The adaptive value of migrations for the bivalve *Macoma balthica*

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The adaptive value of migrations for the bivalve *Macoma balthica*

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CHAPTER 1

General introduction

Animals move from one place to another for a variety of reasons. This study is about the movements of a coastal marine bivalve, *Macoma balthica*, that migrates over several kilometres between the adult habitat on low-lying tidal flats and nurseries for the juveniles at the high flats. Dingle (1996) defined a migration as a 'persistent and straightened out movement, effected by the animal's own locomotion or active embarkation on a vehicle'. The definition excludes random dispersal, foraging movements and other small-scale and short-term movements. It includes the movements of *M. balthica*.

MIGRATORY BENTHOS OF INTERTIDAL AREAS

Occurrence of migratory benthos

This and the next sections give an overview of the migration of benthos species in the Wadden Sea and other temperate tidal flat areas, especially for species using nurseries. I primarily examined bivalves and polychaetes in these sections. Sometimes, however, the more mobile crustaceans or fish are also used as examples. The specific questions addressed in this chapter are 1) which species migrate, 2) which methods do benthos use for migration and what distances are covered, 3) what are the costs and benefits of the migrations?

Most of the macrozoobenthic species of the Wadden Sea have been caught in the water column in a non-larval stage (Günther 1992; Armonies 1994a; Jaklin & Günther 1996). Günther (1992) gives an extensive overview of all Wadden Sea species that migrate of show changing distribution during their life history. Many of these species are present in the water column because they change habitats and are actively

migrating. These migrations probably increase the mortality for benthic species, because they have to leave their burrow and become available for pelagic predators such as fish, which they normally do not encounter, and they run the risk to end up in unsuitable habitats. Therefore, the change of habitat must offer major advantages to the migrant.

A common life-history feature of benthic animals that makes migrations necessary and apparently profitable is the use of nurseries. A nursery is an area where juveniles of a species grow before recruiting to the adult population. The nurseries are spatially separated from the areas where adults live and are characterised by an increased growth or reduced mortality of juveniles. In the Wadden Sea, nurseries are often located in the high intertidal zone (*Macoma balthica*, Beukema 1993a, *Arenicola marina*, Farke *et al.* 1979).

Figure 1 gives an example of a lugworm *Arenicola marina* nursery in the Dutch Wadden Sea. Densities of juveniles are highest at the highest level stations, which are within 1 km from the mainland. Highest concentrations of adults are found 2 to 4 km from the shore. Since the nursery and the adult habitat are spatially separated, the juveniles that recruit to the adult population have to migrate. Other reasons for benthos to undertake migrations are spawning locations that are spatially separated from the regular living areas and seasonal changes in the abiotic and biotic environment.

Although some of the species are probably passively resuspended by waves or current, a large fraction of all benthos species show 'active' migrations during one or more of their life stages. Migrations can be divided in 3 types: 1) migrations to and from nurseries, 2) spawning migrations and 3) seasonal migrations.

Migration to and from nurseries

When a species uses a nursery that is spatially separated from the adult habitat and when this species does not settle as a planktonic stage in the nursery, a migration to and from the nursery has to be undertaken. The migration to the nursery is often described as secondary settlement. This settlement is distinct from the primary settlement, when larvae settle for the first time after a planktonic phase. Table 1 shows the species from the Wadden Sea for which there are indications that they use nurseries. Also, the location of the nurseries and some information on the timing of migrations are given.

Most species that use nurseries migrate out of the nursery within 1 year. Only *Nereis virens* lives in the nursery for several years. Most nurseries are located in the high intertidal and on silty sediments. However, the main conclusion is that, except for *M. balthica* and *Arenicola,* knowledge on the nursery use of intertidal benthic species is scarce and incomplete.

Figure 1. Numerical densities of small (○) and big (●) lugworms *Arenicola marina* on tidal flats at various distances from the coast, during late summer (data from a single sampling of 99 transects scattered over the Dutch Wadden Sea, grouped according to distance from the coast, n =11 to 19 per group) (Beukema & De Vlas 1979).
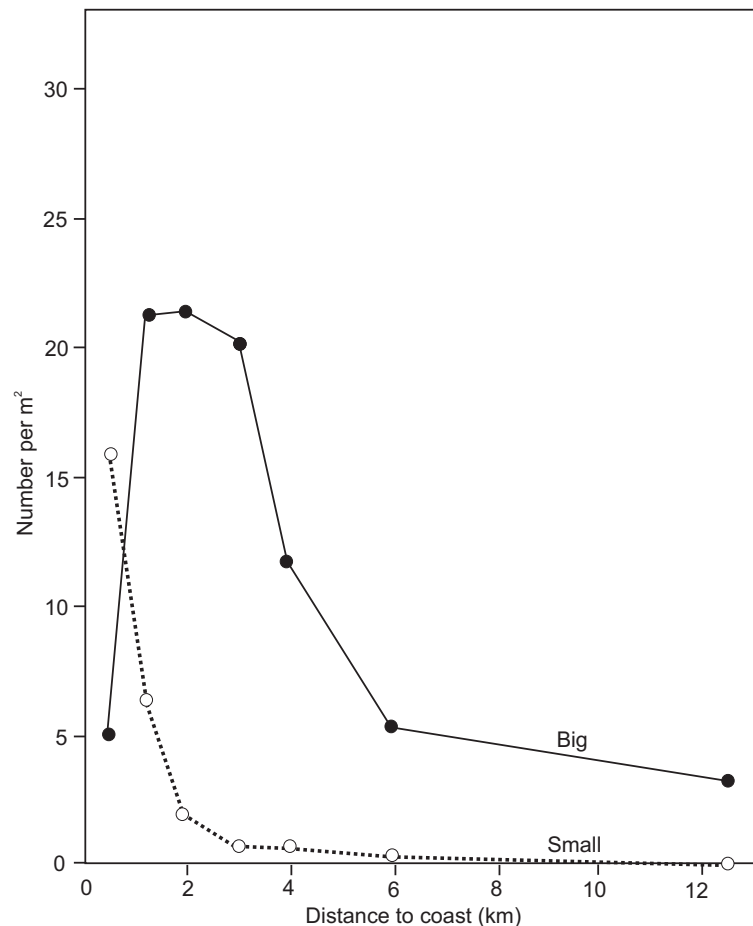
For some of the species in Table 1, like *Heteromastus filiformis*, *Nereis diversicolor* and *Scoloplos*, it is doubtful whether the nurseries described in Table 1 are really nurseries. Especially for *Scoloplos* juveniles, that are concentrated at locations close to where the egg mass hatched, it is doubtful whether this may be called a nursery, because it the result of the concentration of *Scoloplos* eggs in a larger capsule and in fact not spatially separated from the locations where the adults live. The pelagic dispersal of juvenile *Corophium volutator* is probably also related to some form of nursery use.

Seasonal and spawning migrations

Spawning migrations are often seasonal. Of all benthic species, only a few polychaete species (almost all are *Nereis* species) show seasonal and spawning migrations (Table 1). For the nereids, however, it is not clear whether the spawning movements can be really called migrations, as they only move from the sediment to the water column. De Wolf (pers. comm.) found an accumulation of large *Hydrobia ulvae* on the saltmarsh in summer. This cannot be considered a nursery or be seen as a spawning migration. Maybe it is only passive displacement. More information on seasonal and spawning migrations is given by Günther (1992).

Table 1. Intertidal benthic animals (Wadden Sea) that undertake migrations that relate to nursery use, spawning or seasonal migrations

| Group	Species	Type of migration	From	To	Age at migration (year)	Season/moment of Migration	Source
Crustacea	Corophium volutator	Dispersal	Estuary	Landward flats		Nocturnal high tides, before spring tide	(Essink et al. 1989; Lawrie & Raffaelli 1998)
Bivalve	Ensis directus	Nursery	Subtidal	?			(Armonies 1996)
Bivalve	Macoma balthica	Nursery	High intertidal Silt	Low intertidal	¾	Winter	(Wolff & De Wolf 1977; Beukema & De Vlas 1989; Armonies & Hellwig-Armonies 1992; Beukema 1993a; Armonies 1996)
Bivalve	Mya arenaria	Nursery	Low intertidal Sand	High intertidal			(Matthiessen 1960)
Bivalve	Mytilus edulis	Nursery	Filamentous substrates	Sub- and intertidal musselbed	¼	Summer	(Bayne 1964; Pulfrich 1996)
Crustacea	Carcinus maenas	Nursery	High intertidal	Low intertidal/subtidal	½	Autumn	(Klein Breteler 1976)
Crustacea	Crangon crangon	Nursery	High intertidal	Low intertidal/subtidal	½	Autumn	(Kuipers & Dapper 1984; Beukema 1992)
Gastropod	Hydrobia ulvae	Nursery	High intertidal Silt	Intertidal		Summer	(Armonies & Hartke 1995; Sola 1996)
Polychaete	Arenicola marina	Nursery	High intertidal Sand	Low intertidal Sand	1½	Winter	(Farke et al. 1979; Flach & Beukema 1994)
Polychaete	Heteromastus filiformis	Nursery	Indications of secondary settlement				(Shaffer 1983)
Polychaete	Marenzelleria viridis	Nursery	High intertidal Silt	Intertidal Sand	½	Summer	(Essink & Kleef 1993)
Polychaete	Nephtys hombergi	Nursery	Subtidal	Intertidal	½	Winter	(Warwick & Price 1975)
Polychaete	Nereis diversicolor	Nursery	Saltmarsh Silt	Estuary	½	Autumn	(Dankers & Binsbergen 1984)
Polychaete	Nereis diversicolor	Nursery	Adult interspace				(Reise 1979b)
Polychaete	Nereis virens	Nursery	High intertidal High organic content	Low intertidal	3-4		(Miron & Desrosiers 1990)
Polychaete	Scoloplos armiger	Nursery	Patches close to hatching locations				(Reise 1979b)
Gastropod	Hydrobia ulvae	Seasonal	Tidal flats	Saltmarsh		Summer	(De Wolf pers comm)
Crustacea	Crangon crangon	Seasonal	Coastal and intertidal areas	Sea		Winter	(Boddeke 1976)
Polychaete	Nereis virens	Seasonal	Estuary	Sea		Winter	(Dean 1978; Berger & Khalaman 1996)
Polychaete	Marenzelleria viridis	Spawning	Low salinity	High salinity		Winter	(Essink & Kleef 1993)
Polychaete	Nereis succinea	Spawning	Burrow	Water column			(Hartman-Schröder 1971)
Polychaete	Nereis virens	Spawning	Burrow	Water column		Winter	(Dean 1978; Berger & Khalaman 1996)
Polychaete	Nereis virens	Spawning	Burrow	Water column		April, spring tide	(Korringa 1947; Korringa 1950)
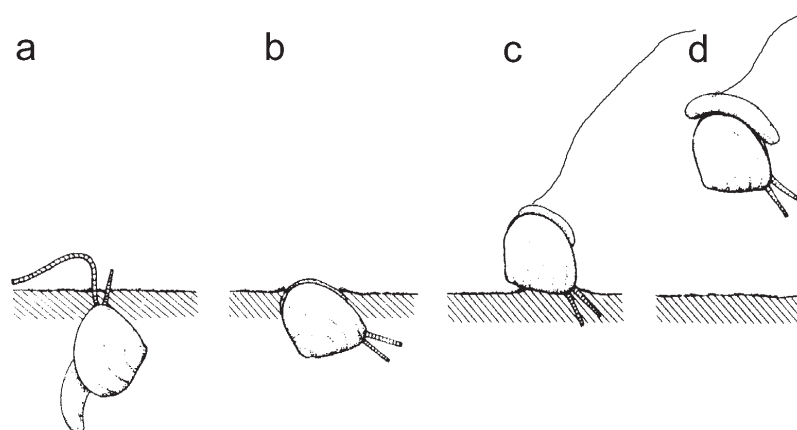
Figure 2. The floating behaviour of *Macoma balthica*. From left to right: a) Normal feeding position in the sediment. b) The animal reacts to stimuli, performs burrowing movements in the sediment, and withdraws the siphons from the sediment surface. c) Shell slightly opened and the foot protruded. d) Free floating in the water column, note the shape and the extreme protrusion of the foot. From: Sörlin (1988).

Most species that have been recorded in the water column are not included in Table 1 or 2 because no incentive for pelagic presence in the water column is known. Possibly, passive resuspension is the reason for the presence of the majority of benthic species in the water column. So far, however, nursery use is the most common understood reason for benthic species to undertake migrations.

METHODS USED TO MIGRATE BY BENTHIC ANIMALS

Mechanisms to move

Most benthic animals in the Wadden Sea can move themselves in some way. This section describes how benthic animals use their motility to disperse or migrate.

A) CRAWLING:
Crawling is not a way of potential long-distance migration for benthos, because the distances that can be covered by crawling are too small. *Hydrobia ulvae* can crawl 2 cm per minute (Anderson 1971; Barnes 1998), young *Mytilus galloprovincialis* up to a meter in a few days (Caceres Martinez *et al.* 1994). Only in polychaetes crawling distances covered more than 1 m within minutes, but never reach the distances of kilometres that have been observed as migration distances in the Wadden Sea; from Figure 1 we can conclude *that Arenicola marina* has to migrate 1 to 12 km to migrate from the nursery to the locations where the adults live.
The only benthic species that can walk substantial distances are crabs. Juveniles of the Chinese mitten crab *Eriocheir sinensis* walk from the sea, where they were born, to their inland living locations, sometimes even crossing dry land. In the Elbe they have

been found 700 and in China 1300 km upstream. They can cover 1-3 km per day when walking upstream. When walking downstream they profit from the current and can cover 8-12 km per day (Adema 1991) and references therein). Adult shore crabs *Carcinus maenas* walk from the Wadden Sea to the North Sea in autumn and back in spring (Broekhuysen 1936).

B) PASSIVE RESUSPENSION

Passive resuspension may also result in 'migrations' over large distances. Passive resuspension of benthos is caused by high current speeds and wave action; the animal is suspended together with the sediment it lives in. Therefore, passive resuspension is not a way *used* by benthos for migration, but it can have a large influence on distribution patterns of benthic species.

Correlations between presence of benthos in the water column and high bedload transports indicate that the presence of benthos in the water column is frequently due to passive resuspension (Grant 1981; Emerson & Grant 1991; Zühlke & Reise 1994).

C) BYSSUS DRIFTING

Many species of bivalves can use byssus drifting as a means of dispersal. Byssus drifting is described for most common bivalves of the Wadden Sea, like *Mytilus edulis* (De Blok & Tan-Maas 1977; Lane *et al.* 1982; Lane *et al.* 1985; Caceres Martinez *et al.* 1994*), Macoma balthica* (Sörlin 1988; Beukema & De Vlas 1989) and *Cerastoderma edule* (De Montaudouin 1997). The byssus thread is a 1 to 4 μm diameter monofilament and consists of acid mucopolysaccharides (Sigurdsson *et al.* 1976; Beaumont & Barnes 1992). The thread is excreted by greatly enlarged glands, which discharge the secretion through a ducted complex at the base of the foot (Lane *et al.* 1982). The thread can be up to two orders of magnitude longer than the shell (Sigurdsson *et al.* 1976) (Figure 2).

Due to an increase in drag force on the animal due to the byssus thread, the sinking rate of juvenile molluscs is decreased strongly. Sinking rates for small bivalves can be up to 5 times slower and are dependent on shell size and thread length (Sörlin 1988; Beukema & De Vlas 1989; Beaumont & Barnes 1992; De Montaudouin 1997). For post-larval *Mytilus edulis* sinking rates as low as 0.1 cm s^{-1} while byssus drifting were recorded. For departure from the sediment surface, current velocities of 0.1 cm s^{-1} were sufficient (Lane *et al.* 1985). Byssus drifting is recorded for bivalves with shell lengths up to 6 mm, but usually the maximum lengths are between 0.5 to 2.5 mm (Lane *et al.* 1985; Sörlin 1988; Beukema & De Vlas 1989; Beaumont & Barnes 1992). The gastropod *Lacuna* and the polychaete *Pectinaria koreni* show a similar behaviour, using a mucous thread to become suspended in the water column (Martel & Chia 1991; Thiebaut *et al.* 1996).

However, some authors doubt whether the byssus only acts as a drifting device and assume that the principal function of the thread is to facilitate anchoring to substrates (De Blok & Tan-Maas 1977). Because the byssus easily adheres to filamentous substrates, this indeed can be the cause of settlement of post-larval mussels on algae and hydroids (Caceres Martinez *et al.* 1994)**.**

Due to the large drag increase by the byssus thread, potential migration distances while byssus drifting are large. Beukema (1989) assumes that byssus drifting *Macoma balthica* cover distances up to 15 kilometres. Armonies (1996) recorded migration distances of 1 kilometre for several species of bivalve spat.

d) Floating

Floating through crawling on the underside of the water surface has been observed in aquaria for the gastropods *Hydrobia ulvae* (Newell 1962; Anderson 1971; Little & Nix 1976a), *Potamopyrgus jenkinsi*, *Rissoa parva*, *Lacuna palliluda* and several species of nudibranchs (Little & Nix 1976a). Floating of *Hydrobia ulvae* has also been observed in field situations, some authors assume floating is a frequently performed behaviour (Newell 1962; Anderson 1971), while others call it an 'accidental phenomenon' (Little & Nix 1976a; Wolff & De Wolf 1977).

Anderson (1971) describes how *Hydrobia ulvae* can become buoyant on the underside of the water surface. Usually, the snails let themselves dry out during ebb tide. Before that, they sometimes climb on a high object. When the water comes in, the shell becomes buoyant because it is dried out. Subsequently, the snail secretes a mucous raft that attaches the snail to the water surface and the snail extends its foot to get hold on the water surface. Only when the weather is calm, *Hydrobia* can remain buoyant. However, Barnes (1981) doubts whether floating is an active behaviour and assumes that floating is the result of drying out of *Hydrobia* on a hard object and not an active or intended strategy. Barnes explains floating and climbing behaviour from other behaviour than dispersal, but admits that floating occurs and may result in changing distribution patterns of *Hydrobia* (Barnes 1998).

Little & Nix (1976a) and Anderson (1971) assume that floating may aid species dispersal. Contrary, Newell (1962) assumes that *Hydrobia* float to graze the water surface. Armonies & Hartke (1995) found that *Hydrobia ulvae* covered distances up to 1 km, probably by floating, since *Hydrobia ulvae* can crawl only 2 cm per minute (1 km in 35 days) (Anderson 1971). Floating may explain the accumulation of *Hydrobia* on the saltmarsh in summer (De Wolf pers. comm., Table 1).

e) Swimming

Swimming as a means of entering and staying in the water column is only described for polychaetes and crustaceans. The polychaete *Nereis diversicolor* swims in an eel-like way, but also moves the parapodia (Gray 1939). *Nereis virens* and *Nephtys hombergi* also swim in this way, although *N. hombergi* does not use its parapodia while swimming (Gray 1939; Dean 1978). It was observed in the field that *Nereis virens* sank back to the bottom when it was not actively swimming (Dean 1978).

Active swimming is also observed for juvenile *Arenicola marina* (Benham stages) in the laboratory. A juvenile enters the water column but stays connected to the sediment with a mucous thread. In the water column, the polychaete secretes a gelatinous tube enclosing the whole body. When the thread ruptures, the juvenile *Arenicola* swims in the tube with the posterior end in front. If the worm stops wriggling, it sinks back to the bottom (Benham 1893; Farke & Berghuis 1979). Beukema & De Vlas (1979) assume

that swimming *Arenicola* can easily cover distances of several kilometres.

The amphipod *Corophium volutator* uses active swimming as a means of entering and staying in the water column (Hughes & Horsfall 1990; Hughes & Gerdol 1997; Ford & Paterson 2001) and may thus be transported over distances of tens of meters to kilometres (Essink *et al.* 1989; Lawrie & Raffaelli 1998). The sandy-beach isopod *Eurydice pulchra* uses vertical swimming in wave-induced currents as a control mechanism of intertidal migration (Warman *et al.* 1991).

Mechanisms to achieve directional migration

To enter the water column and let oneself transport by the water current is already complicated for sessile and normally immobile benthos, but to use the currents as a means of directional transport is way more complicated. However, for some species directional migrations have been recorded. For example, catches of *Macoma balthica* in a tidal channel in winter were much higher during ebb than during flood. This results in a seaward direction of the migration (Beukema & De Vlas 1989). The polychaete *Pectinaria koreni* was mainly caught at flood tide in the Seine Bay. This resulted in an accumulation of *Pectinaria* close to the shore (Thiebaut *et al.* 1996).

How do such benthic animals "know" where to migrate? Most species are widespread and thus the directions of the low tidal flats, high tidal flats and open sea are not equal at all locations. It is not probable that they have an innate sense of direction and an internal map. Three hypotheses that may explain directional tidal transport of estuarine organisms have been formulated:

a)   Transport of organisms in or out of the estuary is a passive process

b)   Organisms use a simple environmental clue to discern between ebb and flood currents and react on this by activity

c)   A suite of factors associated with tidal flux at particular locations may act as the 'zeitgeber' for an endogenous rhythm of activity with a tidal periodicity (Boehlert & Mundy 1988).

