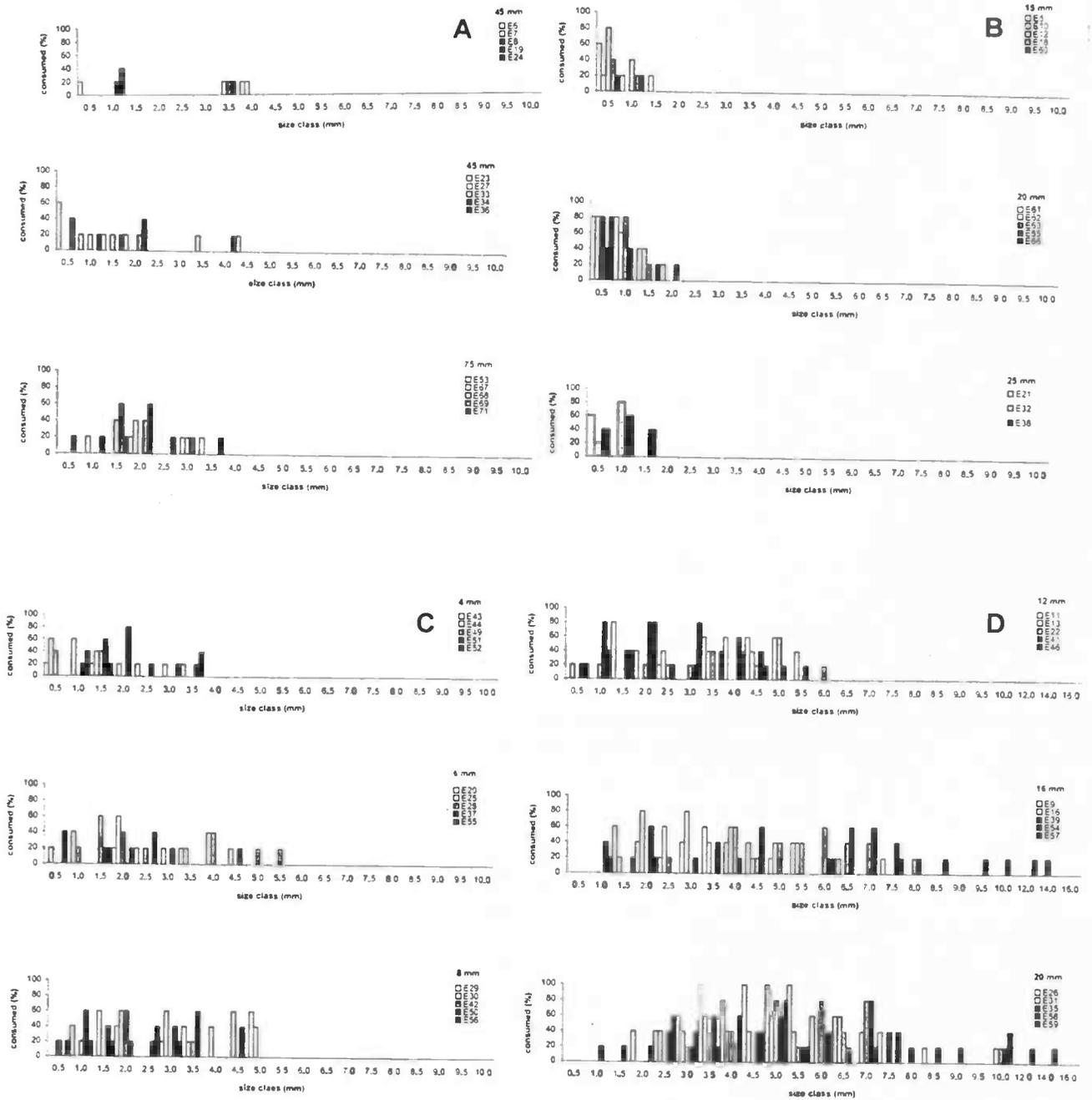


Fig III a-c. Results of the predation experiments. a) *Pomatoschistus microps*, *Pleuronectes platessa* and *Plathichthys flesus*. b) *Crangon crangon* with a length of 15, 20 and 25 mm c) *Carcinus maenas* with a carapace width of 4, 6 and 8 mm. d) *Carcinus maenas* with a carapace width of 12, 16 and 20 mm. Experiments (E) are numbered in chronological order.