Forward and Tankersley (2001) give an extensive review of selective tidal-stream transport of marine animals. Therefore, I will not go into much detail in this section.

AD A) PASSIVE PROCESSES

There are some examples of directional transport of passive animals. Spaargaren (1980) assumes that the seasonal migration of the shrimp *Crangon crangon* in and out of the Wadden Sea requires no active migration behaviour. Since the viscosity of cold water is higher than that of warm water, the sinking speed of shrimps is lower in cold water. If temperature differences between the ebb and the flood current exist, and if shrimps show a random swimming behaviour, this will automatically result in a seasonal migration in the direction of warm water, without orientational behaviour of the shrimps. De Wolf (1973) assumes no behaviour is necessary for the inshore movement of barnacle larvae in the Wadden Sea, because they are transported in the same way by the tidal currents as inert suspended particles.

Higher numbers of migrating juvenile *Macoma balthica* on ebb tides during winter (Beukema & De Vlas 1989), may be explained from the higher concentration of juveniles in the high intertidal. The difference in juvenile density in down- and upstream areas will, even if the migratory behaviour has no tidal rhythm at all, always result in higher numbers of migrating juveniles on ebb than on flood tides.

AD B) BEHAVIOURAL RESPONSES TO ENVIRONMENTAL CLUES
Possibly, one or more factors can direct the migrations of benthic animals. In a laboratory study on *Macoma balthica*, Sörlin (1988) found that the combination of low temperatures and current were necessary to induce migrations of *M. balthica*. These factors mainly affect the timing of migration (in winter) and make sure the *M. balthica* is transported by current, but give no clue on directionality. For *Arenicola marina* ice periods seem to stimulate the migration of the juveniles (Werner 1956; Flach & Beukema 1994). This will also more affect the timing of the migration than the direction. Temperature may give a clue of direction, since temperatures at the high tidal flats are more extreme (higher in summer, lower in winter) than at low tidal flats and the subtidal.

For some other epibenthic species, however, the interaction between abiotic factors and reactions of the animal that cause directional tidal transport has been described (Table 2). The postlarvae of plaice *Pleuronectes platessa* that are heading for nurseries in the Wadden Sea, use a very simple rule. When they encounter enough food, they remain at that location. When, however, food is scarce, the fish swim. Due to the residual transport, they finally will end up at the tidal flats of the Wadden Sea, at locations with plenty of food. Other factors, like temperature, salinity and smell of the water did not affect their swimming behaviour (Creutzberg *et al.* 1978). The swimming crab *Liocarcinus holsatus* migrates from the Wadden Sea towards the North Sea in autumn. *Liocarcinus* swims in decreasing salinity water and rests in increasing salinity water. This results in swimming at ebb tides, and thus the crab is transported out of the Wadden Sea (Venema & Creutzberg 1973). Other examples in Table 2 show that the main factors on which the migrating animals react, are changes in salinity and hydrostatic pressure. For such direction regulating mechanisms only simple factors like salinity or food abundance need to be recorded by the animals. All these factors can be used as a clue for the start of the ebb or flood by a steady animal. However, if a single clue such as salinity is used as a stimulus for swimming behaviour, there is no mechanism for the animals to detect the end of the flood tide. Because the drifting animals will remain in the same water mass until it mixes with the next tide, considerable down- or upstream transport may occur (Boehlert & Mundy 1988). The species *Penaeus plebejus*, however, shows only 3 h of activity following increasing pressure, which may be a way to prevent this downstream flushing.

In estuaries, there often exists a stratification, with a fresher water layer on top and a saltier layer near the bottom. This stratification can be used by animals to identify the water layer they are in and therefore for directed transport. In general, animals that

want to migrate upstream have to stay in the bottom layer, which on average moves upstream, animals that want to migrate downstream should stay in the freshwater layer moving downstream. Jager (1999) showed how flounder larvae can accumulate inside estuaries by adjusting their level in the water column.

Ad c) Endogenous tidal rhythm

Boehlert and Mundy (1988) propose a conceptual model for the role of stimuli and behaviour in fish movements to estuarine areas. They divided the inshore migration into 4 phases. In each phase, the stimuli the fish reacts on are different. For us, the 2 inshore phases are most interesting: channel or mouth and the estuary. Boehlert and Mundy (1988) assume that in the 'channel
or mouth' phase, a suite of factors associated with tidal flux at particular locations may act as the 'zeitgeber' for an endogenous rhythm with a tidal periodicity, that makes highly directional migrations possible. They assume that an endogenous tidal rhythm is necessary because if a single clue such as salinity is used as a stimulus for swimming behaviour, there is no mechanism for the animals to detect the end of the flood tide. An animal with a circatidal endogenous rhythm 'knows' the moment of the end of the flood. Inside the estuary, the fish larvae also show appetitive behaviour. This is behaviour where the larvae reduce their swimming activity in suitable habitats, while they increase their activity in unsuitable habitats. This behaviour results in retention in nurseries, and was described for plaice (Creutzberg *et al.* 1978) (Table 2) and juvenile surgeonfish *Acanthurus triostegus* (Sale 1969).
Forward and Tankersley (2001) suggest that if animals react on environmental clues, it is likely that they react on a sequence of clues and not on a single clue.

Concluding, one can say that there is little evidence for the first hypothesis of passive transport of tidal flat benthos. The second hypothesis is supported by many laboratory and field studies showing that animals react on simple physical or chemical factors in a way that may facilitate directional tidal transport. The third hypothesis assumes an endogenous circatidal rhythm in fish larvae and benthic invertebrates. In the literature, we can find examples of an endogenous circatidal rhythm in bivalves (Kim *et al.* 2001), gastropods (Gray & Hodgson 1999), many crustaceans and fish (Forward & Tankersley 2001), but not for polychaetes.

Costly migration and ontogenetic niche shifts

Costly migration

Migration may be profitable if another habitat has a higher quality than the current one. However, migration takes time, uses energy and the journey may be dangerous. Both mortality and fecundity (and thus fitness) are likely to be affected by migration: by its energy cost, by its effect on food supply and by its dangers. Therefore, migration costs have to be traded against the benefits of living in a more favourable environment.

Table 2. Examples of mechanisms for directional migration used by estuarine organisms, to enter or leave an estuarine area on the tidal current.

Group	Species	What to detect	Way of detection	Reaction	Reference
Bivalve	*Macoma balthica*	Ebb in winter	Current and cold water	Start byssus drifting	(Sörlin 1988)
Crab	*Callinectes sapidus*	Flood	Increasing salinity	High swimming activity	(Devries *et al*. 1994)
Crab	*Liocarcinus holsatus*	Ebb	Decreasing salinity	Swimming	(Venema & Creutzberg 1973)
Crab	*Pinnaxa sp.*	Flood	Increasing hydrostatic pressure	High swimming activity	(Devries *et al*. 1994)
Crab	*Pinnotheres sp.*	Flood	High current speed	High swimming activity	(Devries *et al*. 1994)
Shrimp	*Penaeus duorarum*	Flood	Increasing salinity	Start swimming	(Hughes 1969)
Shrimp	*Penaeus plebejus*	Flood	Increasing hydrostatic pressure	3 h swimming activity	(Rothlisberg *et al*. 1995)
Fish	*Anguilla anguilla*	Fresh water	Fresh water odour	Benthic orientation	(Creutzberg 1961)
Fish	*Paralichthys olivaceus*	Flood	Increasing salinity	Swim to surface	(Burke *et al*. 1995)
Fish	*Pleuronectes platessa*	Nurseries	Food	Stop swimming	(Creutzberg *et al*. 1978)

Thus, whether to migrate or not, is a major question of life-history strategy.

There are 3 main situations that may promote costly movement (Greenwood-Lee & Taylor 2001). The first of these requires kin effects: the cost to the disperser is compensated by the increase in fitness of relatives who are left behind, due to reduced competition (Hamilton & May 1977). The second relies on environmental variation in both time and space (McPeek & Holt 1992). For example, seasonal variation in the carrying capacities of habitats can result in selection for migration, provided that the 2 habitats show fluctuations that are asynchronous. For a bird, a migration to another temperate northern hemisphere country may not help it to avoid the winter, but a migration to Africa (with asynchronous or no seasons) does result in avoiding the winter.

The third situation that may explain the evolution of migration patterns is environmental variation in space only. Theoretical studies show that dispersal in constant environments can be an evolutionary stable strategy only when animals migrate a second time, directed back to the original location (Greenwood-Lee & Taylor 2001). This conclusion follows from the assumption that (in an equilibrium situation) an animal that migrates to a location where residents are already present, has a selective disadvantage, because it has to pay the cost of migration. Therefore, migrants cannot invade a non-migrant population. When, however, the migrants migrate to the locations whence they originated (e.g. for reproduction), they compete only with animals that stayed at this location. Here they may have an equal over even larger fitness if animals that did not migrate suffered a higher mortality in the period that the migrants were in the other habitat (Figure 3).

Ontogenetic niche shifts

An ontogenetic niche shift is a change in niche of an organism somewhere during its development, that provides the maximum possible benefit for an individual (Werner &

Gilliam 1984). This niche shift may involve a costly migration or metamorphosis. The evolution of costly ontogenetic niche shifts can be explained from the second (asynchronous temporal variation) and third (spatial variation in a constant environment) of the 3 above situations.

The environment of *Macoma balthica* in the Wadden Sea shows seasonal variations in temperature and food and predator abundance, but these variations are synchronous in space at source and sink locations of *M. balthica*. Therefore, *M. balthica* migrations may not be explained from the second situation that explains costly migrations from asynchronous temporal variation only. There is no reason to assume that fitness consequences of migration in a situation with both spatial variation and seasonal variation, that is synchronous in space, are different from situations with spatial variation only, because the difference in habitat qualitity is constant in space. Therefore, fitness consequences of migrations for *M. balthica* probably do not deviate from in the situation with variation in space only. Another indication that the migrations
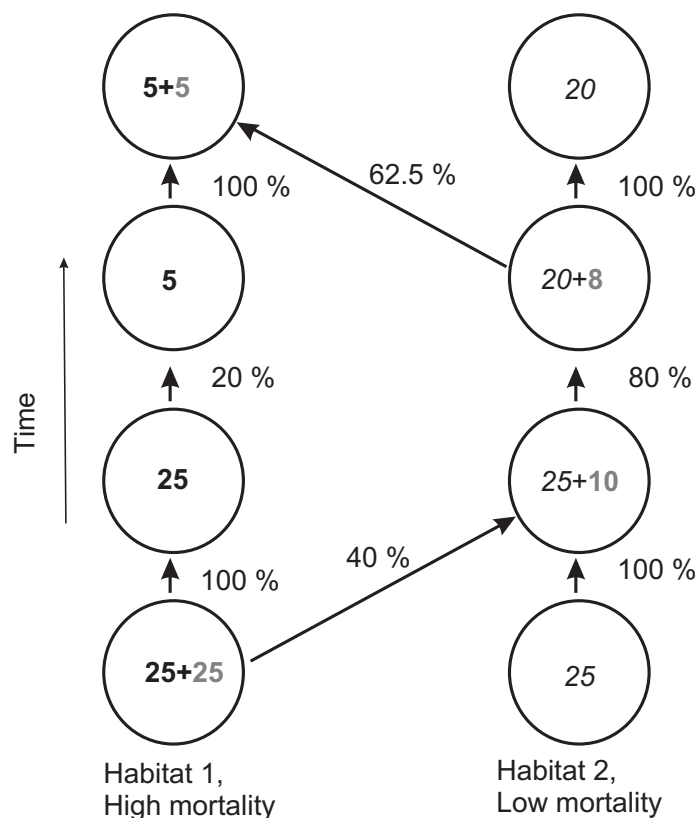
Figure 3. A numerical example of 2 stable populations (bold and italics), in which a fraction (grey) of one population migrates. Survival rates per step are given as percentages, the number of animals per original population with bold and italic figures. A fraction of the habitat 1 population, with high juvenile mortality, migrates to habitat 2, with low juvenile mortality. The migrants have a strong selective disadvantage compared to the non-migrants in habitat 2 (8 surviving after step 2, as compared to 20 non-migrants from habitat 2). Nevertheless, they are equally fit as non-migrants in habitat 1 (5 from both races surviving). This figure illustrates why a one-way migration cannot evolve in a stable environment. In *Macoma balthica* life history, survival in step 2 in habitat 2 (high tidal flat) is higher than in habitat 1 (low tidal flat). Modified from Greenwood-Lee & Taylor (2001).

of *M. balthica* may not be explained from seasonal variations in the environment only is that they only undertake 2 migrations, while they may reach ages of more than 10 year and therefore undergo many seasonal changes.

In populations that consist of juveniles and adults, spatial variation may make costly migration worthwhile because one habitat may be beneficial for juveniles, while it is detrimental for adults and vice versa, due to ecological and physiological differences between juveniles and adults. This can be caused by a wide variety of ecological factors, from food availability to physical factors like salinity and temperature.

Most research on ontogenetic niche shifts has focused on changes in habitat use in relation to food resource distribution and size-selective predation. Examples of ontogenetic niche shifts can be found for most amphibians, many insects and for many marine fish and crustaceans. The example of amphibians is generally known; the larvae are aquatic (tadpoles), while, after a metamorphosis, adults are terrestrial (frogs, toads). In general, niche shifts are confined to species without parental care.

Animals are expected to shift niche in terms of fitness-maximising strategies. Non-reproductive animals have to follow a strategy that increases the probability of survival to adulthood. This can be accomplished by maximising energy gain (growth rate) or/and minimising mortality (predation). Due to an increased growth rate, animals attain adulthood earlier. Moreover, many predators select for small size classes, which the prey may avoid by rapidly growing out of the vulnerable size class. Adults should try to maximise their reproductive output by both surviving and producing many offspring.
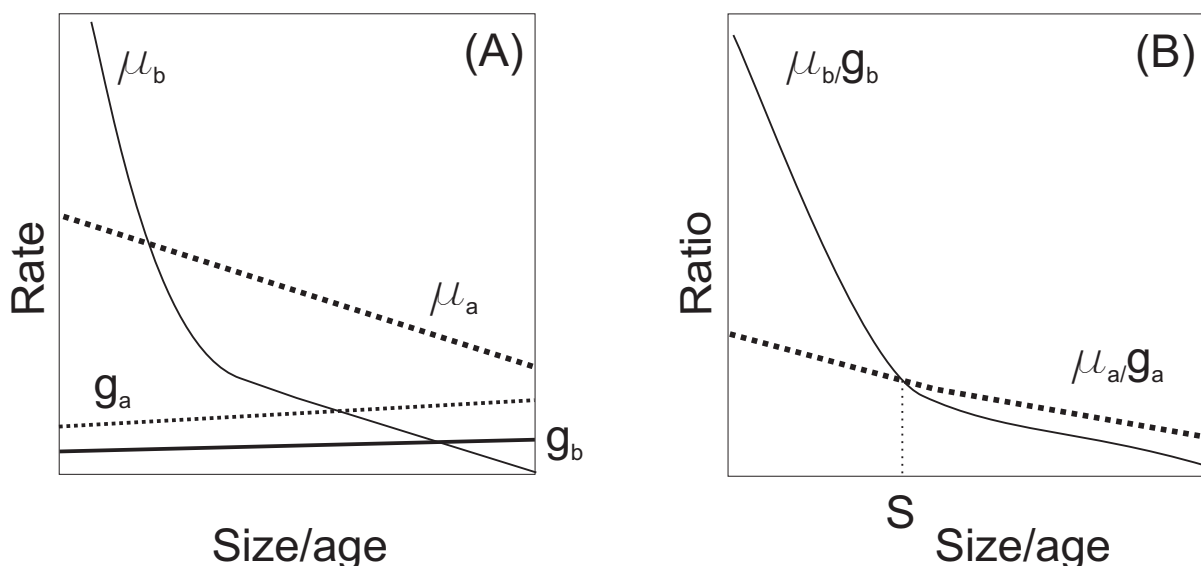

Figure 4. (a). Hypothetical mortality (μ) and growth (g) rates in 2 habitats (a and b). (b). The ratio of mortality to growth rates for the curves in (a). Fitness is maximised for animals that minimise the μ/g ratio; to maximise fitness in this case, an animal should migrate from habitat a to b at size/age S. Redrawn and modified from Werner (1986).

For many species, a trade-off between growth and survival has been described: growth is often fastest in areas with the highest predation risk (Dahlgren & Eggleston 2000). Under such circumstances, Werner & Gilliam (1984) predict that fitness is maximal for animals that live on locations where the mortality to growth (μ/g) ratio is minimised (Figure 4). If this ratio depends on size, age or developmental stage, e.g. due to size-selective predation or growth, and differs between locations, an ontogenetic niche shift may increase fitness. Because niche shifts in response to changing mortality rates and growth rates can result in complex life histories, understanding ecological processes underlying niche shifts is important.

An example of how the minimisation of the μ/g ratio can be applied to amphibian life histories is given by Werner (1986). Bufonids undergo metamorphosis at a small size, as compared to frogs (ranids and hylids). Because the terrestrial phase of bufonids possesses a variety of strong toxins, mortality during the terrestrial phase is probably lower than for frogs. Therefore the μ/g ratio for the terrestrial phase is smaller for toads than for frogs (Figure 4: μ_b curve lower, therefore S at a smaller size), while the μ/g ratio in the aquatic phase probably does not differ much between frogs and toads. When minimising the μ/g ratio, a toad should therefore switch to the terrestrial phase at a smaller size. The bufonids thus have conquered the problems of predation risk on land and can take advantage of high growth rates available there.

Above considerations assume that a niche shift has no costs. For species in which there are costs associated with the shift (energetic costs, increased mortality during migration or metamorphosis), these costs have to be known to be able to evaluate the adaptive value of the niche shift. Only if the short-term costs are outweighed by long-term increases in reproductive output, a niche shift is worthwhile.

In this thesis, I will attempt to analyse the migrations of *Macoma balthica* as a case of ontogenetic niche shift in which the population migrates between niches with different survival and growth rates for juveniles and adults. I will investigate the survival and growth in both niches as well as the costs of migration. Finally, I will consider if migration is worthwhile for *Macoma balthica*. Before doing so, I will review the current knowledge on the costs and benefits of migration by *M. balthica* and other benthic organisms.

COSTS AND BENEFITS OF HABITAT SHIFTS AND MIGRATION FOR INTERTIDAL BENTHOS

Costs

For vertebrates like salmon and birds, the dangers of changing habitat and migration are obvious to humans. Predation, food deprivation and becoming lost are often observed and cause death. In migratory birds for example, 1-10% dies during migration

to their winter stations (Berthold 1993). The interaction between locomotion costs and predation risk makes migration even more dangerous; for example, the bird blackcap (*Sylvia atricapilla*) stores much fat as fuel for migration, but due to impaired predator avoidance caused by this high load, the large fat reserves place them at increased risk of predation during migration (Kullberg *et al.* 1996).

Migration itself has always a cost, because of the risk of mortality and the costs of secretion of mucus or byssus or the costs of swimming behaviour. Thus, the costs of the migration have to be traded off against the benefits of the new habitat. In this chapter costs and benefits of migratory behaviour for Wadden Sea benthos are summarised and compared. Attention is focused on costs and benefits of nursery use because it is the most common identified reason for migration.

The main costs of migration for benthic species are, unlike for birds, fish and mammals (Baker 1978), not the costs of locomotion. Since benthic species use water currents for migration, the locomotion costs are confined to the mechanisms of entering and staying in the water column, like secreting a byssus thread or mucus for molluscs, or swimming movements of polychaetes. The mortality risk is probably the most important cost of migration for benthos. Benthic species that are normally hidden (buried), are vulnerable to pelagic and epibenthic predators during migration. Moreover, because benthos use currents for migration, they may drift to unsuitable locations.

For benthos, there are no direct studies on increased mortality during migrations, but there are some indications that migrations do have costs. It was observed that *Nereis virens*, migrating in winter under ice in the USA, were eaten by fish (Dean 1978). Migrating lugworms *Arenicola marina*, were found in the stomach of the pelagic fish *Osmerus eperlanus* that is unable to dig out deep living polychaetes (Kühl 1970). Only 5 % of the *Arenicola* population that migrated at the Balgzand in winter, could be recovered by Flach and Beukema (1994); this suggests high mortality rates of migrating lugworms. The tube-dwelling amphipod *Corophium volutator*, that migrates pelagically over distances of several km's in the Ems-Dollard estuary (Essink *et al.* 1989), was found in the stomachs of pelagic fish (herring *Clupea harengus*), which cannot dig out buried *Corophium* (Stam 1981). The tube-dwelling amphipod *Corophium volutator* suffers enhanced mortality from predation by shrimps when disturbance by *Arenicola marina* and *Cerastoderma edule* forces it to leave the sediment (Flach & De Bruin 1994). In *Macoma balthica* in the Baltic Sea, physical disturbance also increased mortality due to predation by the isopod *Saduria*, while physical disturbance alone did not have any influence on mortality (Bonsdorff *et al.* 1995). Thus, leaving their burrow in the presence of predators may be dangerous for infaunal benthos.
There are no studies on the fate of benthos that disperse out of a suitable habitat due to migrations. The fact that there is a large variation in growth and predation rates between locations for many benthic species may be an indication that many individuals fail to migrate to the optimal location (Beukema 1993a). Chapter 2 and 3 will elucidate on the risks of migration for *Macoma balthica*.