APPENDIX III

Table I. Statistical analysis on the data obtained from 5 predation experiments with 4 shrimp each. Shrimp length = 1.5 mm

Analysis of Variance					
Source	Sum of Squares	Df	Mean Square	F-Ratio	P-Value
Between groups	10604.0	19	558.105	11.63	0.0000
Within groups	3840.0	80	48.0		
Total (Corr.)	14444.0	99			

Multiple Range Tests

Method: 95.0 percent LSD			
macsizes	Count	Mean	Homogeneous Groups
10	5	0.0	X
9.5	5	0.0	X
2	5	0.0	X
2.5	5	0.0	X
3	5	0.0	X
3.5	5	0.0	X
4	5	0.0	X
4.5	5	0.0	X
5	5	0.0	X
5.5	5	0.0	X
6	5	0.0	X
6.5	5	0.0	X
7	5	0.0	X
7.5	5	0.0	X
8	5	0.0	X
8.5	5	0.0	X
9	5	0.0	X
1.5	5	4.0	X
1	5	20.0	X
0.5	5	44.0	X

Variance Check

Cochran's C test: 0.708333 P-Value = 0.0832233
 Bartlett's test: 1.44413 P-Value = 0.137443

Table II. Statistical analysis on the data obtained from 5 predation experiments with 4 shrimp each. Shrimp length = 2.0 mm.

Analysis of Variance					
Source	Sum of Squares	Df	Mean Square	F-Ratio	P-Value
Between groups	36556.0	19	1924.0	20.91	0.0000
Within groups	7360.0	80	92.0		
Total (Corr.)	43916.0	99			

Multiple Range Tests

Method: 95.0 percent LSD			
macsizes	Count	Mean	Homogeneous Groups
9	5	0.0	X
9.5	5	0.0	X
10	5	0.0	X
2.5	5	0.0	X
3	5	0.0	X
3.5	5	0.0	X
4	5	0.0	X
4.5	5	0.0	X
5	5	0.0	X
5.5	5	0.0	X
6	5	0.0	X
6.5	5	0.0	X
7	5	0.0	X
7.5	5	0.0	X
8	5	0.0	X
8.5	5	0.0	X
2	5	8.0	X
1.5	5	24.0	X
1	5	52.0	X
0.5	5	72.0	X

Variance Check

Cochran's C test: 0.608696 P-Value = 0.0668042
 Bartlett's test: 1.38861 P-Value = 0.190451

APPENDIX III

Table III. Statistical analysis on the data obtained from 3 predation experiments with 4 shrimp each. Shrimp length = 2.5 mm.

Analysis of Variance					
Source	Sum of Squares	Df	Mean Square	F-Ratio	P-Value
Between groups	9100.0	19	478.947	5.32	0.0000
Within groups	7200.0	80	90.0		
Total (Corr.)	16300.0	99			

Multiple Range Tests

Method: 95.0 percent LSD			
macsizes	Count	Mean	Homogeneous Groups
10	5	0.0	X
1.5	5	0.0	X
2	5	0.0	X
2.5	5	0.0	X
3	5	0.0	X
3.5	5	0.0	X
4	5	0.0	X
4.5	5	0.0	X
5	5	0.0	X
5.5	5	0.0	X
6	5	0.0	X
6.5	5	0.0	X
7	5	0.0	X
7.5	5	0.0	X
8	5	0.0	X
8.5	5	0.0	X
9	5	0.0	X
9.5	5	0.0	X
1	5	20.0	X
0.5	5	40.0	X

Variance Check

Cochran's C test: 0.555556 P-Value = 0.834019
 Bartlett's test: 1.00623 P-Value = 0.83354

Table IV. Statistical analysis on the data obtained from 5 predation experiments with 1goby each. Length of the fish = 45 mm.

Analysis of Variance					
Source	Sum of Squares	Df	Mean Square	F-Ratio	P-Value
Between groups	1516.0	19	79.7895	2.49	0.0025
Within groups	2560.0	80	32.0		
Total (Corr.)	4076.0	99			

Multiple Range Tests

Method: 95.0 percent LSD			
macsizeg	Count	Mean	Homogeneous Groups
9	5	0.0	X
9.5	5	0.0	X
2	5	0.0	X
2.5	5	0.0	X
1.5	5	0.0	X
10	5	0.0	X
4	5	0.0	X
4.5	5	0.0	X
5	5	0.0	X
5.5	5	0.0	X
6	5	0.0	X
6.5	5	0.0	X
7	5	0.0	X
7.5	5	0.0	X
8	5	0.0	X
8.5	5	0.0	X
0.5	5	4.0	XX
3.5	5	8.0	XX
3	5	12.0	X
1	5	12.0	X

Variance Check

Cochran's C test: 0.5 P-Value = 0.25
 Bartlett's test: 1.1547 P-Value = 0.555084

APPENDIX III

Table V. Statistical analysis on the data obtained from 5 predation experiments with 1 plaice each. Length of the fish = 45 mm.

Analysis of Variance					
Source	Sum of Squares	Df	Mean Square	F-Ratio	P-Value
Between groups	3664.0	19	192.842	2.47	0.0027
Within groups	6240.0	80	78.0		
Total (Corr.)	9904.0	99			

Multiple Range Tests

Method: 95.0 percent LSD			
macsizep	Count	Mean	Homogeneous Groups
8	5	0.0	X
7.5	5	0.0	X
6.5	5	0.0	X
2.5	5	0.0	X
3	5	0.0	X
9	5	0.0	X
10	5	0.0	X
9.5	5	0.0	X
5	5	0.0	X
5.5	5	0.0	X
6	5	0.0	X
6.5	5	0.0	X
7	5	0.0	X
3.5	5	4.0	XX
4.5	5	4.0	XX
4	5	4.0	XX
1.5	5	12.0	XX
1	5	12.0	XX
2	5	16.0	X
0.5	5	20.0	X

Variance Check

Cochran's C test: 0.512821 P-Value = 0.0089517
 Bartlett's test: 1.49294 P-Value = 0.114696

Kruskal-Wallis Test

Test statistic = 39.5997 P-Value = 0.00369189

Table VI. Statistical analysis on the data obtained from 5 predation experiments with 1 flounder each. Length of the fish = 75 mm.

Analysis of Variance					
Source	Sum of Squares	Df	Mean Square	F-Ratio	P-Value
Between groups	7404.0	19	389.684	4.53	0.0000
Within groups	6880.0	80	86.0		
Total (Corr.)	14284.0	99			

Multiple Range Tests

Method: 95.0 percent LSD			
macsizef	Count	Mean	Homogeneous Groups
7.5	5	0.0	X
8.5	5	0.0	X
9	5	0.0	X
8	5	0.0	X
10	5	0.0	X
9.5	5	0.0	X
4	5	0.0	X
4.5	5	0.0	X
5	5	0.0	X
5.5	5	0.0	X
6	5	0.0	X
6.5	5	0.0	X
7	5	0.0	X
2.5	5	4.0	XX
0.5	5	4.0	XX
3.5	5	8.0	XX
1	5	8.0	XX
3	5	12.0	X
1.5	5	24.0	X
2	5	32.0	X

Variance Check

Cochran's C test: 0.395349 P-Value = 0.0960252
 Bartlett's test: 1.45535 P-Value = 0.142857

APPENDIX III

Table VII. Statistical analysis on the data obtained from 5 predation experiments with 1crab each. Carapace width = 4 mm.