Benefits

Benefits of migration to benthos are related to spatial differences in predation pressure, parasite infestation, food availability and abiotic conditions. Only if these factors are both size-selective and spatially inhomogeneous, an animal can benefit from an ontogenetic niche shift. Therefore, in this section I will focus on examples from the marine intertidal that show an interaction between location and size/age

A) MIGRATION OF POSTLARVAL STAGES INCREASES THE SEARCHING TIME FOR A GOOD HABITAT
The postlarvae of the mussels *Mytilus edulis*, *M. galloprovincialis* and *Perna canaliculus* undertake secondary migrations (Bayne 1964; Caceres Martinez *et al*. 1994; Buchanan & Babcock 1997). Bayne (1964) and Pulfrich (1996) assume that postlarval *Mytilus* use filamentous substrates as nurseries, before settling on adult mussel beds, thus reducing intraspecific competition between adults and juveniles. However, Caceres Martinez (1993; 1994) assumes that the secondary dispersal phase of postlarval mussels is used to prolong the searching period for a good habitat. Due to the byssus thread, used while drifting, mussels attach easily to filamentous substrates and are therefore primarily found on these substrates.

B) CHANGING FOOD PREFERENCE OF DEVELOPMENTAL STAGES
Juvenile *Nereis virens* is detrivorous while adults are carnivorous. Therefore, juveniles live on silty locations on tidal flats, while adults live on low tidal flats (Miron & Desrosiers 1990).

C) GROWTH DIFFERENCES OF ADULT AND JUVENILE BENTHOS AT DIFFERENT HABITATS
Net growth is often easily measured; it depends on food availability, food intake (in many intertidal animals controlled by immersion time), the amount of biomass lost to siphon cropping, tail or palp nipping (partial predation) and the basal metabolic rate (controlled by temperature). To get an insight in motives for nursery use, one should try to separate the effects of food availability and temperature on growth rates from the effects of partial predation.
For most intertidal species and age groups, growth rate seems to decrease with increasing emersion time (Wanink & Zwarts 1993). For *Macoma balthica*, growth of juveniles is faster in the nurseries high in the intertidal in most studies, while adult growth is usually fastest in the low intertidal (Beukema 1993a), although there seems to be a large variation between locations (Harvey & Vincent 1990; Harvey & Vincent 1991; Armonies & Hellwig-Armonies 1992; Vincent *et al*. 1994; Hummel *et al*. 1996).

D) DIFFERENT VULNERABILITY TO BIOTURBATION
Adult *Arenicola* exert intensive bioturbatic effects on their environment and thus on other infauna. At frequently occurring densities of some tens of adults per m^2, lugworms turn over the entire upper sediment layer within 1 year due to their feeding

activity (Cadée 1976). Both juvenile and adult *Arenicola* are negatively affected by high densities of bioturbating adult lugworms. Juveniles seem to be even more susceptible to this disturbance than adults and cannot live among adults (Flach & Beukema 1994) and are therefore confined to high intertidal locations (Farke & Berghuis 1979). The negative effect of *Arenicola* and *Cerastoderma* on *Corophium* and juvenile bivalves was extensively studied (Flach 1992a; Flach 1992b; Flach & De Bruin 1993; Flach 1993; Flach & De Bruin 1994; Flach 1996). The digging activity of both bioturbators seems to have a negative effect on all small benthic species.

E)   AVOIDANCE OF JUVENILE-ADULT INTERACTIONS

Adult bivalves can have a negative effect on juvenile abundance due to their foraging activity. Suspension-feeding adults of species like *Cerastoderma edule* and *Mya arenaria*, filter out planktonic larvae and therefore inhibit larval settlement on locations with large adult concentrations (Andre & Rosenberg 1991). Adult *Macoma balthica* had no or only a small effect on juvenile abundance, however (Ratcliffe *et al.* 1981; Strasser *et al.* 1999; Richards *et al.* 2002).

F)   SIZE AND SITE-SELECTIVE PREDATION OF TERRESTRIAL PREDATORS

Birds are the only terrestrial predators hunting on the intertidal flats of the Wadden Sea. Because waders, shelducks and gulls can only forage at emerged flats or in very shallow water, they only have a short foraging time at low intertidal levels. Whether or not they do forage most of the time in the high intertidal is not important from the viewpoint of the prey. The *availability* of an area to a predator makes an area unattractive to benthos and may thus affect nursery use.
Oystercatcher *Haematopus ostralegus* and Knot *Calidris canutus* only take *Macoma balthica* >11 mm (Hulscher 1982; Zwarts & Blomert 1992; Piersma *et al.* 1994). Oystercatchers do not take small *Scrobicularia plana*, *Mya arenaria* (no <15 mm), *Cerastoderma edule* (>10 mm is preferred) and *Mytilus edulis* (only ones >20 mm are eaten) (Zwarts & Wanink 1984; Moreira 1994a). *Nereis diversicolor* <20 mm were not eaten by Black-tailed Godwits *Limosa limosa* (Moreira 1994b). For these benthos species, many more examples of size selection by waders can be found in the literature. Thus, by selection of large prey and their restriction by the tide, waders make high intertidal sites unattractive for adult benthos, leaving small benthos unaffected.

G)   SIZE AND SITE-SELECTIVE PREDATION OF EPIBENTHIC MARINE PREDATORS

Since most aquatic predators can only forage when tidal flats are submerged, high tidal flats may offer a refuge from predation by aquatic predators. For some aquatic predators, size selection has been observed. The shrimp *Crangon crangon* can only eat *Macoma balthica* <5 mm and prefer *M. balthica* of 1-2 mm (Keus 1986). The crab *Carcinus maenas* can eat both nursery and adult-size *Cerastoderma edule* (Sanchez-Salazar *et al.* 1987a; Kaiser *et al.* 1990; Mascaro & Seed 2001). Size selection for small *Mytilus* by *Carcinus* becomes stronger if many mussels are offered in a group (Burch & Seed 2000). Since these predators select for (small) juvenile benthos, it may be profitable for juvenile benthos to use nurseries high in the intertidal. Chapter 4

describes size and site-selective predation by epibenthic predators on *Macoma balthica*.

H)   SIZE-SELECTIVE PREDATION OF INFAUNAL MARINE PREDATORS

The effect of infaunal polychaetes on meiofaunal and juvenile macrofaunal abundance has been studied at many locations. Infaunal polychaetes had little effect in some studies (Reise 1979a; Kennedy 1993) and large impact in others (Commito 1982; Ambrose 1984a; Ambrose 1984b; Commito & Shrader 1985; Ronn *et al.* 1988; Desroy *et al.* 1998; Tita *et al.* 2000). In all studies, only an effect on the smallest animals was found. The number of meiofaunal organisms that is killed by disturbance in these cases can be much higher than the number that is actually eaten (Tita *et al.* 2000). Therefore, polychaete predation may be a reason for juvenile benthos to avoid locations with many polychaetes, but no examples of such an interaction are known at this moment. Chapter 5 describes size and site-selective predation of infaunal predators on *Macoma balthica*.

I)   DIFFERENT RATES OF PARASITIC INFESTATION

Macoma balthica infested with the digenetic trematode *Parvatrema affinis* show a crawling behaviour on the sediment surface, that makes predation by the final host of the parasite, birds, more probable (Swennen 1969; Swennen & Ching 1974). Infection rates increase with tidal level for *Macoma balthica* (Hulscher 1973; Zwarts 1991), and large shellfish are more frequently infested with these parasites than small ones (Hulscher 1973; Lim & Green 1991). Although many other intertidal species are infected by parasites (e.g. trematodes for *Hydrobia* and *Littorina*), in no other species the interaction between tidal level, age and parasitic infection has been described in detail (Curtis 1990; Galaktionov 1992; Sola 1996), although increasing infection rates with size are a common phenomenon in many bivalves (Lauckner 1983; Curtis 1990; Sola 1996).

J)   PHYSICAL DISTURBANCE DOES MAINLY AFFECT JUVENILE BENTHOS

Settling larvae of intertidal benthos are usually around 300 µm in length, the size of a sand grain (Armonies 1994b). Therefore, these juveniles are susceptible to passive resuspension with the sediment, possibly resulting in mortality (Zühlke & Reise 1994). Juveniles of *Macoma balthica*, *Scoloplos armiger*, *Pygospio elegans* and *Hydrobia ulvae* and the small polychaete *Microphthalmus sczelkowii* were washed out at locations with a high sediment turnover (Zühlke & Reise 1994). Juveniles of *Mya arenaria* disappeared or were relocated at high-energy sandflats (Emerson & Grant 1991). Bouma *et al.* (2001) found that the decrease in numbers of small *Macoma balthica* (0.3-1 mm) was smallest at high tidal flats, and that the decrease in numbers of the bivalves was positively correlated with sediment-turnover and current-velocities. However, for *M. balthica* >2 mm, decrease in numbers was lowest at the low, dynamic locations. Bonsdorff *et al.* (1995) showed that physical disturbance of the sediment alone did not affect survival of juvenile *Macoma balthica,* but that the combination of physical disturbance and predation increased mortality. Since physical disturbance is

generally higher in the low intertidal than in the high intertidal, it may be profitable for young benthos to live at high intertidal sites.

κ)   DIFFERENT INFLUENCE OF TEMPERATURE

Temperature is generally very important for poikilotherm benthic organisms. Since high tidal flats are exposed to air longer, in summer temperatures are higher and in winter temperatures are lower in high tidal flat nurseries than on the low tidal flats. Therefore, shell growth of *M. balthica* in spring starts earlier in the high intertidal (Harvey & Vincent 1990) and it has been shown that some benthic species experience higher mortality rates in the high intertidal during cold periods (Beukema 1985).

There is little knowledge on different temperature tolerances of adult and juvenile benthos, in relation to nursery use. Young *Cerastoderma glaucum* show a greater resistance to short exposures to high temperatures than adults (Ansell *et al*. 1981). However, *C. glaucum* is not an intertidal species and does not use nurseries. Also, juveniles of *Macoma balthica* are more tolerant of temperatures higher than 30 °C than adults (Ratcliffe *et al.* 1981). Juveniles showed no mortality at 39.5 °C for 6 h, while mortality among adults was 30 %. However, differences in tolerance between adults and juveniles were found above sediment temperatures of 30 °C only, a temperature which is very rarely exceeded in the Wadden Sea (Niesel 1999). Juvenile *M. balthica* is more sensitive to freezing than adults in the St. Lawrence estuary (Bourget 1983), but tolerates temperatures below –10°C, while adults can survive temperatures below –15°C.

Summarising, there seems to be many examples of factors that affect juveniles different from adults and therefore may stimulate juveniles to live at other locations than adults.

THE ADAPTIVE VALUE OF MIGRATION AND HABITAT SHIFTS IN TIDAL-FLAT BENTHOS

A migration is the result of the decision to change habitat. It is worthwhile if it increases the fitness of animals. Many intertidal benthic species do migrate, but usually only a few times and thus they use only few different habitats. In the previous sections of this chapter we saw that many methods are used by migrating benthos, but most species do have in common that they use the current to have themselves transported. The active part of the migration aims at becoming suspended in the water column. Thus, locomotion costs of migrations are low, especially when compared to some vertebrates that migrate over very long distances and have to move actively. There are many examples of benthic species that use tidal currents as directional means of transport. The fact that benthic species only use few habitats in their life-time, makes it possible to analyse and quantify the effect of these decisions in the life-history on fitness, since it is possible to analyse all factors that may affect fitness at the different locations. This analysis is much easier than for more mobile animals, that make decisions about habitat use several times every day.

Nursery use seems to be the most common reason for migrations of benthic organisms. We should keep in mind, however, that the label the migration gets, is based on the assumed reasons for the migration. Thus, a migration to a nursery probably is called so without knowing why this is a nursery.

Several factors seem to promote nursery use and migrations in intertidal benthic invertebrates. The factors that have been mentioned in the literature to make migrations or nursery use beneficial are:
(The number of species mentioned per item is shown between brackets).
· prolonged searching period for a good habitat (3)
· different food preferences of juveniles and adults (1)
· differential growth of adults and juveniles (1)
· bioturbation (2)
· juvenile-adult interactions (2)
· size- and site-selective predation by terrestrial predators (4)
· size- and site-selective predation by marine predators (2)
· age and site-selective parasitic infestation (1)
· size-selective physical stress (6)
· temperature (2)

Of the above factors, some seem to be relevant to many species, while others are of interest for only one species. However, when interpreting the pattern in the number of species shown between brackets, one has to take into account that this number may reflect the lines of interest of ecologists. Size-selective predation by waders has been studied extensively by many authors for example, while size selection by parasites has not received much attention.
From this overview, prolonged searching time, size-selective predation and size-selective physical stress seem to be the more important factors that can be incentives for migrations. Avoiding unfavourable circumstances, like predation or disturbance seems to be more common as a governing factor in the distribution pattern than searching for better growth or feeding circumstances. Possibly, the nursery-strategy aims more at surviving until adulthood, than at maximising growth rates.

The major costs or risks of migration are probably the risk of predation while migrating and the possibility to end up in unfavourable locations. There are some indications that migration, i.e. entering the water column and leaving their burrow, is dangerous for benthos, but no studies have quantified this risk so far.

Concluding, currently there is some knowledge on the factors that can make nursery use and migrations beneficial. While some of the factors, like size-selective predation by birds and the effect of physical stress, have been covered extensively by research, other factors like growth, parasites and the risks of migration are not well studied and should get future attention. Most factors still have to be quantified, in a way that makes comparison of the different factors possible.

For the Wadden Sea species *Macoma balthica* and *Arenicola marina* nursery use is studied best, and several factors that may cause migration and nursery use have been identified and quantified (Beukema 1993a; Flach & Beukema 1994).

HABITAT SHIFT, MIGRATION AND NURSERY USE OF *MACOMA BALTHICA*

Although the term 'nursery' is often used in marine biological papers, there exist no studies in which the adaptive value of nursery use for marine species, including the costs of migration, has been evaluated. This thesis makes an attempt to estimate the costs and benefits of nursery use for one species. The bivalve *Macoma balthica* was chosen as a model organism to study the fitness consequences of migrations and nursery use.

Macoma balthica is a small bivalve that is found in coastal areas in temperate regions (Beukema and Meehan, 1985) and is one of the most common and widespread bivalves in the Wadden Sea (Beukema 1993a). Juveniles of this species are mainly found on 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, the early life history of *M. balthica* includes 2 migrations.
M. balthica spawns in late March and April (Honkoop & Van der Meer 1997). The eggs and larvae are pelagic for a short period; in the Wadden Sea larvae settle mainly on the low tidal flats at a length of 190 µm to 300 µm (Günther 1991; Armonies & Hellwig-Armonies 1992). This settlement on low tidal flats is probably dictated by hydrography (Armonies & Hellwig-Armonies 1992; Bouma *et al*. 2001). In May the postlarvae (300 µm) migrate to the nurseries (spring migration) at high, silty tidal flats (Armonies & Hellwig-Armonies 1992) (Figure 5). After the first growing season, the juvenile *M. balthica* (5 mm) embark on a winter migration between December and March, from the nurseries to the low intertidal flats and the subtidal of the Wadden Sea and North Sea (Beukema & De Vlas 1989).
M. balthica migrates by byssus drifting (Figure 2). Byssus drifting has been described for most common bivalves of the Wadden Sea, such as the blue mussel *Mytilus edulis* (De Blok & Tan-Maas 1977; Lane *et al*. 1982; Lane *et al*. 1985; Caceres Martinez *et al*. 1994) and the cockle *Cerastoderma edule* (De Montaudouin 1997). The byssus drifting of *M. balthica* has been described by Sörlin (1988) and Beukema and De Vlas (1989). Due to an increase in drag force by a byssus thread, the sinking rate of juvenile molluscs decreases strongly. Sinking rates for small bivalves with byssus thread can be up to 5 times slower than those without and are dependent on shell size and thread length (Sörlin 1988; Beukema & De Vlas 1989; Beaumont & Barnes 1992; De Montaudouin 1997). For departure from the sediment surface, current velocities of 0.1 cm s^{-1} are sufficient (Lane *et al*. 1985).

The major questions that I try to answer in this thesis are:

1.   What and how large are the migration costs for *Macoma balthica*? What mechanisms may explain increased mortality during migration?

2.   Are there differences in growth rate between high and low tidal flats?

3.   How are *M. balthica*-predators distributed over the low and high tidal flats and what sizes of *M. balthica* do they eat? Does size-selective predation by epibenthic, infaunal and bird predators make it beneficial for juvenile *M. balthica* to live in the high intertidal and for adult *M. balthica* to live in the low intertidal?

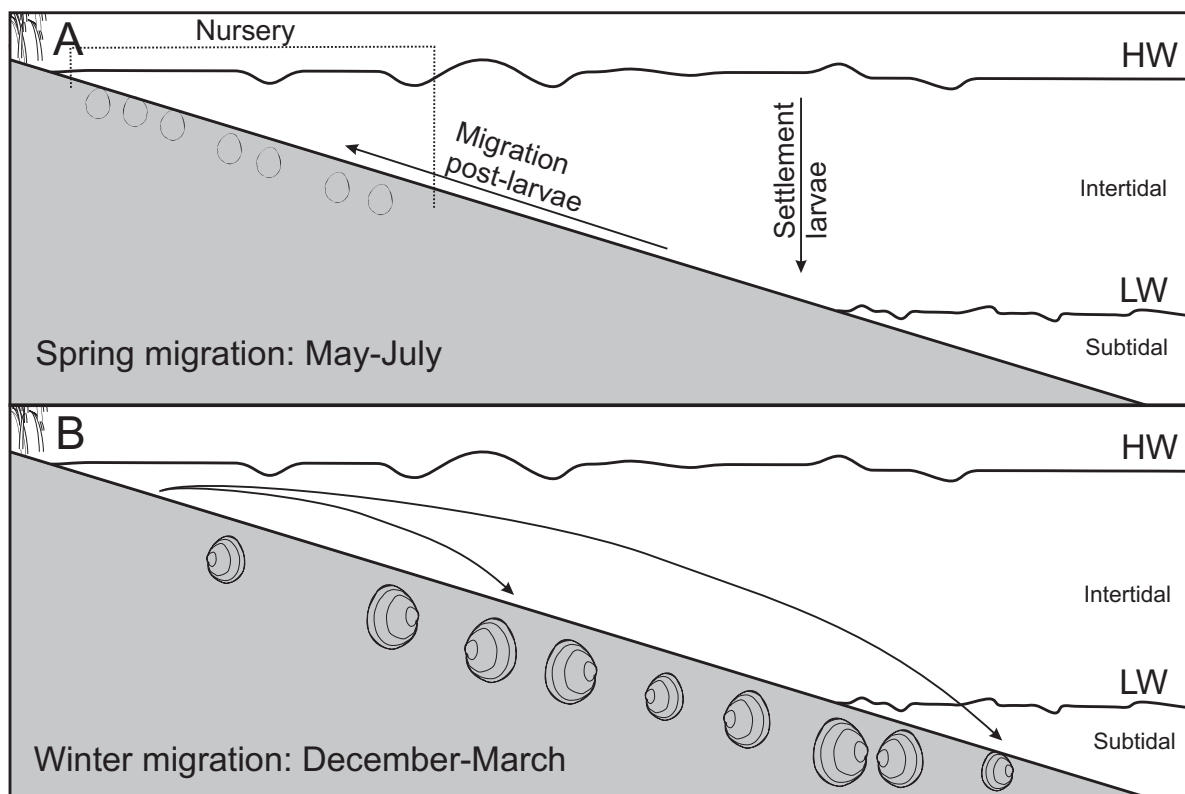Figure 5. The two successive migrations of young *Macoma balthica* in the Wadden Sea. A) Settlement of larvae in the low intertidal and subsequent migration of the post-larvae to the nurseries in the high intertidal. B) Winter migration of the approximately 5 mm long *Macoma* to the low intertidal and subtidal, after a stay of 7 to 10 months at high tidal flats. Redrawn and modified from Beukema (1993a).

4.   Are the benefits of nursery use larger than the migration costs?

OUTLINE OF THIS THESIS

Chapter 2 describes a field study that estimates changes in density of the 1998-yearclass of *Macoma balthica* on the Groninger Wad, with additional stations in tidal channels and the North Sea. From changes in density, mortality rates for the periods in between and during the spring and winter migration were calculated. From these, the additional mortality caused by the migration was estimated.

Chapter 3 tries to explain these higher mortality rates during the migration periods from increased predation by fishes and crabs on migrating *M. balthica*. Predation was studied in a 'carousel', a circular stream tank that allowed *M. balthica* to migrate in the laboratory, under illuminated and dark conditions. Additional field studies examined stomachs of pelagic fish for the presence of *M. balthica* and diurnal rhythms in the migration of *M. balthica*.

Chapter 4 examines the predation of shrimps, crabs and fish on buried *M. balthica*. Predator densities were estimated at the Groninger Wad. Size selection was examined in laboratory experiments and from stomach content analysis. Caging experiments in the field explored the interaction of predator abundance and size selection in relation to tidal level.

A similar study for infaunal predators is described in **Chapter 5**. Laboratory experiments showed that the infaunal polychaetes *Nereis diversicolor* and *Arenicola marina* and the gastropod *Retusa obtusa* could eat *M. balthica* spat. Stomach contents analysis, density estimates and density manipulation experiments showed how important these species are as predators on juvenile and adult *M. balthica*.

Chapter 6 describes a model that was used to evaluate to what extent mortality of *Macoma balthica* on tidal flats of the Groninger Wad could be explained from consumption by predators and additional mortality caused by migration.

Chapter 7 uses the model that was described in Chapter 6 to evaluate the adaptive value of migrations for *Macoma balthica*. Empirical data and literature values were used to calculate the reproductive output of animals using different migration strategies. Additional to the predators and processes studied in earlier chapters, parasites and birds were included in this model.

Chapter 8 contains a general discussion of the major findings.

CHAPTER 2

Changes in distribution and decrease in numbers during migration of the bivalve *Macoma balthica*

J. G. HIDDINK & W.J.WOLFF

ABSTRACT

The population development of the 1998 year-class of the bivalve *Macoma balthica* was studied by repeated sampling of a tidal flat area in the eastern Dutch Wadden Sea from May 1998 to August 2000. The juveniles migrated twice, once in mid-1998 from their primary settlement locations in the low sandy intertidal to the nursery in the high intertidal (spring migration, 25 % of all juvenile *M. balthica* relocated from low to high intertidal) and once in late 1998/early 1999 from the nursery to the low intertidal and the subtidal (winter migration, between 8 and 15% of all 0-group *M. balthica* relocated from high to low intertidal). During winter, *M. balthica* migration was most intensive at the lowest temperatures. Relative to the abundance on the tidal flats, 1+ group *M. balthica* was rare in the tidal channels of the Wadden Sea and was only slightly more common in the North Sea adjacent to the tidal inlet.

During both the spring and winter migration, many bivalves disappeared from the tidal flat population. This could partly be explained by normal mortality and by emigration to the subtidal channels and the North Sea. The remaining mortality was probably due to the risks inherent in migration; predation during pelagic floating or not reaching the right locations. The number of bivalves that disappeared was very high. In spring, slightly more disappeared than relocated. In winter, more than four times more bivalves disappeared than relocated. Migration is obviously a very dangerous activity, therefore great advantages must be associated with the nursery use that makes such migrations necessary. An analysis of literature data on the density of *M. balthica* shows that in the eastern Dutch Wadden Sea, 90% of the population lives in the intertidal, about 10% in the adjacent North Sea, and a negligible fraction in the subtidal channels of the Wadden Sea.

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 & Beukema 1994). A nursery is an area inhabited by many juveniles but few adults of a species. This is typical, 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 & Dapper 1984) and the bivalve *Macoma balthica* (Beukema 1993a).

It is assumed that these nurseries provide juveniles of these benthic species with protection against predation by marine organisms such as shrimps, crabs and small fish (Beukema 1993a), that physical disturbance is less (Flach 1992b) and that perhaps feeding conditions are better (Armonies & Hellwig-Armonies 1992). However, when nurseries are spatially separated from the locations inhabited by adults, juveniles must migrate to and from the nurseries. Many marine benthic animals (including *M. balthica*) migrate by drifting on the current while suspended in the water column (Sigurdsson *et al.* 1976; Forward & Tankersley 2001). This migration to and from the nursery is a phase with potentially very large risks: the animals are easy victims for pelagic and epibenthic predators such as fishes and risk ending up in the wrong locations.

For benthic animals, the risks of migration have not been studied, but there are some indications that they do have costs. Migrating lugworms, *Arenicola marina*, are eaten by the pelagic fish *Osmerus eperlanus,* which is unable to dig out deep-living polychaetes (Kühl 1970). The tube-dwelling amphipod *Corophium volutator* suffers enhanced mortality from predation by shrimps when disturbance by *A. marina* and *Cerastoderma edule* causes it to leave the sediment (Flach & De Bruin 1994). In *M. balthica* in the Baltic Sea, physical disturbance increased mortality due to predation by the isopod *Saduria entomon*, while physical disturbance alone did not have any influence on mortality (Bonsdorff *et al.* 1995). Thus, leaving their burrow in the presence of predators may be dangerous for bivalves, polychaetes and crustaceans.

There are no studies on the fate of benthic animals that migrate from a suitable habitat. The fact that there is a large variation in growth and mortality rates between locations for many benthic species may be an indication that many individuals fail to migrate to the optimal location (Beukema 1993a).

M. balthica is one of the most common and widespread bivalves in the Wadden Sea. Its early life history includes 2 migrations. *M. balthica* spawns in late March and April (Honkoop & Van der Meer 1997). The eggs and larvae are pelagic for a short period; in the Wadden Sea larvae settle mainly on the low tidal flats at a length of 190 to 300 µm (Günther 1991; Armonies & Hellwig-Armonies 1992). This settlement on low tidal flats is probably dictated by hydrography (Armonies & Hellwig-Armonies 1992). In May the postlarvae (300 µm) migrate to the nurseries (spring migration) on high, silty tidal flats (Armonies & Hellwig-Armonies 1992). After the first growth season, the juvenile *M. balthica* undertake a winter migration between December and March, from the

nurseries to the low intertidal flats and the subtidal of the Wadden Sea and North Sea (Beukema & De Vlas 1989). However, migration patterns in the Westerschelde estuary (outside the Wadden Sea) showed different migration patterns, with primary settlement on the high-tidal flats and migration to low-tidal flats during the summer (Bouma *et al.* 2001).

M. balthica migrates by byssus drifting. Byssus drifting has been described for most common bivalves of the Wadden Sea, such as the blue mussel *Mytilus edulis* (De Blok & Tan-Maas 1977; Lane *et al.* 1982; Lane *et al.* 1985; Caceres Martinez *et al.* 1994) and the cockle *Cerastoderma edule* (De Montaudouin 1997). The byssus drifting of *M. balthica* has been described by Sörlin (1988) and Beukema and De Vlas (1989). Due to an increase in drag force by a byssus thread, the sinking rate of juvenile molluscs decreases greatly. Sinking rates for small bivalves with a byssus thread can be up to 5 times slower than of those without, and are dependent on shell size and thread length (Sörlin 1988; Beukema & De Vlas 1989; Beaumont & Barnes 1992; De Montaudouin 1997). Current velocities of 0.1 cm s^{-1} are sufficient to enable ascent from the sediment surface (Lane *et al.* 1985).

For *M. balthica,* some of the factors that may promote nursery use have been identified. Beukema (1993a) concluded that juvenile *M. balthica* avoid the low intertidal because of the high abundance of epibenthic predators such as shrimp and crabs, which select for small shellfish (Reise 1978; Kaiser *et al.* 1990). Adult *M. balthica* are predominantly eaten by birds, which can forage for longer daily periods in the high than in the low intertidal (Hulscher 1982). Growth rates have been studied at many locations, but no distinction between 0-group and older animals was made in most studies (Wanink & Zwarts 1993; Harvey *et al.* 1993; Beukema 1993a). Further, maximum growth rates were found in the high intertidal in some studies, while in other studies the highest growth rates were found in the low intertidal. However, whether the migration to and from the nursery itself has any negative fitness consequences has never been investigated. Therefore, the total costs and benefits of nursery use for the *M. balthica* population cannot be evaluated.

Metapopulation ecology stresses the importance of migrations between populations for the survival of the metapopulation (Hanski 1999). The theory stresses the importance of estimating the costs of migrations, as the cost of migration is equivalent to the cost of living in a metapopulation. Further, it leads to some interesting questions, such as whether subtidal *M. balthica* represent a population, because it is not clear if the species can survive without intertidal nurseries. On the other hand, the subtidal population may be important for the survival of the intertidal population in the case of extreme physical harshness, such as extremely cold winters. Metapopulation theory was largely developed in terrestrial habitats and still has to demonstrate its validity in the marine environment. This paper contributes to the latter aim, by describing a migration pattern not encountered on land.

The present paper presents the costs and benefits of nursery use by a *M. balthica* population in the Groninger Wad, eastern Dutch Wadden Sea, focussing on the population consequences of migration. We describe the migration from the low intertidal to the nursery in spring and from the nursery to the low intertidal and subtidal in the next winter for 1 year-class of *M. balthica*. We try to quantify the migration flows of *M. balthica* as it migrates to and from the nursery. Further, we attempt to estimate the additional mortality caused by these migrations.

METHODS

Study area

Our study was carried out at the Groninger Wad, which is part of the Lauwers basin, in the eastern Dutch Wadden Sea (6° 31' E, 53° 27' N) (see Figure 1). The average tidal range is 2.4 m. The tidal flat area ranges from –1.4 to +1.0 m NAP (Dutch Ordnance level, which is 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. At the salt marsh side, brushwood groynes of former land reclamation works enclose the tidal flat area above +0.3 m NAP. Sediments range from fine sand to fine silt. The study area (7.9 km^2) is enclosed by salt marsh on the south side, the shallow shipping gully to Noordpolderzijl on the eastern side, the deep (10 m) tidal channel Zuidoost-Lauwers on the northern side and partly by another shallow tidal channel on the western side. Additional density data were collected in the tidal channels of the Lauwers basin and adjacent North Sea. The mouths of the main tidal channels Lauwers and Eilanderbalg are close to each other. It is impossible to deduce the origin of *M. balthica* (Zuidoost-Lauwers or Eilanderbalg) in the North Sea from their geographical position in the area. Therefore, Wadden Sea data for these areas were also combined. Figure 5 gives the boundaries of these tidal basins based on De Boer (1978), Ridderinkhof et al. (1990) and Louters and Gerritsen (1994). The North Sea area considered is defined by the area enclosed by lines heading straight north-west of the centres of the barrier islands of Schiermonnikoog and Rottumerplaat to 14 km offshore. The area extends more to the west than to the east because ebb currents from the Wadden Sea are directed westwards in this area (De Boer 1978). Residual currents are directed eastwards in the southern North Sea, but are of little importance to migrating *M. balthica* as these bivalves are probably mainly present in the water column during ebb tides. The tidal basin consists of 139 km^2 of tidal flats and 48 km^2 of tidal channels. Tidal channels reach a maximum depth of 18 m below NAP. The studied part of the North Sea has an area of 265 km^2 and a maximum depth of 20 m.

Our study required that there was no net migration to or from other tidal flat areas that were not sampled, because this could lead to either an over- or an underestimate of mortality. We assumed that the net displacement of *M. balthica* across the western and eastern boundaries of this area was negligible since the currents over the tidal flats are

mainly directed north-south and vice versa (Essink 1978) and because this assumption was a prerequisite for making estimates at all. We also assumed that net exchange across the major tidal channel, Zuidoost-Lauwers, was negligible since this channel has strong tidal currents running west-east and vice versa.

Set-up

The density *of Macoma balthica* of the 1998 year-class was monitored at the tidal flat area studied from May 1998 to August 2000. During this period, the density of *M. balthica* was estimated 21 times at 57 intertidal stations. Mortality was estimated from the rate of decrease in population size. By comparing mortality, or rather disappearance, before, during and after the migration, the amount of additional 'mortality' caused by the migration can be estimated. Subtidal densities of 1998 and 1999 year-class *M. balthica* were examined in October 1999.

Intertidal benthic sampling

The size of the *M. balthica*-spat population on the tidal flat was estimated from 7 May 1998 to 16 August 2000 by repeated sampling of 57 stations (Figure 1). Of these 57 stations, 25 were located in the high intertidal (between 0.3 and 1.2 m above NAP) and 32 were located in the low intertidal (between 0.5 m below and 0.2 m above NAP). The height levels of stations and all areas were obtained from Rijkswaterstaat depth charts of the Wadden Sea surveyed in 1994. Although MLW was 1.4 m below NAP and some stations were horizontally close to MLW, the height of the lowest stations was 0.5 m below NAP. This is because the transition of the Zuidoost-Lauwers tidal channel to the adjacent tidal flats has a relatively steep slope (1:20).

Table 1 gives the dates on which the stations were sampled. Sampling started in early May, because at this time, further settlement of postlarvae was assumed to be rare and therefore the population had become 'closed', a prerequisite for our calculations. With decreasing densities and increasing size of *M. balthica*, the sample size and sieve mesh size were increased from 13 cm^2 and 125 µm on 7 May 1998 to 415 cm^2 and 1000 µm at the end of the study (Table 1). On some of the sampling dates, 1 or 2 of the lowest stations could not be sampled due to high water levels at low tide. We did not correct for these missing values.

The samples were stored at -25°C until sorting. Samples were sieved through 1000, 500, 300 and 125 µm mesh (only those mesh sizes equal or larger than the mesh size used in the field on a date were used). The fractions were sorted at 6 to 25 x magnification under a binocular dissecting microscope. The shellfish were classified in year-classes by counting year-rings on the shells and the number of *M. balthica* in the 1998 year-class per sample was counted.
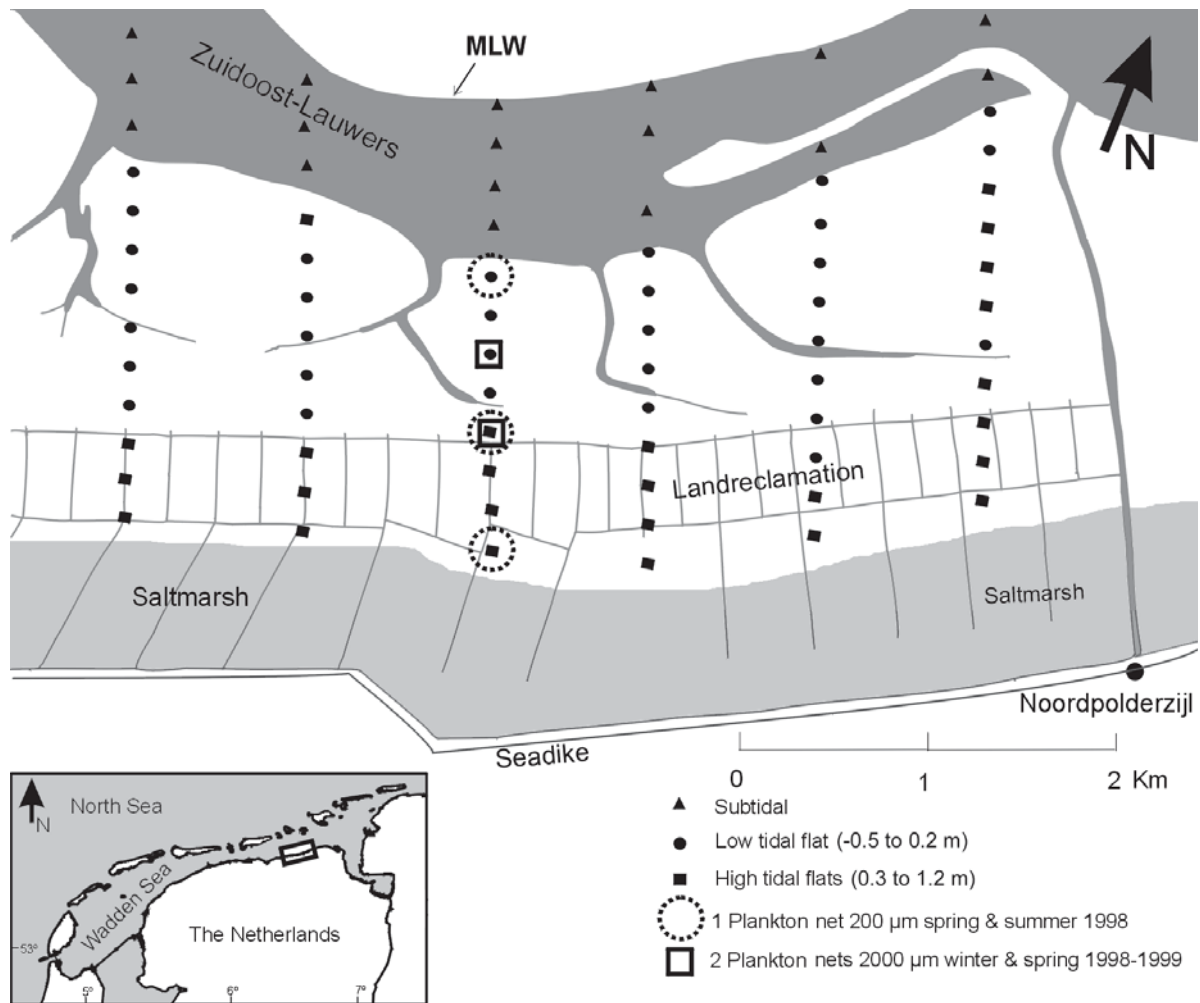
Figure 1. Sampling stations at the Groninger Wad, eastern Dutch Wadden Sea. The locations of plankton nets (200 µm, a single net per location) in spring and summer 1998 are indicated with a dotted circle. The locations of the coarse plankton nets (2000 µm, two nets per location) in winter and spring (1998-1999) are indicated with a square. MLW = Mean low water level.

Subtidal benthic sampling

Since *M. balthica* can also migrate to and from the subtidal, subtidal densities of *M. balthica* spat and newly migrated adults were examined. On 5 October 1999, *M. balthica* were sampled in the subtidal tidal channels, just north of the study area (Figure 1). At 17 stations, 3 or 4 0.2 m² Van Veen-grabs per station were taken, sieved over 2 mm, and pooled per station. Samples were sorted in the laboratory. The depths of these stations range from 1.5 to 10 m below NAP (= 0.1 to 8.6 m below MLW). Samples were stored at –20°C until sorting. For each pooled sample, the numbers of 1998 and 1999 year-class *M. balthica* were counted. In the same week, densities of the 1998 and 1999 year-classes in the intertidal were estimated as described in the preceding subsection (6 October 1999: see Table 1).

Table 1. Intertidal benthic and plankton sampling of *M. balthica*. Sampling dates, number of stations, area sampled, mesh sizes of sieves and plankton nets and the water temperature for the sampling dates in winter are listed.

Date	Number of stations	Area sampled (cm^2)	Mesh size smallest sieve (µm)	Water temperature (°C)	Mesh size plankton nets (µm)
7-May-98	55	13	125		200
19-May-98	57	13	125		200
3-Jun-98	57	13	125		200
18-Jun-98	56	22	300		200
7-Jul-98	56	22	300		200
21-Jul-98	57	22	300		200
4-Aug-98	56	22	300		200
19-Aug-98	56	22	300		200
14-Oct-98	56	43	300		200
2-Dec-98	57	83	500	-1.0	2000
15-Dec-98	56	83	500	8.0	2000
13-Jan-99	56	83	500	1.5	2000
28-Jan-99	56	83	500	4.0	2000
10-Feb-99	56	83	500	-1.5	2000
25-Feb-99	56	83	500	5.0	2000
11-Mar-99	57	83	500	3.5	2000
30-Mar-99	56	83	500	12.0	2000
11-May-99	56	83	500	17.0	2000
6-Oct-99	56	249	1000	12.5	2000
10-Apr-00	57	415	1000		No fishing
16-Aug-00	57	83	1000		No fishing

Pelagic sampling

The timing of migration by *M. balthica*-spat was estimated from samples obtained with plankton nets in the intertidal during high tide. The net opening had a diameter of 19 cm and the net could rotate freely on a pole (see figure 1E in Armonies 1994a). The bottom side of the opening of the net was placed 5 cm above the sediment surface. On every sampling date, the plankton nets were placed on the tidal flats for 24 h, starting at low water. Nets fished passively on the current during the immersion periods (approximately 2 x 4 h). In spring a mesh size of 200 µm was used, in winter a mesh size of 2000 µm (Table 1). From May to October 1998, single nets were used at 3 locations (-0.3, 0.0 and 0.8 m above NAP) (Figure 1). From October 1998 to October 1999, 2 nets were used at 2 locations (both at 0.0 m NAP). The number of *M. balthica*-spat per net was counted in the laboratory on the same day.

Analysis

The period from May 1998 to October 1999 was divided in 4 periods: spring migration period, first summer period, winter migration period and second summer onwards (Table 2), based on the number of migrating *M. balthica* caught in the plankton nets and the changes in distribution on the tidal flats. A period of migration was defined as a

period with both numerous migrating *M. balthica* and a change in distribution on the tidal flats. We could not distinguish between active migration and passive dislocation (due to strong currents) with our methods. For each of these periods, the rate of disappearance could be estimated, assuming an exponential population decrease, according to the formula:

$$N_t = N_0 \cdot e^{-Z.t}$$

where Z is the instantaneous disappearance rate, t is time, N_0 the original population size, and N_t population size at time t. Disappearance could be estimated by rewriting the formula as $-Z.t = Ln(N_t/N_0)$ and doing a regression of $ln(N_t/N_0)$ on t. The differences in disappearance rate between these periods were tested by comparing the slopes (Z values) of the regressions.