Analysis of Variance					
Source	Sum of Squares	Df	Mean Square	F-Ratio	P-Value
Between groups	11536.0	19	607.158	3.61	0.0000
Within groups	13440.0	80	168.0		
Total (Corr.)	24976.0	99			

Multiple Range Test

Method: 95.0 percent LSD			
macsize	Count	Mean	Homogeneous Groups
8	5	0.0	X
7.5	5	0.0	X
10	5	0.0	X
9	5	0.0	X
8.5	5	0.0	X
9.5	5	0.0	X
4	5	0.0	X
4.5	5	0.0	X
5	5	0.0	X
5.5	5	0.0	X
6	5	0.0	X
6.5	5	0.0	X
7	5	0.0	X
3	5	8.0	XX
2.5	5	8.0	XX
3.5	5	16.0	XX
2	5	20.0	XX
0.5	5	24.0	XX
1	5	24.0	XX
1.5	5	36.0	X

Variance Check

Cochran's C test: 0.357143 P-Value = 0.184321
 Bartlett's test: 1.37667 P-Value = 0.225744

Table VIII. Statistical analysis on the data obtained from 5 predation experiments with 1crab each. Carapace width = 6 mm.

Analysis of Variance					
Source	Sum of Squares	Df	Mean Square	F-Ratio	P-Value
Between groups	6416.0	19	337.684	2.22	0.0073
Within groups	12160.0	80	152.0		
Total (Corr.)	18576.0	99			

Multiple Range Tests

Method: 95.0 percent LSD			
macsize	Count	Mean	Homogeneous Groups
7.5	5	0.0	X
6.5	5	0.0	X
8	5	0.0	X
6	5	0.0	X
10	5	0.0	X
7	5	0.0	X
9.5	5	0.0	X
9	5	0.0	X
8.5	5	0.0	X
5.5	5	4.0	XX
5	5	4.0	XX
3.5	5	8.0	XXX
3	5	8.0	XXX
4.5	5	8.0	XXX
1	5	12.0	XXX
0.5	5	12.0	XXX
4	5	16.0	XXX
2	5	16.0	XXX
1.5	5	20.0	XX
2.5	5	28.0	X

Variance Check

Cochran's C test: 0.197368 P-Value = 0.670026
 Bartlett's test: 1.28011 P-Value = 0.444002

APPENDIX III

Table IX. Statistical analysis on the data obtained from 5 predation experiments with 1 crab each. Carapace width = 8 mm.

Analysis of Variance					
Source	Sum of Squares	Df	Mean Square	F-Ratio	P-Value
Between groups	15264.0	19	803.368	3.16	0.0002
Within groups	20320.0	80	254.0		
Total (Corr.)	35584.0	99			

Multiple Range Test

Method: 95.0 percent LSD			
macsize	Count	Mean	Homogeneous Groups
6	5	0.0	X
8.5	5	0.0	X
7	5	0.0	X
6.5	5	0.0	X
9	5	0.0	X
9.5	5	0.0	X
10	5	0.0	X
7.5	5	0.0	X
8	5	0.0	X
5.5	5	0.0	X
2.5	5	8.0	XX
0.5	5	8.0	XX
4	5	8.0	XX
5	5	20.0	XXX
4.5	5	20.0	XXX
1.5	5	24.0	XX
3.5	5	28.0	XX
3	5	28.0	XX
1	5	28.0	XX
2	5	36.0	X

Variance Check

Cochran's C test: 0.15748 P-Value = 1.0
 Bartlett's test: 1.19562 P-Value = 0.684232

Table X. Statistical analysis on the data obtained from 5 predation experiments with 1 crab each. Carapace width = 12 mm.

Analysis of Variance					
Source	Sum of Squares	Df	Mean Square	F-Ratio	P-Value
Between groups	21544.3	22	979.289	2.86	0.0002
Within groups	31520.0	92	342.609		
Total (Corr.)	53064.3	114			

Multiple Range Tests

Method: 95.0 percent LSD			
macsize	Count	Mean	Homogeneous Groups
7	5	0.0	X
9	5	0.0	X
8	5	0.0	X
7.5	5	0.0	X
8.5	5	0.0	X
12	5	0.0	X
16	5	0.0	X
14	5	0.0	X
10	5	0.0	X
9.5	5	0.0	X
6.5	5	4.0	XX
6	5	4.0	XX
5.5	5	12.0	XXX
0.5	5	12.0	XXX
2.5	5	20.0	XXXX
3	5	24.0	XXX
1.5	5	28.0	XX
5	5	28.0	XX
1	5	28.0	XX
3.5	5	32.0	XX
2	5	32.0	XX
4	5	32.0	XX
4.5	5	36.0	X

Variance Check

Cochran's C test: 0.142132 P-Value = 1.0
 Bartlett's test: 1.47917 P-Value = 0.0965378

APPENDIX III

Table XI. Statistical analysis on the data obtained from 5 predation experiments with 1 crab each. Carapace width = 16 mm.