In periods without migration, all bivalves that disappear will have died; thus, disappearance equals mortality. In periods with migration, disappearance is equal to mortality plus emigration or minus immigration. In this study, 'disappearance' indicates that bivalves died or otherwise disappeared. 'Mortality' is used only in cases were it can be safely assumed that the shellfish actually died. The additional mortality and disappearance caused by the migration was estimated by subtracting the average disappearance before and after migration from the disappearance during migration.

Order-of-magnitude calculations

We made an order-of magnitude-calculation on the population size of *M. balthica* during the migration period (Table 3) based on: initial population size - final population size = normal mortality + additional mortality ± migration. As we assumed a closed population, bivalves could only migrate within the study area. The final and initial population sizes were calculated by multiplying density by the total tidal-flat area. Normal mortality is the mortality that would have occurred without migration. For the spring migration, we assumed that this was equal to the mortality of the following summer. Additional mortality is the difference between the disappearance measured during migration and the assumed normal mortality. Both disappearance rates (normal and additional) were calculated for the whole population. The difference between the calculated number after normal and additional mortality at a location (based on the mortality of the whole population) and the actual number found must be migration (within the study area). 95% confidence intervals of population sizes were calculated from the low and upper confidence intervals for the density estimates.

As our sampling comprised only 1 year-class during 2 years and only a small tidal flat and channel area close to the mainland, additional density data of *M. balthica* from the subtidal and intertidal of the Lauwers tidal basin and the adjacent North Sea were obtained from earlier investigations.

RESULTS

Intertidal density

Figure 2 shows the time course in densities of *M. balthica* (1998 year-class) on high- and low-tidal flats. Initial settlement occurred mainly in the low intertidal, on the sandy flats close to the main tidal channel. This is reflected by much higher densities on 7 May 1998 in the low intertidal (22 098 m^{-2}) than in the high intertidal (8244 m^{-2}). *M. balthica* undertook a spring migration in May and June 1998. At that time densities increased in the high intertidal and decreased greatly in the low intertidal. The density of *M. balthica*-spat in the high intertidal was significantly higher on 3 June than on 7 May (ANOVA, p = 0.05). Settlement after 7 May 1998 can largely be excluded, since after this date, few newly-settled *M. balthica* <300 μm were found in all samples. The density of *M. balthica* <300 μm was 433 m^{-2} on 7 May, 76 m^{-2} on 19 May and 13 m^{-2} on 3 June. After 3 June no *M. balthica* <300 μm was found on the tidal flats. This indicates that after the first sampling date, hardly any new settlement of *M. balthica* larvae occurred in the study area, and implies a migration from the low to the high intertidal. During summer of 1998, densities in the high intertidal remained higher than in the low intertidal (ANOVA, p = 0.000).

A second migration occurred in winter, between December and February. In this period *M. balthica* migrate from the high tidal flats to the low tidal flats. This is visible on Figure 2 as the crossing of the lines of densities for the high- and low-intertidal stations between 15 December 1998 and 13 January 1999. Density in the low intertidal did not increase significantly between these dates (ANOVA, p = 0.45), but the density in the high intertidal did decrease significantly (ANOVA, p = 0.05). After the migration (from February 1999 onwards), densities in the low intertidal stayed higher than in the high

Figure 2. Density of *M. balthica*-spat (1998 year-class) (left axis) ±95% confidence limits at high and low tidal flats of the Groninger Wad from May 1998 to August 2000. Fast changes in ratio (rigth axis) of the densities on the low and the high tidal flats point to migration. An asterisk (*) indicates that the density differed significantly between high and low tidal flats at a date (t-test on log-transformed data, p<0.05).
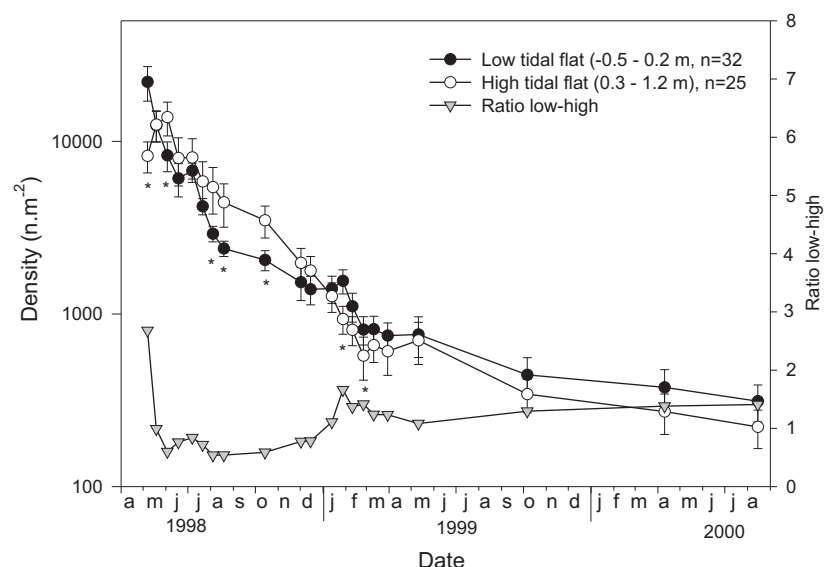
intertidal (ANOVA, p = 0.003). A 2-factor ANOVA on the log-transformed densities for all sample dates, with date and tidal level as factors shows that the interaction between these 2 factors was significant (2-way ANOVA, date x tidal level, p = 0.000); thus the spatial distribution changed significantly over time.

Subtidal density

Densities of *M. balthica* in the subtidal channels, for both the 1998 and the 1999 year-class in October 1999, were much lower than in the intertidal. The 1999 spat had a density of 0.2 m^{-2} in the subtidal, while the average density in the intertidal at this time was 980 m^{-2}. The 1998 group (1.5 year old) had an average density of 15 m^{-2} in the subtidal and 400 m^{-2} in the intertidal at that time. The density of 1998 *M. balthica* in the shallow North Sea off the Lauwers (see Figure 5) in March 1999 was 30 ± 74 (SD) m^{-2} (M. F. Leopold, pers. comm.).

Plankton catches, determination of migration periods and disappearance per period

The numbers of *M. balthica*-spat caught in spring and summer 1998 in the 200 µm plankton nets (Figure 3), were very low compared to the benthic densities at that time. At 4 June, the highest numbers were found in the nets (13 net^{-1}). The number of migrating *M. balthica* in winter reached the highest value of 1055 net^{-1} on 10 February 1999. Only 1 individual of another bivalve species, a 1 year old *Scrobicularia plana*, was caught. The numbers of *M. balthica* caught in the plankton nets in winter were significantly negatively correlated with the water temperature (R^2= 0.48, p = 0.04, Figure 4) indicating that *M. balthica* migrates in winter. However, during winter, temperatures vary widely with temperatures of -1 and +8°C recorded in December (Table 1). Thus, the bivalves responded to water temperature.

The times of start and end of the migrations were estimated from the changes in distribution pattern (Figure 2) and the time course of the plankton catches (Figure 3). Figure 2 shows the ratio of densities on the low and the high tidal flats. A fast-changing ratio in May and June 1998 and in January and February 1999 suggests a fast-changing distribution pattern in these months. These periods also showed the highest planktonic catches, but these catches suggest a longer migration period (Figure 3). Table 2 gives the dates of the approximate start and end of the migration and intervening periods. For each period, the disappearance rate (including immigration and emigration) of the whole *M. balthica* population (1998 year-class) was estimated from the decrease in densities over the entire (low + high) tidal flat area. It is likely that mortality rates between high and low tidal flats differ. Nevertheless, disappearance rates were calculated for the whole tidal flat area with no distinction between high and low tidal flats, because migrations make it impossible to calculate disappearance rates otherwise.

Figure 3. Number of *M. balthica*-spat (1998 year-class) ± SD, caught in an intertidal plankton net in 24 h at the Groninger Wad, with a mesh width of 200 µm (spring and summer 1998) or 2000 µm (winter 1998-1999).
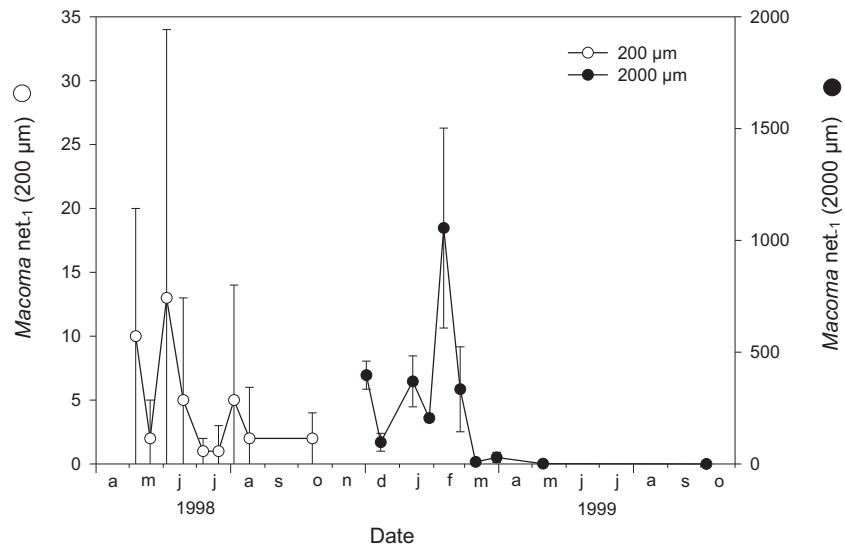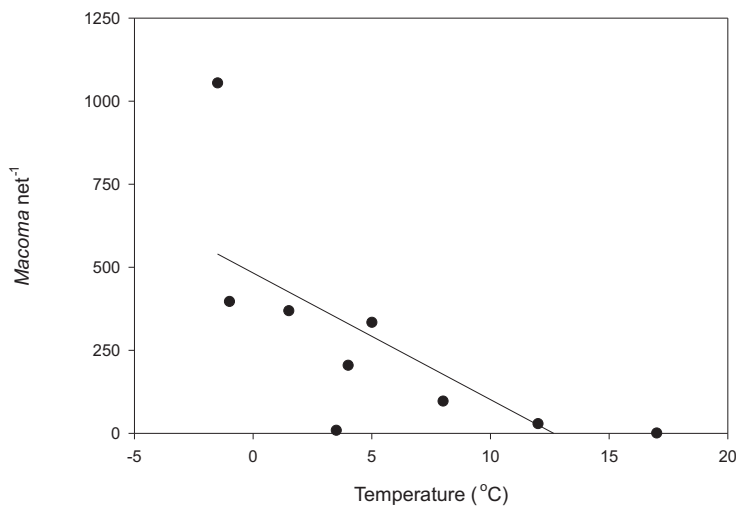
Figure 4. The number of *M. balthica* (1998 year-class) caught in a plankton net in 24 h at the Groninger Wad, at various water temperatures from December 1998 to May 1999. R^2=0.48, p=0.04.

The disappearance rate was significantly higher during the spring migration (0.0125 d^{-1}) than during the subsequent first summer period (0.0084 d^{-1}). Disappearance during the winter migration was higher than during the first and second summer period (0.0107 vs 0.0084 and 0.0020d^{-1} respectively). All disappearance rates were significantly different from each other.

We found a few *M. balthica* in the plankton nets after the spring migration (7 July 1998). It is not clear whether this was active migration or passive dislocation.

Order-of-magnitude calculations

SPRING MIGRATION

In the Groninger Wad, densities of juvenile *M. balthica* in summer, after the spring migration, were higher in the high intertidal than in the low intertidal, and were almost zero in the subtidal of the tidal channels. Because the area of low intertidal in the study area was larger than the area of high intertidal, the total number of juvenile *M. balthica* in the 2 areas was approximately equal (Table 3A: 29 x 10^9). The distribution and migration of juvenile *M. balthica* in this study resembles the patterns described for the German Wadden Sea by Günther (1991), Armonies & Hellwig-Armonies (1992) and

Table 2. Disappearance rates of *M. balthica* (1998 year-class) during four periods in their first 2.5 year.

Period	Approximate start date	Approximate end date	Disappearance rate (d^{-1})
Spring migration	7 May 1998	7 July 1998	0.0125
First summer	7 July 1998	2 December 1998	0.0084
Winter migration	2 December 1998	25 February 1999	0.0107
1+ group	25 February 1999	15 August 2000	0.0020
Average	May 1998	15 August 2000	0.0052

Armonies (1996), and in the western Dutch Wadden Sea by Beukema (1993a).

During the spring migration, the actual disappearance rate measured during migration was 0.0125 d^{-1}, while the normal disappearance rate was 0.084 d^{-1} (Table 2). Hence, the additional disappearance rate was 0.0041 d^{-1}. As the duration of the spring migration was 61 d, 25 % of the initial intertidal population disappeared during migration (either due to mortality during the migration period or emigration to the subtidal). During this process, the normal disappearance (of 0.0084 d^{-1}) of buried *M. balthica* also continued. In Table 3A, the numbers of migrating and disappearing *M. balthica* during the spring migration were calculated from the observed density changes. The number of normal disappearances was calculated from the normal disappearance rate for the period of migration (61 d) and the initial population size. The number of additional migration disappearances was calculated from the number after normal disappearances and the additional disappearance rate for the period of

Table 3. The population size of *M. balthica* (1998 year-class, in 10^9 individuals) at the Groninger Wad. Bold values were actually measured or come from calculation in other tables, other values were calculated from these bold figures (see text). The net number of migrants is the difference between the calculated number of *M. balthica* 'After additional migration disappearance' and the observed 'Final population size' at a location. A: spring migration. B: winter migration.

A: Spring migration 7 May to 7 July 1998

Location	Stations	Area (km^2)	Initial population size	Pop. size after normal disappearance	Pop. size after additional migration 'disappearance'	Net number of immigrants	Final population size
Total	**57**	**7.9**	**125**	75	58		**58**
High intertidal	**26**	**3.6**	**29**	17	13	15	**29**
Low intertidal	**31**	**4.3**	**95**	57	44	-15	**29**

B: Winter migration. 2 December 1998 to 25 February 1999

Location	Stations	Area (km^2)	Initial population size	Pop. size after normal disappearance	Pop. size after additional migration 'disappearance'	Net number of immigrants	Final population size
Total	**57**	**7.9**	**14.0**	8.9	5.6		**5.6**
High intertidal	**25**	**3.6**	**7.1**	4.6	2.9	-0.8	**2.1**
Low intertidal	**32**	**4.3**	**6.9**	4.4	2.8	0.8	**3.5**
Subtidal	**19**	**2.4**	**0.0$^+$**	0.0	0.0	0.0	**0.0***

$^+$ Assumption, based on density of 1999-year-class in October 1999
* Stations sampled in October 1999

migration (61 d). The difference between the number 'After additional migration disappearance' and the 'Final population size' is the number that migrated.

Table 3A gives the absolute numbers of *M. balthica* in the low- and high-tidal flats before and after spring migration. Most *M. balthica* spat settled initially in the low intertidal. Subsequently, about 12% of the initial numbers migrated from the low flats to the high-tidal flat nurseries between May and July, while 23 % of the population stayed in the low intertidal. The rest of the population disappeared in this period. The numbers staying in the low intertidal constitute 50% of the final numbers in the intertidal, so half of all surviving bivalves continued to live in the low intertidal. The numbers of *M. balthica* in the high intertidal before and after the migration were equal, while the number in the low intertidal decreased greatly. 53 % of the initial numbers disappeared during the migration period, including the normal mortality of 40%. The additional 13% ($17 \pm 5 \times 10^9$ individuals) mortality outnumbers the $15 \pm 6 \times 10^9$ that migrated from the low- to the high-tidal flats. Since the bivalves probably did not settle in the subtidal in spring, this disappearance is presumably due to additional mortality during the migration.

WINTER MIGRATION

The order-of-magnitude calculation in Table 3B also show the number of migrating and disappearing *M. balthica* during the winter migration. The total disappearance rate during the winter migration was 0.0107 d^{-1}. Parallel to normal disappearance, the additional disappearance rate (due to mortality or emigration) of 0.0055 d^{-1} (see Table

Table 4. Average density ($\pm$ SD) and population size of *M. balthica* 1998 year-class in the Lauwers tidal basin and the adjacent North Sea in 1999. Data from North Sea from M.F. Leopold (pers. comm.).

Location	Area (km^2)	Month 1999	Density 1998-*Macoma* (n.m^{-2})	Population ($\times 10^9$)	N
Intertidal	139	March	684 $\pm$ 478	95.1	56
Intertidal	139	October	401 $\pm$ 218	55.7	56
Tidal channels	48	October	15 $\pm$ 27	0.7	19
North Sea	195	March	30 $\pm$ 74	5.8	62

Table 5. Population size (in 10^9 individuals) of *M. balthica* (1998 year-class), in the Lauwers tidal basin and adjacent North Sea in winter 1998/1999. The net number of migrants is the difference between the calculated number of *M. balthica* 'After additional migration disappearance' and the observed 'Final population size' at a location.

	Area Km^2	Initial population size (x 10^9)	Pop. size after normal disappearance	Pop. size after additional migration disappearance	Net number of migrants	Final population size
High intertidal	23	45	29	22	-9.3	13
Low intertidal	116	185	118	92	2.7	94
Tidal channel	48	0	0	0	0.7	1
North Sea	195	0	0	0	5.8	6

2, the difference in disappearance rate between the average of the first and second summer (0.0052) and during winter migration (0.0107)) over 85 days resulted in 36% of the initial intertidal population disappearing.

Table 3B gives the absolute numbers of *M. balthica* on the low- and high-tidal flats before and after winter migration. Most *M. balthica* spat lived in the high intertidal throughout summer. Subsequently, about 21% of the initial numbers migrated from the high-tidal flat nurseries to the low-intertidal flats between December and February. This was 13% of the initial population on the high tidal flats. 60% of the initial numbers disappeared during the migration period, including the normal mortality of 36%. The additional 24% ($3.4 \pm 0.6 \times 10^9$ individuals) mortality outnumbered the 0.8×10^9 that migrated from the high- to the low-tidal flats and subtidal channel. If all the disappearing individuals from our study area alone migrate to the coastal North Sea (to a depth of 20 m, an area of 195 km^2), this would result in an average density of 11 bivalves m^{-2} in the North Sea outside the Lauwers tidal basin.

Winter migration of 1998 year-class in whole Lauwers tidal basin and adjacent North Sea

In order to calculate the actual density of the 1998 group of *M. balthica* in the North Sea in 1999, we must consider the entire tidal basin of the Lauwers and Eilanderbalg. This basin consists of 139 km^2 of tidal flats and 48 km^2 of tidal channels. Density in the intertidal was about 20 times the density in the North Sea and tidal channels (Table 4), indicating that almost 95% of the *M. balthica* 1998-year-class was still in the intertidal in 1999 at the end of the winter migration (Table 4).

Table 5 shows an order-of-magnitude calculation of the migration of *M. balthica* in the Lauwers tidal basin during the winter migration, assuming that the sampled area of subtidal and intertidal area sampling in the Groninger Wad is representative of the whole Lauwers basin. In these calculations, we used North Sea and tidal channel densities from Table 4, ignoring differences in sampling month, since these densities were very low compared to intertidal densities.

Of the 9.3×10^9 (7.8 to 10.6×10^9 95% CL) migrants that leave the high intertidal, 62% migrate to the North Sea and only 30% to the low intertidal. A small fraction of 7% migrates to the tidal channels. There are however still an additional 34×10^9 (28 to 40×10^9 95% CL) individuals disappearing during migration. This is thus more than 9 times the number arriving in the North Sea. Therefore, taking the North Sea population into the calculations does not explain a large proportion of disappearing *M. balthica*. Comparison of Table 3 and Table 5 changes our picture of the migration flow drastically. Taking migration to the North Sea into the calculations reveals that migration from the high to the low intertidal is only of minor importance, with two-thirds of the bivalves migrating to the North Sea.

Table 6. Sources giving densities of *M. balthica* from the subtidal and intertidal of the Lauwers tidal basin (Wadden Sea) and adjacent North Sea.

Source	Habitat	Location	Sampling date	Method	Number of stations	Area per station (m²)	Density (n.m⁻²) 0-group	1-group	Total
De Vlas (1981)	Intertidal	Pieterburenwad, Andelbult & Wantij Rottum	**July 1981**	Corer	23	0.060	10	82	438
Lindeboom et al., (1996)	Intertidal	Boschwad & Mothoek	July 1994	Corer	4	0.028			13
This study	Intertidal	Groninger Wad	March 1999	Corer	58	0.008	0	684	556
This study	Intertidal	Groninger Wad	March 2000	Corer	9	0.042	0	173	395
This study	Intertidal	Schiermonnikoog	March 2000	Corer	4	0.042	0	63	140
RIKZ (pers. comm.)	Intertidal	Groninger Wad	1976 to 1999	Corer	5, at least twice a year	0.077	279		675
Van Scheppingen and Groenewold (1990)	North Sea	Whole area	May 1989	Van Veen-grab	19	0.068			118
Duineveld (1992)	North Sea	Offshore station	May 1992	Boxcore	1	0.068			18
Duineveld and Belgers (1993)	North Sea	Offshore station	May 1993	Boxcore	1	0.068			3
Holtmann et al., (1995)	North Sea	Offshore station	May 1994	Boxcore	1	0.068			3
Holtmann et al., (1996)	North Sea	Offshore stations	May 1995	Boxcore	2	0.068			29
Holtmann et al., (1997)	North Sea	Offshore stations	May 1996	Boxcore	2	0.068			249
Holtmann et al., (1998)	North Sea	Offshore stations	May 1997	Boxcore	2	0.068			132
Leopold (pers. comm.)	North Sea	Whole area	June 1997	Van Veen-grab	62	0.200	0	3	10
Leopold (pers. comm.)	North Sea	Whole area	May 1998	Van Veen-grab	62	0.200	0	7	12
Holtmann et al., (1999)	North Sea	Offshore stations	May 1998	Boxcore	2	0.068			59
Leopold (pers. comm.)	North Sea	Whole area	March 1999	Van Veen-grab	62	0.200	0	30	61
De Vlas (1981)	Tidal channels	Whole Zuid-Oost Lauwers	July 1981	Van Veen-grab	18	0.200	4	18	38
Lindeboom et al., (1996)	Tidal channels	Spruit & Boschgat	July 1994	Boxcore	16	0.060	6	26	101
This study	Tidal channels	Southern Zuid-Oost Lauwers	October 1999	Van Veen-grab	19	0.6-0.8	1	14	28

Densities in the subtidal Wadden Sea and adjacent North Sea in other years

Additional density data for *M. balthica* from the subtidal and intertidal of the Lauwers tidal basin and the adjacent North Sea from earlier studies (Figure 5) are given in Table 6. These densities were used to calculate the average density per compartment (North Sea, tidal channels and tidal flats). Whenever available, densities of 0-group, 1-group and older individuals were calculated separately. Together with the area of each of these compartments, the average total population size of *M. balthica* per age-class was calculated from these data.

Most studies sampled the North Sea from March to May. Postlarval *M. balthica* settle in April and are small (<2 mm) until early June, and therefore pass through the coarse sieves used in subtidal sampling. Thus, few studies sampled in the North
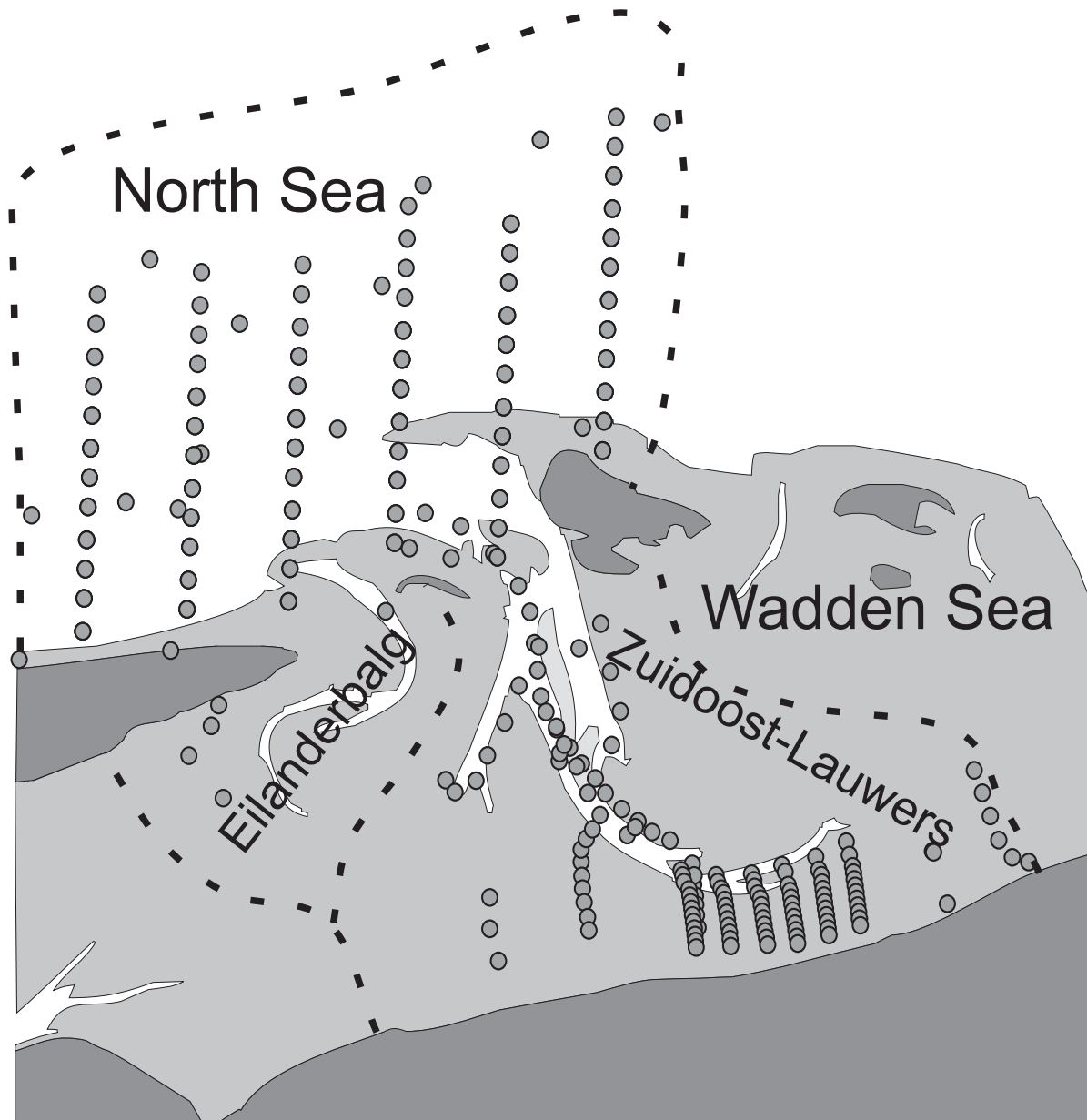
Figure 5. Sampling stations from the sources giving densities of *M. balthica* from the subtidal and intertidal of the Lauwers tidal basins (Wadden Sea) and adjacent North Sea (See Table 6). The boundaries of the Lauwers and Eilanderbalg basin are indicated with dashed lines.

Sea in the months that 0-group *M. balthica* were present and large enough to be retained in the sieves. This can explain why in none of the studies in Table 6, 0-group *M. balthica* was found in the North Sea. For older (and thus larger) age-classes, the sampling month was not so important, since between-year-class differences in density are much larger than between-month differences (Beukema *et al.* 1996).

Table 7 gives the average densities in the different habitats. In the North Sea, older *M. balthica* were found to a depth of 20 m. Densities of 1-group individuals were generally low (densities of 0 to 790 m^{-2} at individual stations) in the subtidal of both the tidal channels and the North Sea. In the intertidal *M. balthica* was more numerous, up to 7300 m^{-2}. Only 10% of the population of the Lauwers basin dwelt in the North Sea in

Table 7. Average density of *M. balthica* (1-group animals) (± SD) from the Lauwers tidal basin and the adjacent North Sea, from all sources in Table 6.

Area	Area (km^2)	Density 1-group *Macoma*			Population (*10^6)	n
Intertidal	139	511	±	490	71029	88
Tidal channels	48	17	±	42	833	49
North Sea	265	30	±	56	7966	207

the studied period, and thus the majority were in the intertidal (Table 7). Since both the density of *M. balthica* and the area of the tidal channels were low, the population size in the tidal channels was negligible.

When comparing densities and population size of the 1998 year-class after 1 year (Table 4) with the data for many year-classes from 1976 to 2000 (Table 7), the correspondence in densities at the locations is striking: around 10% of the population dwelt in the North Sea, only 1% in the tidal channels and the rest on tidal flats in both tables. The absolute population size deviates by <30 %. Therefore, we can conclude that the distribution of 1998 year-class *M. balthica* in 1999 is representative for other years.

DISCUSSION

When estimating mortality in a population, it is necessary that the population be closed. In this study, settlement was very low after the start of the observations and therefore did not interfere with the estimates of disappearance rates. However, migration into and from the research area was not examined. Since, according to detailed maps of the area, sediment and other physical and biological circumstances are quite homogeneous inside and outside the research area, and since currents over the flats are mainly north-south and vice versa, it was assumed that there was no net lateral migration in and from the area. Im- and emigration from and to the subtidal cannot be excluded but is probably not a significant process (Armonies 1996).

Low water temperatures accompanied the winter migration. Sörlin (1988) had already found this in a laboratory study. It is unclear if this temperature dependency is only a trigger, or if it also has a functional component. It is known that *M. balthica* is somewhat sensitive to freezing (Ibing & Theede 1975).

Effect of sampling month and mortality values

The effect of differences in sampling months, differences in mortality between the habitats, and the interaction between these needs some consideration. Densities in the North Sea and on the tidal flats were sampled directly after the winter migration, while densities in the tidal channels could only be sampled half a year later (Table 4). As mortalities in these different habitats are probably not equal, densities cannot be compared without reservation. Actual mortality values in the subtidal channels and

North Sea were not measured and are not reported in the literature.

The ratio between individuals older than 1 year and 1-group individuals can give an idea of the mortality at a location: a low ratio suggests a high mortality and vice versa. In October 1999, we found 9% 2 year and older *M. balthica* in the tidal channels and 17% of these animals in the intertidal. This suggests a higher mortality in the tidal channels. The North Sea data do not allow an estimation of mortality. The densities of some year-classes at stations sampled in early spring in 3 consecutive years (1997, 1998 and 1999) seemed to increase (M.F. Leopold, pers comm.). This suggests a further migration of *M. balthica* to the North Sea at an older age. The origin and migration mechanism of these older individuals still need to be clarified. Older individuals can also migrate pelagically: in January 2001, we found 5 1-group *M. balthica* together with 2241 migrating 0-group in a plankton net on the Groninger Wad tidal flats. Together, these differences in mortality and sampling month will have led to an (unquantifiable) underestimate of migration to the tidal channels and the North Sea.

Explaining disappearance

During both migration periods, many *Macoma balthica* disappeared from our study area. For the winter migration, part of this disappearance can be explained by migration to the North Sea. This pattern of increased mortality during spring and winter is not found for non-migrating populations of *M. balthica* (for example in the Baltic Sea, Bonsdorff *et al*. 1993) or for non-migrating species like *Cerastoderma edule* (Jensen 1992; Guillou & Tartu 1994). Therefore, the high disappearance rates during the migration period were probably not caused by a higher predation rate on buried *M. balthica*. The rest of the disappearing individuals were possibly a victim of predators, although many other factors co-varied. Laboratory experiments showed that *M. balthica* is indeed more vulnerable to epibenthic predators such as flatfish and the crab *Carcinus maenas,* during migration than when they remain buried (Chapter 3). It is, however, not clear whether this can quantitatively explain the disappearance of all migrating *M. balthica*.

Densities of the shrimp *Crangon crangon*, the crab *Carcinus maenas* and the goby *Pomatoschistus* sp. on the tidal flats are generally lower during the spring and winter migration, than before and after these migrations (Beukema 1991; Beukema 1992). The fact that disappearance is higher in a period when predators are scarce means that the actual impact of migration losses on the population size may be even larger than the estimated it this study.

General

Macoma balthica spat were more abundant in high- than on low-tidal flats during their first summer. Since there is more low- than high-tidal flat, half of the spat lived in the high intertidal while the other half lived in the low intertidal. Adults lived in both the high-

and low-tidal flats, but were more common on the low tidal flats. Therefore, nursery use is not obligatory for juvenile *M. balthica,* and adults can live in the nurseries. Still, *M. balthica* undertake migrations. As no juveniles were found in the North Sea, the Wadden Sea tidal flats must serve as an exclusive nursery for the North Sea population.

This study shows that there is a large risk associated with migration. Therefore, nursery use has to have a large advantage for the juvenile *M. balthica*. Beukema (1993a) summarised the knowledge on differences in growth and survival between juvenile and adult *M. balthica*. Many of these differences may indeed promote nursery use. Several studies have shown that circumstances are more favourable for juveniles in the high intertidal nurseries and in the low intertidal for adults.

The advantages and disadvantages for adults and juveniles of living in the North Sea have not been investigated. It is difficult to evaluate the disadvantages for 0-group *M. balthica* in the North Sea, as these rarely occur outside the tidal flats. We assume that, for spat, environmental condition are not so good, as they do not occur there. We hypothesise that this is caused by predation by flatfish, the shrimp *Crangon crangon* and the crab *Carcinus maenas* on small *M. balthica*, and that spat are thus forced to live in the high intertidal, where these predators are scarce.

The winter migration to the North Sea is especially dangerous, since the number of individuals disappearing during this migration is much higher than the number arriving in the North Sea. This implies that living in the North Sea is of great advantage for the adults. The nature of this advantage has never been investigated. Possibly, survival of adults is much higher in the North Sea, as very old adults are much more numerous there than in the intertidal. In the long run, the North Sea population might ensure survival of the metapopulation in the case of extremely cold winters.

However, most *Macoma balthica* either stay in the high intertidal or migrate to the low intertidal. We cannot exclude the possibility that migration to the North Sea in winter is no more than a side effect of migration from the high to the low intertidal, whereby low-intertidal arrivals have the advantage of migration (Chapter 4 and 7), while the North Sea individuals have passed the best places.

CHAPTER 3

Active pelagic migrations of the bivalve *Macoma balthica* are dangerous

J.G. HIDDINK, R.P. KOCK & W.J. WOLFF

ABSTRACT

The bivalve *Macoma balthica* migrates twice during the benthic part of its life cycle. During the spring migration (May-June), the newly settled spat (0-group) migrates to the nurseries in the high intertidal. Seven to nine months later, the bivalves migrate back to the low tidal flats and the subtidal (winter migration, 1-group). Both 0- and 1-group *M. balthica* use byssus threads for active pelagic migrations. As many *M. balthica* disappear during these migrations, we examined experimentally the importance of predation on 0- and 1-group *M. balthica*. Laboratory experiments using a circular aquarium determined predation rates on buried (no current) and drifting (current) 0- and 1-group *M. balthica* by several fish species (plaice, flounder, goby and whiting) and the shore crab. Under illuminated conditions, more *M. balthica* were consumed when migrating than when buried, whereas there was no difference between experiments in conditions of darkness. For the 0-group, predation rates on migrating and buried *M. balthica* in dark were lower than in light. The stomachs of pelagic fish in the Wadden Sea and Oosterschelde estuary did not contain *M. balthica* during winter migration. In the Wadden Sea, 1-group *M. balthica* primarily migrated at night.
In conclusion, enhanced predation on drifting as compared to buried *M. balthica* may be the mechanism that explains enhanced mortality during migration in light and may explain why *M. balthica* mainly migrates at night in the field. As we found no *M. balthica* in stomachs of pelagic fish, we do not know whether predation on byssus drifting *M. balthica* exists in the field. There are however, some indications for fish predation on infaunal polychaetes during pelagic migrations.

INTRODUCTION

Migration is the consequence of a preference for one habitat relative to the present habitat. Migration takes time, uses energy and the journey may be dangerous. The advantages or benefits of migration must exceed the costs, such as energy consumption and exposure to predators.
These benefits are found in the difference between locations. For example, seasonal migrations enable animals to exploit resources that are not available year-round. Migrations to and from nursery and spawning areas are both related to reproduction. Often nursery use of juveniles makes spawning migrations by adults necessary. A well-known example is the salmon (*Salmo salar*), which has to migrate from the sea to rivers to spawn, as the juveniles grow up in rivers, while adults live in the sea. Salmon also illustrate the costs of migrations very well. The energetic costs of locomotion are high, as much energy is used in long distance migrations. Further, migrating animals are under a higher predation risk during the migration than during their normal life. Migrating salmon, for example, are eaten by fishing bears that they do not encounter during their oceanic life.

Macoma balthica is one of the most common and widespread bivalves in the Wadden Sea. The early life history of benthic *M. balthica* includes 2 migrations. In May the postlarvae (300 µm, 1-3 months in age) migrate from the low tidal flats, where they settle initially, to the nurseries (spring migration) on high silty tidal flats (Armonies & Hellwig-Armonies 1992). In the following December through March, *M. balthica* (3-7 mm length, 8-11 months in age) migrate from their nurseries to the low intertidal flats and the subtidal of the Wadden Sea and North Sea (= winter migration) (Beukema & De Vlas 1989).

Migration occurs via byssus drifting, where increased drag on byssus threads decreases sinking rates (Sigurdsson *et al.* 1976; Sörlin 1988). Due to an increase in drag force by a byssus thread, the sinking rate of juvenile molluscs decreases strongly (Sigurdsson *et al.* 1976). Sinking rates for small bivalves with a byssus thread can be up to 5 times slower than those without a thread, depending on shell size and thread length (Sörlin 1988; Beukema & De Vlas 1989). For departure from the sediment surface, current velocities of 0.1 cm s^{-1} are sufficient (Lane *et al.* 1985). Sigurdsson *et al.* (1976) studied the physics of byssus drifting in more detail.

Many benefits of nursery use have previously been identified for *M. balthica* (Beukema 1993a; Chapter 4 and 5), but the costs of migration to and from the nursery have been considered in only one paper (Chapter 2); many individuals disappeared during both the spring and winter migrations. The present study examines the importance of predation on byssus drifting *M. balthica*. First, migrating 0-group *M. balthica* (2-3 months old) were investigated for the presence of a byssus thread to determine whether the spring migration is active (byssus drifting) or passive (resuspension), as some authors doubt whether the spring migration is an active process (Günther 1991;

Beukema 1993a). Secondly, stomach contents of several pelagic fishes were examined for the occurrence of *M. balthica.* Thirdly, we counted the number of *M. balthica* migrating during daylight versus darkness in the field, to examine possible avoidance of visual predators by nightly migrations. Finally, laboratory experiments with fish and crabs determined predation rates on drifting versus buried *M. balthica* in both daylight and dark conditions.

METHODS

In the present study, we considered both the spring and the winter migration of *Macoma balthica*. During the spring migration, *M. balthica*-spat is only 2-3 months old. In this paper, we call these *M. balthica* the 0-group and when we refer to the 0-group, we are referring to the spring migration. During the winter migration, from December to February of their first winter, the bivalves are 8-11 months old. These animals are called the 1-group, although they are not quite 1 year old yet.

Collection of experimental animals

Both 0- and 1-group *M. balthica* were collected on the tidal flats of the Groninger Wad (Figure 1). For 0-group *M. balthica*, the top-layer of the sediment was collected and sieved through 500 and 1000 μm mesh in the laboratory. *M. balthica* that passed through 1000 mesh but were retained on 500 μm were used in the laboratory study and were stored in aerated seawater on a flat tray with a shallow layer of sand. For 1-group *M. balthica* (3-7 mm)*,* the top layer was sieved through 1 mm mesh in the field. In the laboratory, these bivalves were sorted according to age, based on annual rings, and 1-group specimens were stored in containers with flowing, aerated seawater.
Predators for the carousel experiment were collected at a wide range of locations with different techniques. Predators for 0-group carousel experiments were collected on the tidal flats at the Groninger Wad with a pushnet, days to weeks before the experiments.
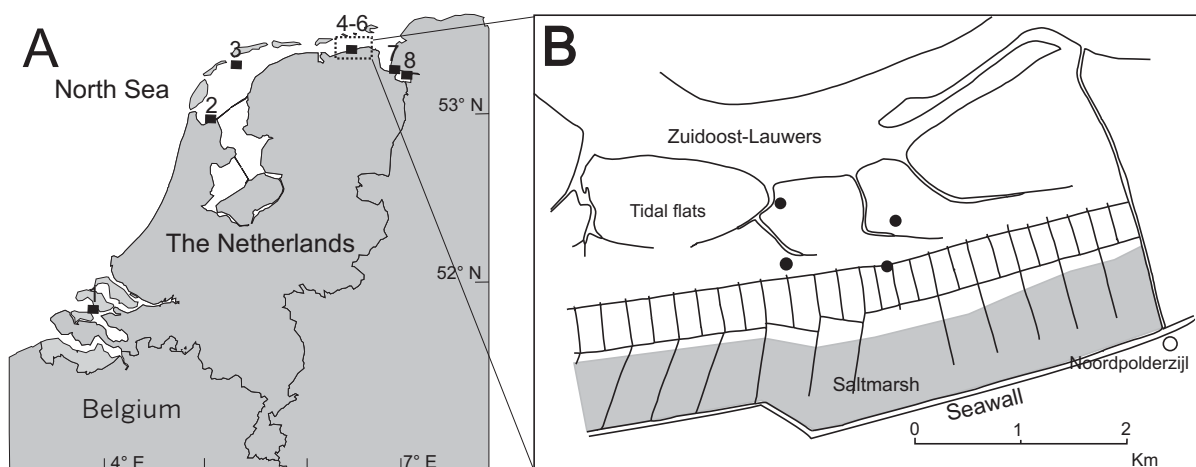

Figure 1. Map of the study area in The Netherlands. A: Locations where fish were caught for stomach content analysis (For location numbers see Table 1). B: Locations on the Groninger Wad, where plankton nets were fished.