Analysis of Variance					
Source	Sum of Squares	Df	Mean Square	F-Ratio	P-Value
Between groups	16556.5	22	752.569	1.87	0.0205
Within groups	36960.0	92	401.739		
Total (Corr.)	53516.5	114			

Multiple Range Tests

Method: 95.0 percent LSD			
macsize	Count	Mean	Homogeneous Groups
0.5	5	0.0	
16	5	0.0	X
9	5	0.0	X
8.5	5	0.0	X
12	5	4.0	XX
10	5	4.0	XX
9.5	5	4.0	XX
14	5	4.0	XX
8	5	8.0	XX
1	5	12.0	XXX
7.5	5	16.0	XXXX
7	5	20.0	XXXX
1.5	5	20.0	XXXX
6	5	20.0	XXXX
2.5	5	20.0	XXXX
6.5	5	24.0	XXXX
5.5	5	24.0	XXXX
3.5	5	24.0	XXXX
3	5	28.0	XXX
5	5	28.0	XXX
4.5	5	28.0	XXX
4	5	36.0	XXX
2	5	40.0	XX
			X

Variance Check

Cochran's C test: 0.121212 P-Value = 0.826574
 Bartlett's test: 1.41814 P-Value = 0.138793

Table XII. Statistical analysis on the data obtained from 5 predation experiments with 1 crab each. Carapace width = 20 mm.

Analysis of Variance					
Source	Sum of Squares	Df	Mean Square	F-Ratio	P-Value
Between groups	51568.7	22	2344.03	5.41	0.0000
Within groups	39840.0	92	433.043		
Total (Corr.)	91408.7	114			

Multiple Range Tests

Method: 95.0 percent LSD			
macsize	Count	Mean	Homogeneous Groups
9.5	5	0.0	
16	5	0.0	X
0.5	5	0.0	X
1.5	5	4.0	X
8	5	4.0	X
12	5	4.0	X
14	5	4.0	X
9	5	4.0	X
1	5	4.0	X
8.5	5	8.0	X
2	5	12.0	XX
10	5	20.0	XXX
7.5	5	24.0	XXX
6.5	5	36.0	XXX
3	5	36.0	XXX
2.5	5	36.0	XXX
5.5	5	40.0	XX
7	5	44.0	XX
6	5	44.0	XX
4.5	5	44.0	XX
4	5	44.0	XX
3.5	5	52.0	XX
5	5	76.0	X

Variance Check

Cochran's C test: 0.128514 P-Value = 0.631776
 Bartlett's test: 1.64429 P-Value = 0.00894121

Kruskal-Wallis Test

Test statistic = 67.47 P-Value = 0.00000164411

APPENDIX III

Table XIII. Statistical analysis on the data obtained from a total of 30 predation experiments with juvenile crab of different sizes.

Analysis of Variance for consumed - Type III Sums of Squares

Source	Sum of Squares	Df	Mean Square	F-Ratio	P-value
MAIN EFFECTS					
A:predlength	28715.8	5	5743.16	16.48	0.0
B:macsize	62121.4	22	2823.7	8.10	0.0
RESIDUAL	215004.0	617	348.467		
TOTAL (CORRECTED)	299283.0	644			

All F-ratios are based on the residual mean square error.

Multiple Range Tests for consumed by predlength

Method: 95.0 percent LSD

predlength	Count	LS Mean	Homogeneous Groups
4	100	4.44928	X
6	100	4.44928	X
8	100	8.04928	XX
12	115	12.6957	XX
16	115	16.1739	X
20	115	23.4783	X