Predators for the 1-group carousel experiments were collected at various locations in the Wadden Sea and Oosterschelde estuary (locations 1, 4-6, 7 and 8 in Table 1 and Figure 1), generally between a year and 3 months before the experiments. Predators were kept in aquaria with flowing seawater and were fed 3 times a week with *Artemia* and pieces of saithe and salmon, but not on the day before the experiments. 0-group experiments were carried out at a temperature of 15°C, animals were stored at a light/ dark cycle of 16/8 h. 1-group experiments were carried out at 10°C, animals were stored at a 12/12 h light/dark cycle. All experiments were done at a salinity of 30 (±2) psu.

Byssus drifting of 0-group *Macoma balthica*

We investigated the byssus drifting of 0-group using a vertical Perspex tube with fine mesh netting (250 μm) on the bottom (Sigurdsson *et al.* 1976). An upward current of 0.2 cm s^{-1} induced byssus drifting of *M. balthica* . Drifting animals were collected with a pipette and put in a petridish with Alcian blue solution, thereby staining mucopolysaccharides in byssus threads blue. Subsequently, individuals were examined for the presence of a byssus thread under a binocular microscope at 25 x magnification.

Predator species and stomach contents in the Wadden Sea and Oosterschelde estuary in winter

Potential fish predators on migrating *M. balthica*, were collected with different fishing gears at 6 locations in the Oosterschelde estuary and Wadden Sea, at locations where we expected migrating *M. balthica* (Figure 1A) at 8 dates in winter (Table 1). Stomach contents of pelagic fish were examined for the presence of bivalves with a binocular microscope. Demersal species were not examined, because the pelagic origin of *M. balthica* in stomachs of these species was not guaranteed.

Diurnal migration rhythms of 1-group *M. balthica* in winter

Predation pressure by visual predators is generally assumed to be stronger in during the day than at night (McIntosh & Townsend 1995; Forward, Jr. & Rittschof 2000; De Robertis *et al.* 2000).

Table 1. Locations, sampling dates and gear used for sampling pelagic fishes in estuarine areas in winter (For location map see Figure 1A).

Nr	Location	Date	Gear and mesh
1	Oosterschelde	07-Feb-00	Beamtrawl, 4 mm
2	Den Oever	29-Feb-00	Plankton net 1 m^2, 1 mm
3	Terschelling	03-Mar-00	Plankton net 1 m^2, 1 mm
4	Noordpolderzijl	09-Dec-99	Plankton net, 0.019 m^2, 2 mm
5	Noordpolderzijl	27-Jan-00	Plankton net, 0.019 m^2, 2 mm
6	Noordpolderzijl	16-Mar-01	Plankton net, 0.019 m^2, 2 mm
7	Ems	26-Mar-01	Anchor seine, 1 cm
8	Dollard	26-Mar-01	Large fykes, 1 cm

Table 2. Dates on which the number of 1-group *Macoma balthica*, migrating at day and night-time in winter was estimated. The time of low water (LW, morning 1st day, evening 1st day, morning 2nd day), sunset (evening 1st day) and sunrise (morning 2nd day) and the moon phase are given.

Start date	LW-1	LW-2	LW-3	Sunrise-1	Sunset-2	Sunrise-3	Moon phase
3 January 2001	9.36	21.50	10.30	8.49	16.27	8.48	First quarter
15 January 2001	8.37	20.46	9.20	8.41	16.44	8.41	Last quarter
25 January 2001	5.10	17.15	6.16	8.30	17.02	8.28	New moon
15 February 2001	9.26	21.46	10.16	7.52	17.43	7.52	Last quarter
15 March 2001	8.10	20.25	8.46	6.49	18.36	6.49	Last quarter

Therefore, we predict that the number of migrating bivalves would be higher at night- than during the day, either due to adaptation of the bivalves or a high predation on migrating bivalves in daytime or both processes. From January to March 2001 5 samples were collected with 4 2 mm mesh plankton nets on the tidal flats of the Groninger Wad, in the eastern Dutch Wadden Sea (Figure 1B and Table 2). The nets (diameter 19 cm) were placed 5 cm above the sediment surface and could rotate freely on a pole (see Figure 1E in Armonies 1994a). The nets fished passively on the current during immersion. Sampling dates were chosen so that low water and sunset and sunrise approximately coincided (Table 2 and Figure 2). Day-length in January was less than 8 h while the time between 2 low tides is approximately 12.4 h. The locations of the nets were submerged for approximately 6 h between 2 low tides. Therefore, with a deviation of less than 3 h between LW and sunrise or –set, there was a good separation of day and night catches (Figure 2).

Log transformed catch numbers were analysed in a 3 factor ANOVA (type I), with date, location and day/night as factors. The number of lugworms *Arenicola marina* in the catches was also counted.

Carousel

Experiments determining predation rates on migrating and buried *M. balthica* were conducted in 2 circular tanks or carousels (Figure 3). Carousel A (Figure 3A) was already in use for migration studies in 1973 (Creutzberg *et al*. 1978); carousel B (Figure
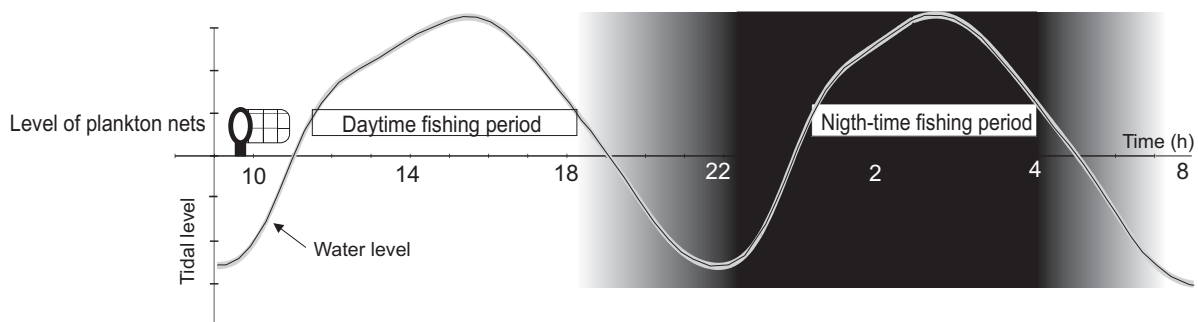

Figure 2. Set-up of the day-night migration sampling in the field, example of a day with a 14 h night. Water level, day and night, and level of the plankton net together determine the day and night fishing period. In this example, LW and sunset/rise are not perfectly synchronised as on all data in Table 3; there is still a good separation of fishing in light and darkness.

Table 3. Carousel experiments. Predator species, number and approximate length, carousel type, duration, *Macoma* number and age, light and replication are given.

Predator species & number	Length (cm)	Carousel	Duration (min)	*Macoma* age	# *Macoma* start	Replication			
						Light Current	Light No current	Dark Current	Dark No current
None		A	120	0	500	6	6	0	0
10 *Pomatoschistus microps*	4	B	120	0	500	6	6	0	0
10 *Pleuronectes platessa*	3	B	120	0	500	6	5	4	4
None		B	150	1	150	4	3	0	0
2 *Carcinus maenas*	4	A	80	1	150	7	7	0	0
2 *Merlangius merlangus*	15	B	150	1	150	3	3	0	0
2 *Pleuronectes platessa*	10	B	150	1	150	4	4	0	0
4 *Platichthys flesus*	10	A	150	1	150	4	5	0	0
2 *Platichthys flesus*	10	B	150	1	150	6	8	5	5

3B) (De Jonge & Van den Bergs 1987), was an improvement of carousel A (Venema & Creutzberg 1973). In the carousel, a water current was generated by paddles in the inner cylinder (A) or by 2 concentric cylinders moving with the same angular velocity (B). Both systems were driven by an electric motor with adjustable rotational velocity. The advantage of system B over A is that a laminar water flow is generated at low angular velocities. On the bottom of both systems, there was a 3 cm thick layer of sediment with a grain size smaller than 0.5 mm. Experiments were carried out in the period that migration did occur in the field. Therefore, 0-group migration experiments were carried out from May to July and 1-group migration experiments were done between December and April.

Before an experiment, *M. balthica* (500 0-group or 150 1-group *M. balthica*) were released into a carousel and allowed to bury for 30 minutes. We checked whether they had buried for the 1-group, for 0-group animals this was not possible because individuals were too small to detect on sand with the naked eye. Predators were then added to the carousel. In 'migration' experiments, a current of 5-8 cm s^{-1} was generated that gave *M. balthica* the opportunity to migrate through the water column. Visual observation confirmed that at least some *M. balthica* did migrate in all these experiments. In 'control' experiments, no current was generated; therefore *M. balthica* could not migrate and remained buried.

At the end of the experiment (after 80-150 min, see Table 3) the current was stopped and predators were removed from the carousel with a dip-net. The sediment was passed through a 0.5 (0-group) or 1.0 mm sieve (1-group) to extract *M. balthica* and the number of surviving *M. balthica* (relative to the initial number) were counted. In the analysis, we used the number of disappeared or eaten *M. balthica*. As some bivalves were lost in control experiments without predators (for numbers see Results), the number of disappearing animals was not always exactly the number of 'eaten' *M. balthica*.

Most experiments were done during daylight hours in the light, but we also examined the interaction of darkness and current on the number of eaten *M. balthica* for both the

A

To motor

Waterlevel

Paddles

Sediment

Perspex tank wall

B

65 cm

40 cm

Waterlevel

Perspex cilinders

Sediment

Perspex tank wall

To motor
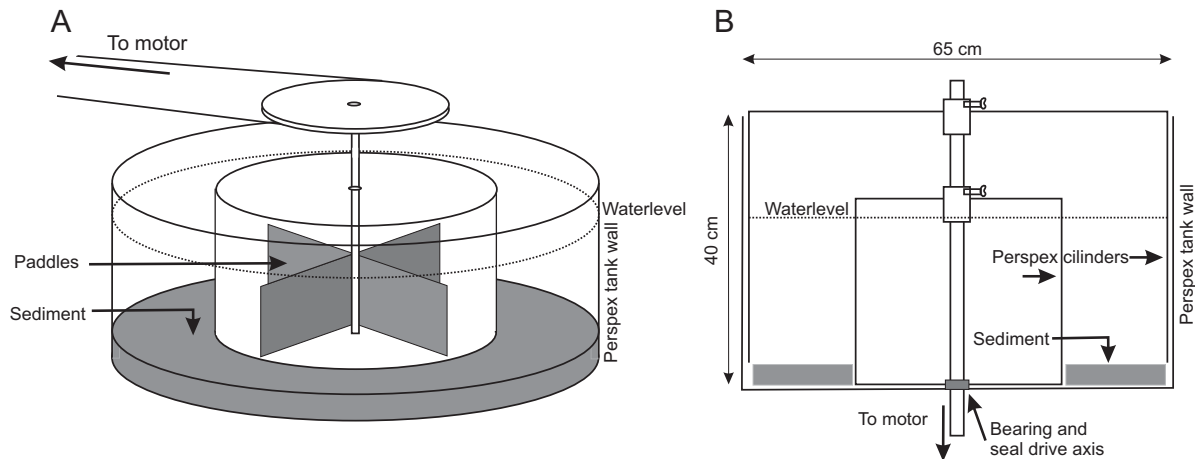
Bearing and
seal drive axis

Figure 3. The carousel as used in laboratory migration experiments. A: Carousel A, redrawn and modified from Creutzberg (1961). B: Carousel B, redrawn and modified from De Jonge & Van den Bergs (1987).

0- and 1-group. Experiments in darkness were carried out in daytime under a black sheet in a dark laboratory with plaice and flounder as predators. In this way, we separated the effect of the rhythm of predators from light conditions, which allowed more precise conclusions on the effect of light.

In addition to the experiments in Table 3, we carried out predation experiments with 1-group *M. balthica* and the fishes common dragonet *Callionymus lyra,* seabass *Dicentrarchus labrax*, goby *Pomatoschistus microps*, stickleback *Gasterosteus aculeatus* and butterfish *Pholis gunnellus.*

In 0-group experiments, individual predators were never used in an experiment more than once, for 1-group experiments, the number of available predators was limited and therefore the same predators were used in every second experiment.

Carousel experiments were analysed in a 2-factor ANOVA, with current and predator or light-condition as factors. The factor 'predator' also included 'no predator'. Data were log-transformed when variances were not homogeneous.

RESULTS

Byssus drifting of 0-group *Macoma balthica*

A byssus thread was observed on many of the migrating 0-group *M. balthica* (Figure 4). In a petridish, the byssus thread was approximately 2 cm in length, whereas in the vertical tube, is was possible to pick up the byssus drifting animals up to 10 cm above the shell. Thus, the length of the byssus thread under more natural circumstances was much longer.
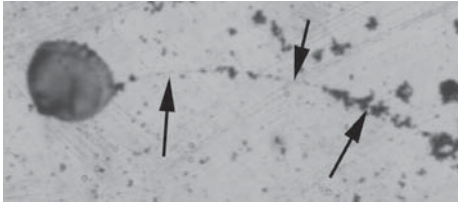
Figure 4. Photograph of a 0-group *Macoma balthica* (approximately 1 mm length) in a petridish, shortly after byssus drifting in a water current, showing a byssus thread. The byssus was coloured with Alcian blue and is indicated with arrows. Particles in the picture are Alcian blue not soluted.

Pelagic fish in estuarine areas in winter

Because different fishing methods were used at every location (see Figure 1), no quantitative data about pelagic fish abundance are given. Herring *Clupea harengus* (location 1 and 7, n=20 stomachs), sprat *Sprattus sprattus* (location 1, 2, 3, 4, 5 and 7, n=58 stomachs), three-spined stickleback *Gasterosteus aculeatus* (location 2, 4 and 8, n=20 stomachs) and smelt *Osmerus eperlanus* (location 2, 4, 5, 7 and 8, n=90 stomachs) were common at all locations. Seabass *Dicentrarchus labrax*, cod *Gadus morhua*, whiting *Merlangius merlangus* and bib *Trisopterus luscus* were common on only 1 of the locations, while many other species were caught in low numbers. No *M. balthica* were detected in the stomachs of pelagic fish, despite the presence of 4 small *Mytilus edulis* (<1mm) and various polychaetes in the stomachs of S*prattus sprattus* (mussel and Phyllodocidae) and *Osmerus* (*Nereis*).

Diurnal migration rhythms of 1-group *Macoma balthica*

The number of migrating *M. balthica* caught in the plankton nets varied by an order-of-magnitude between the sampling dates (Figure 5). The number of migrating *M. balthica* was significantly higher at night- than in daytime, although the effect of location and the interaction between date and day-night effect was also significant (Table 4).

The number of migrating lugworms *Arenicola marina* in winter was higher at night- (0.65 net^{-1}) than in daytime (0.05 net^{-1}). Due to the high number of zero-catches (19 out of 20 in daytime), no statistical test was feasible.

Carousel experiments

Approximately 20% of the *M. balthica* in the experiments with current were byssus drifting.

Control experiments with 0-group *M. balthica* and without predators experienced 5% loss due to handling, irrespective of the presence of current (Figure 6). In the presence of the plaice *Pleuronectes platessa* and the goby *Pomatoschistus microps*, *M. balthica* mortality was significantly higher when migrating (current) than when they stayed buried (no current, Figure 6, Table 5). The predator (presence & species) x current interaction was significant, because current had no effect on the number of surviving *M. balthica* without predators.

More 0-group *M. balthica* were consumed by *Pleuronectes* in daylight with current than in darkness with or without current (Figure 7, Table 6). *Pleuronectes* was inactive during darkness, as the number of *M. balthica* consumed in darkness was less than the number disappearing without predators (compare with Figure 6). It should be noted that

'light' data in Figure 7 are equal to the *Pleuronectes*-data in Figure 6.

Control experiments with 1-group *M. balthica* and without predators experienced a loss of ca. 3 *M. balthica* due to handling, irrespective of the presence of current (Figure 8). The shore crab *Carcinus maenas*, whiting *Merlangius merlangus* and flounder *Platichthys flesus* and plaice *Pleuronectes platessa* consumed more 1-group *M. balthica* that were migrating than that were buried (Figure 8). The 2-factor ANOVA in Table 7 shows that the effect of both predator and current was significant and that the interaction between these was significant, because there was no effect of current in the absence of predators.
Several fish species (*Callionymus lyra, Dicentrarchus labrax*, *Pomatoschistus microps*, *Gasterosteus aculeatus* and *Pholis gunnellus*) did not consume 1-group *M. balthica* in our experiments, either with or without current.

Carousel experiments in light and dark with flounder show that the effect of migration on the predation risks also depended on light conditions for 1-group *M. balthica* (Figure 9). The number of eaten *M. balthica* in light was significantly higher with than without current, while this difference did not exist in dark. Nevertheless, predation in the dark without current was significantly higher than in light.

Discussion

Migration of 0-group *M. balthica* is active, as a byssus thread is secreted by the bivalve and is used as a 'dragline' for transport. This knowledge is important, because if they were transported to the high intertidal passively, living there would not necessarily be beneficial for juvenile *M. balthica*. On the contrary, we can expect nursery use to benefit bivalves if they migrate there actively. The migration, however, incurs a potential cost, as *M. balthica* is more susceptible to predation under daylight conditions. Several potential predators are present in estuarine areas during the winter migration. Thus, this study provides a mechanism that may contribute to explaining higher mortality rates of bivalves and other infaunal organisms during migrations.

As we found that *M. balthica* primarily migrates at night, it is not surprising that we did not find *M. balthica* in the stomachs of pelagic fish that we caught in daytime in the field. Unfortunately, therefore the mechanism cannot be validated. Nevertheless, literature reports suggest fish predation on migrating infauna. The pelagic fish *Osmerus eperlanus,* which is unable to dig out infaunal polychaetes, ate lugworms *Arenicola marina*, apparently during migration (Kühl 1970). Verrill (1873) cf Dean (1978) observed fish predation on migrating polychaete *Nereis virens*. Hostens and Mees (1999) observed a proportion of 1% benthic polychaetes in stomachs of herring *Clupea harengus*. Another striking example of the risks of migration comes from the large amount of the amphipod *Corophium volutator* eaten by pelagic fish, like herring and sprat in the Ems estuary (Stam 1981). These amphipods are not available as food

Figure 5. Number of migrating *Macoma balthica* (+SD) on the tidal flats of the Groninger Wad in winter 2001, at day- and night-time.
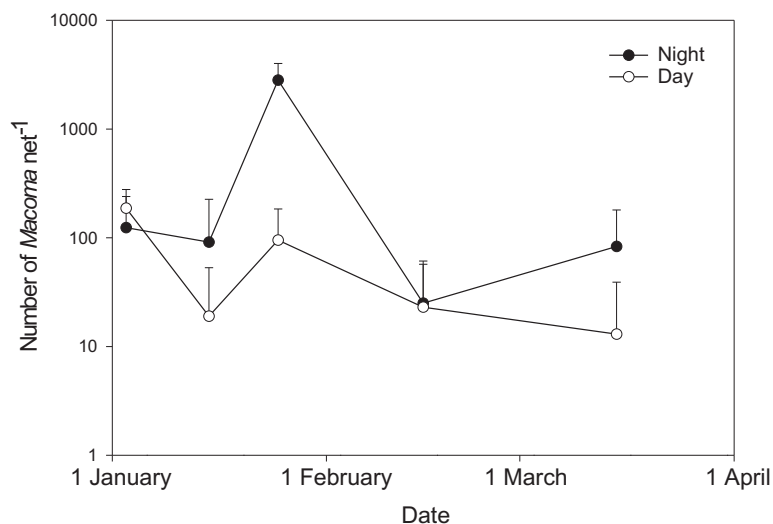

Figure 6. Number of 0-group *Macoma* eaten (+SD) in carousel experiments in light, with and without current, with three types of predators.
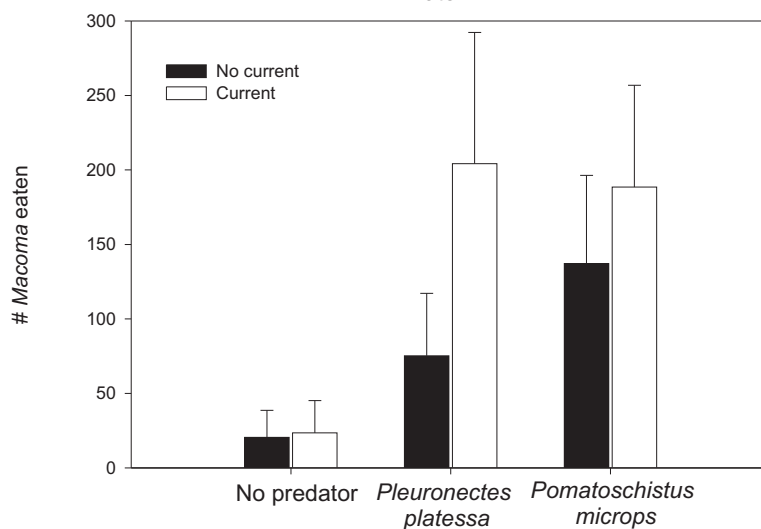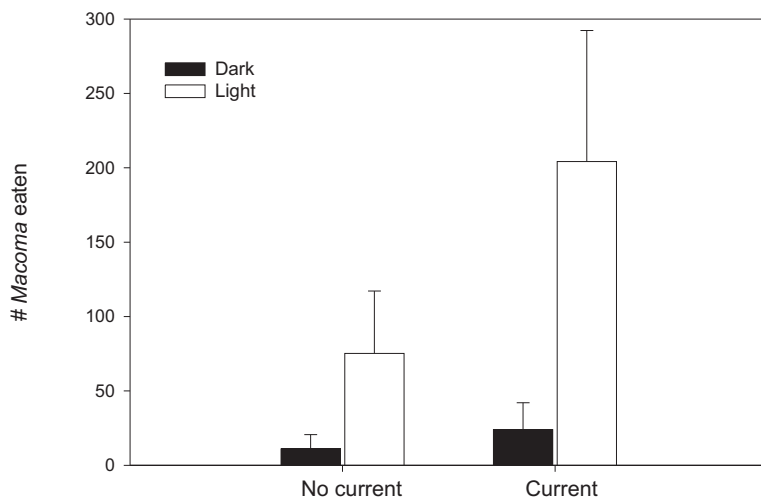

Figure 7. Number of 0-group *Macoma balthica* eaten (+SD) by juvenile *Pleuronectes platessa* in carousel experiments in light and dark, with and without current.

when they are buried in the sediment, but were probably eaten during the pelagic long distance migrations (several km's) they undertake (Essink *et al.* 1989), even though these migrations are largely nocturnal (Lawrie & Raffaelli 1998). These records of infaunal organisms in stomachs of pelagic fishes are an indication that predation on migrating infauna exists. However, recordings of low numbers of bivalves and polychaetes were probably often reported in the category 'other' and were therefore missed in our literature search, because these items are quantitatively unimportant in

Table 4. Three-factor ANOVA (Type I error) of the log-transformed number of *Macoma* net^{-1} at day- and night-time in winter.

Source	Df	Mean square	F-Ratio	P-Value
Date	4	28.5	31.12	0.0000
Location	3	20.3	22.20	0.0000
Day/night	1	20.0	21.93	0.0001
Date x day/night	4	5.5	6.03	0.0013
Residual	27	0.9		

Table 5. Two-factor ANOVA of the number of eaten 0-group *Macoma balthica* in carousel experiments (current, no current) in light with different predators (none, plaice, gobies).

Source	Df	Mean square	F-Ratio	P-Value
Predator	2	67393	22.76	0.0000
Current	1	31510	10.64	0.0029
Predator x current	2	10902	3.68	0.0381
Residual	28	2961		
Total	33			

Table 6. Two-factor ANOVA of the number of eaten 0-group *Macoma balthica* in carousel experiments (current, no current) in dark and light under predation of plaice.

Source	Df	Mean square	F-Ratio	P-Value
Light	1	66368	23.65	0.0003
Current	1	22404	7.98	0.0135
Light x current	1	14951	5.33	0.0368
Residual	14	2806		
Total	17			

Table 7. Two-factor ANOVA of the number of eaten 1-group *Macoma balthica* (log-transformed) in carousel experiments (current, no current) in light with different predators (none, shore crab, plaice, flounder, whiting).

Source	Df	Mean square	F-Ratio	P-Value
Predator	4	1.61	17.83	0.0000
Current	1	0.82	9.10	0.0043
Predator x current	4	0.27	3.05	0.0268
Residual	43	0.09		
Total	52			

the diet of pelagic fishes. Some other studies show an interaction between leaving burrows and predation for infaunal organisms. Disturbance of the amphipod *Corophium volutator* by the lugworm *Arenicola marina* made the amphipod more vulnerable to shrimp predation (Flach & De Bruin 1994). Physical disturbance of the sediment made *Macoma balthica* more vulnerable to predation by the epibenthic isopod *Saduria entomon* (Bonsdorff *et al*. 1995). These observations can be explained by the same mechanism of increased predation on benthic animals that leave their burrow.

Migration in the presence of pelagic and epibenthic predators is dangerous in light for both 0-group and 1-group *M. balthica*, but in the dark no difference exist in predation risk incurred between migrating and staying buried in the sediment. In the field, most 1-group *M. balthica* did indeed migrate during darkness as was also found by Armonies (1992) for 0-group *M. balthica*. In laboratory experiments, Sörlin (1988) found more

Figure 8. Number of 1-group *Macoma* eaten (+SD) in carousel experiments in light, with and without current, with five types of predators.
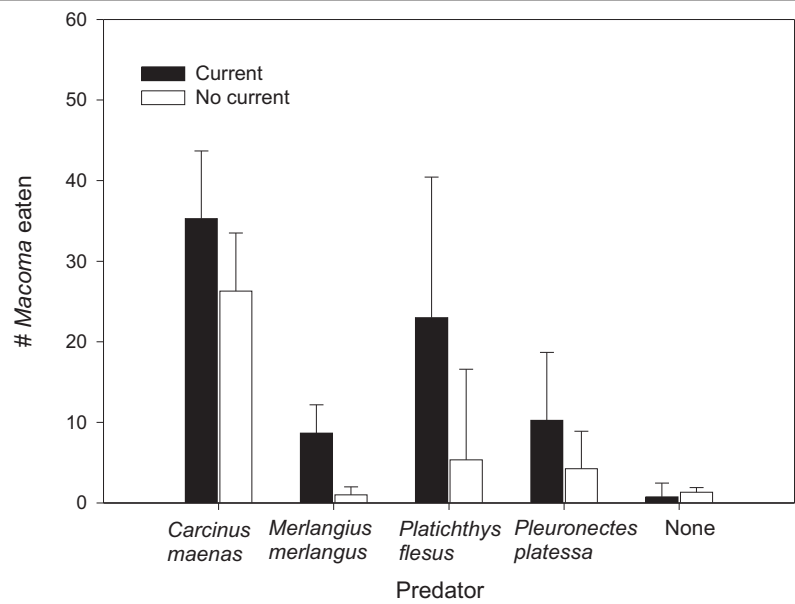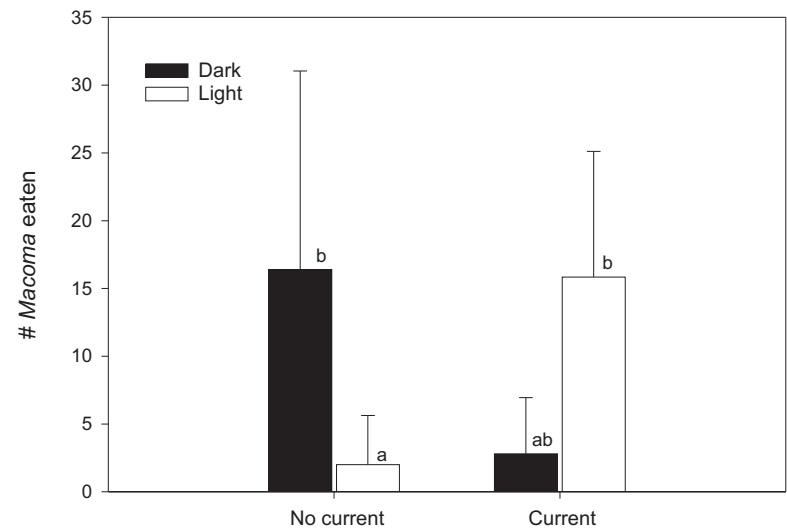

Figure 9. Predation of flounder *Platichthys flesus* on 1-group *Macoma balthica* (+SD) at day and night time, with and without current. Letters (a, b) indicate common groups (Student Newman Keuls-test).

migration activity of 1-group *M. balthica* at night (without predators). Therefore, results indicating that *M. balthica* migrate at night are probably primarily due to the behaviour of *M. balthica* and not to an increase of consumption of *M. balthica* by fish during the daytime. These nightly migrations may be an adaptation to visual predation on pelagic *M. balthica* and can be interpreted as an indication that predation on migrating *M. balthica* plays a role.

Our conclusions are not biased by the absence of dark controls because the chance of losing animals due to handling is probably larger when animals are migrating and we expect higher migration rates in the dark, at the same time predation is expected to in the dark.

Dark-experiments were conducted in daytime, therefore the difference in predation between light and dark really represents the difference in visibility and not diurnal rhythms of the predators or *M. balthica*. The diurnal rhythms of juvenile flatfish in field studies are not clear, but some studies have found high activity in the daytime, while others have detected mostly nocturnal activity (Nash *et al.* 1994).

Nocturnal migrations pose the question how *M. balthica* distinguishes between day and

night. Although not reported for *M. balthica*, photoreceptors (and even eyes) are a common feature in bivalves (Barber & Land 1967; Nilsson 1994). Therefore, is it likely that these *M. balthica* can detect light in some way or another.

We consider light to be factor affecting the migration risk for *M. balthica.* Turbidity may also be an important factor, but only if the water is very turbid, because prey the size of *M. balthica* are only visible within a very limited field anyway. On the Groninger Wad, we often observed visibilities of only a few cm in winter, although visibility on calm days in summer can be up to 1 m. We expect that a high turbidity has the same effect on visual predation by fish as the absence of light. Some studies found that turbid water reduced consumption rates of estuarine and salmonid fish predators (Hecht & Van Der Lingen 1992; Benfield & Minello 1996; Gregory & Levings 1998), while others found that the predation patterns changed but that the consumption rates stayed the same (Gregory & Levings 1996; Abrahams & Kattenfeld 1997). If turbidity indeed decreases predation rates on migrating *M. balthica,* a smaller risk and a smaller day-night difference of predation for *M. balthica* is expected.

A simple calculation of the energetics of juvenile *M. balthica* shows that the costs of producing a byssus thread are unimportant as compared to the migration risks. A 5 mm *M. balthica* has an AFDW of 1.4 mg and a caloric content of 8 J (Beukema 1997). Even if we assume that a byssus thread of 4 µm thickness and 10 cm length consists entirely of carbohydrates (and no water) with a caloric content of 17.1 J mg^{-1}, the energy content of the byssus thread (0.0000001 J) is negligible compared to the whole animal. Therefore, energetic costs do not seem to be an important factor that the *M. balthica* has to weigh against benefits resulting from migrations.

This study sheds some light onto the neglected processes of benthos migrations. Concluding, enhanced predation on migrating *M. balthica* could be a mechanism that explains high disappearance rates during the migration periods (Chapter 2). The nightly migrations of *Macoma balthica* may be an adaptation to avoid predation by diurnal fish predators. Other mechanisms that may explain differences in disappearance have not been described so far. A likely process is that bivalves migrate to sink populations, where they do not survive. For example, *M. balthica* does occur in fast flowing tidal channels (Chapter 2), but a low food supply and high sediment mobility may cause a quick death on these locations. A single observation of large numbers of dead 1-group on the saltmarsh vegetation in winter shows that migration to wrong locations can cause death.

opportunity to collect fishes during their cruises. Comments of 2 anonymous reviewers and Jim Coyer (University of Groningen) improved an earlier version of the manuscript.

CHAPTER 4

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

J.G. Hiddink, S.A.E. Marijnissen, K. Troost & W.J. Wolff

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 *M. balthica* 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 *M. balthica* remains. These predators selectively preyed on small 0-group *M. balthica*, 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 exclosure experiments (2 mm mesh). There was no effect of epibenthos exclosure on adult *M. balthica.* For 0-group *M. balthica*, densities were higher in exclosures 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 *M. balthica*. Thus, 0-group *M. balthica* 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 *M. balthica* leave the high intertidal. Concluding, the nursery use of *M. balthica*-spat in the high intertidal is probably, at least partly, an adaptation to avoid epibenthic predation.

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 & 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 & 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 1992b) and that growth is faster (Armonies & Hellwig-Armonies 1992). We studied the relation between predation and nursery use of *Macoma balthica*.

Macoma balthica is a small bivalve found in coastal areas in temperate regions (Beukema & 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, *Macoma balthica* has to undertake migrations between these locations. Juvenile *M. balthica* 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 *M. balthica* migrates again, this time back to the low intertidal and the North Sea (Beukema & De Vlas 1989; Chapter 2).

There are 3 groups of predators on *Macoma 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*. 1987b). Shorebirds generally select for relatively large prey. Oystercatchers and Knots for example do not eat *M. balthica* smaller that 10 mm (Hulscher 1982; Zwarts & Blomert 1992). Densities of shorebirds are usually in the range of 1-5 birds 10 000 m^{-2} (Van de Kam *et al*. 1999).

Another important group of predators on *M. balthica* 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 *Crangon crangon*, the crab *Carcinus 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 *Crangon crangon* is known to eat large numbers of bivalve spat (Keus 1986; Van der Veer *et al*. 1998). *Carcinus maenas* can cause large density reductions of *M. balthica* in enclosure experiments (Fernandez *et al*. 1999) and *M. balthica* is found is their stomach (Scherer & 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 & Hesthagen 1981; Jaquet & Raffaelli 1989; del Norte-Campus & Temming 1994e). We know only one study in which the effect of tidal level on mortality of *M. balthica* -spat was examined; Reise (1978) exclosed epibenthic predators at 4 tidal levels 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. A 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 *Macoma 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 *Macoma balthica*. Because high tidal flats are exposed for a long period we expect a high predation pressure of birds on *M. balthica* 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 *M. balthica* 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 *M. balthica* is higher on the high tidal flats due to predation by birds, which select for relatively large prey.
Together, these 2 groups of predators may force *M. balthica* to live in the high intertidal as a juvenile and in the low intertidal as an adult.

Methods

This study was carried out between March and November in the years 1998, 1999 and 2000. What we call 0-group *M. balthica* 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 to 5 mm. 1+ group *M. balthica* 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.

Set-up of the study

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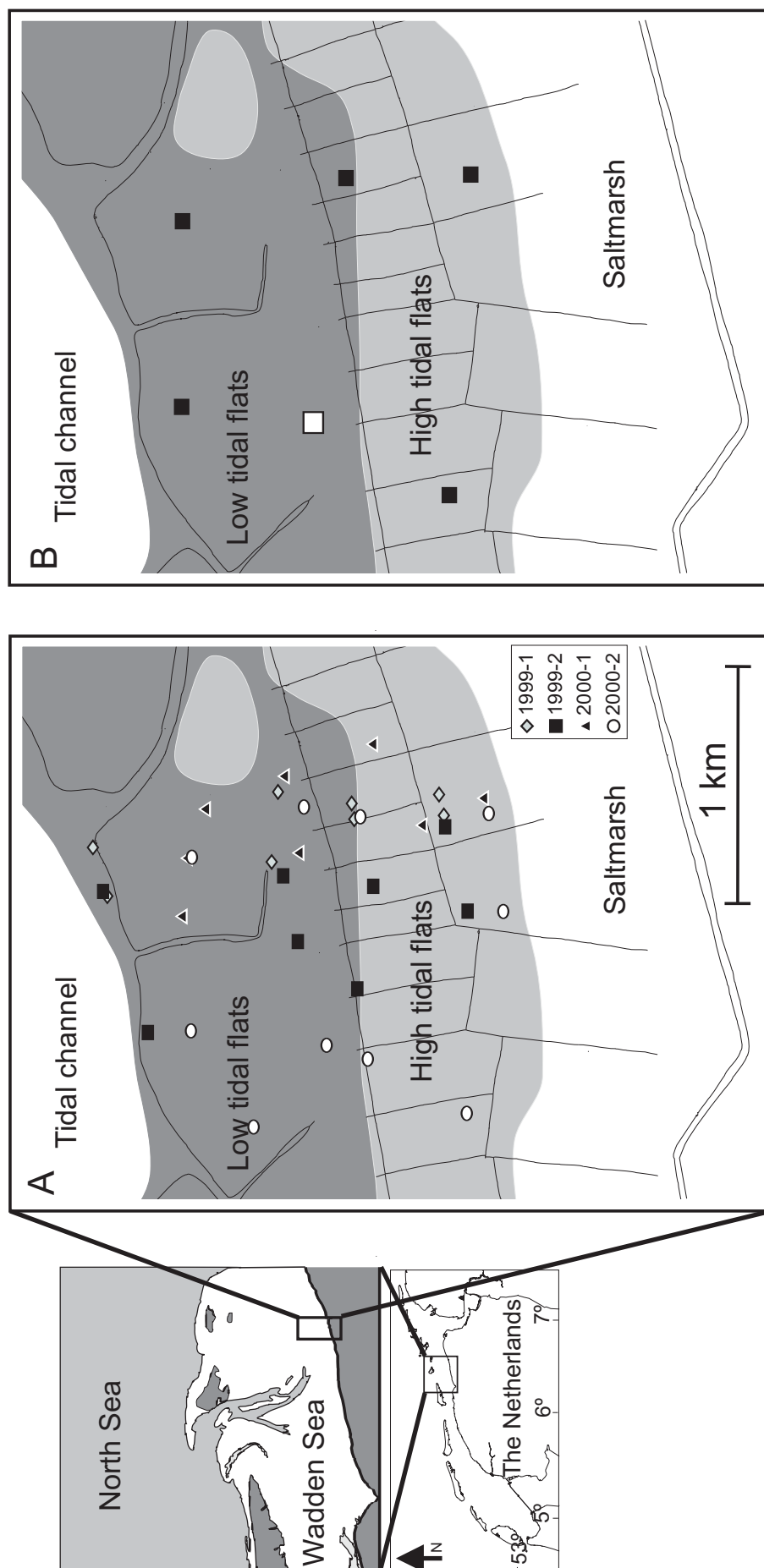
Figure 1. Map of the study area in the Dutch Wadden Sea. (A) Locations of exclosures in the different series on the Groninger Wad tidal flats. Periods of the different series are presented in Table 2. (B) Locations of the transplantation experiments. Solid squares are the locations were treatments were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

- 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+ *M. balthica*. The exclosure experiments also included transplantations of 0-group *M. balthica* to locations where they did not naturally occur.

Study site

Our study was carried out at the Groninger Wad in the eastern Dutch Wadden Sea (6° 31' E, 53° 27' N) (Figure 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.

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 4x4 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 (Figure 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 passively during 2 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 4 easterly locations of series 1999-2 (Figure 1A).

The catch was preserved in the field in 4% formalin and sorted in the lab. 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 2 groups (the 0-group from 0-3 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 (4x4 mm), a 2x2 mm mesh was attached, leaving 5 cm between the 2 nets. After fishing the size of the animals in the 2 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.

Stomach contents of predators

The stomachs of *Carcinus* juveniles and adults*, Crangon, Pomatoschistus 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 10x magnification. In each stomach, the number of recognisable *M. balthica* shell fragments was counted. As most *M. balthica* 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 *M. balthica* >4 mm. We made a new calibration line of hinge + top length on shell length with *M. balthica* <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.

Size selection by epibenthic predators: laboratory experiments

Size selection by *Carcinus, Crangon, Pomatoschistus microps, Pleuronectes* and *Platichthys* was studied in the laboratory. All experiments were conducted in containers of 15x10x13 (l x w x h) cm, with a 4-cm sand layer (grain size <300 µm) on the bottom and a 0.5-mm mesh lid. *M. balthica* 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

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
Carcinus maenas	1	4, 6, 8, 12, 16, 20	6	9 am to 3 pm
Crangon crangon	4	15, 20, 25	24	9 am to 9 am
Pleuronectes platessa	1	45	24	9 am to 9 am
Platichthys flesus	1	75	24	9 am to 9 am
Pomatoschistus microps	1	45	24	9 am to 9 am

experiments, crabs with a carapace width >15 mm did eat *M. balthica* >10 mm. Therefore, in experiments with *Carcinus maenas*, 3 larger size classes were also included: 10-12 mm, 12-14 mm 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). 5 *M. balthica* were assigned to each size class. The total number of *M. balthica* in each experiment was therefore 100 (or 115 in experiments with crabs). The selected *M. balthica* were left to bury in the container for 6 hours. 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 5 times.
After the experiment, the sediment was sieved over 300 µm. All retrieved *M. balthica* 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 *M. balthica* was lost and never more *M. balthica* were retrieved than were added.
The selectivity was estimated by the Electivity index E'. E' is calculated per size class as:

$$E' = \frac{c_i - o_i}{c_i + o_i}$$

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 5 replicas, as in Stamhuis *et al.* (1998).

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 *Macoma balthica* at the low and high tidal flats. The first 'exclosure' experiment examined the effect of epibenthos such as shrimps, crabs and fish and shorebirds in 1x1m plots (Figure 2A). The second 'transplantation'-experiment aimed at epibenthic predation on 0-group *M. balthica* at locations where these small *M. balthica* did not occur. To enable study of growth and mortality of 0-group animals on these locations, 100 0-group *M. balthica* were transplanted to small cages at these locations (Figure 2B).

Five different treatments were applied in the exclosure experiment. Epibenthos and birds were exclosed from cages with 2 mm mesh size (Ex: exclosure, Figure 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 exclosure, allowing epibenthic predator access but otherwise mimicing 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 enclosed in the exclosure. In such cases, the cage was analysed as an epibenthic predator enclosure (En: enclosure). Birds, but not epibenthic predators, were exclosed with wires at 5 and 15 cm above the sediment surface (Bi:

Table 2. Exclosure experiments. Duration, n per treatment, distribution of the locations over high and low tidal flats and applied analyses per exclosure 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 (d)	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	

A

B

2 mm nylon mesh

Level of sediment surface

1 mm nylon mesh
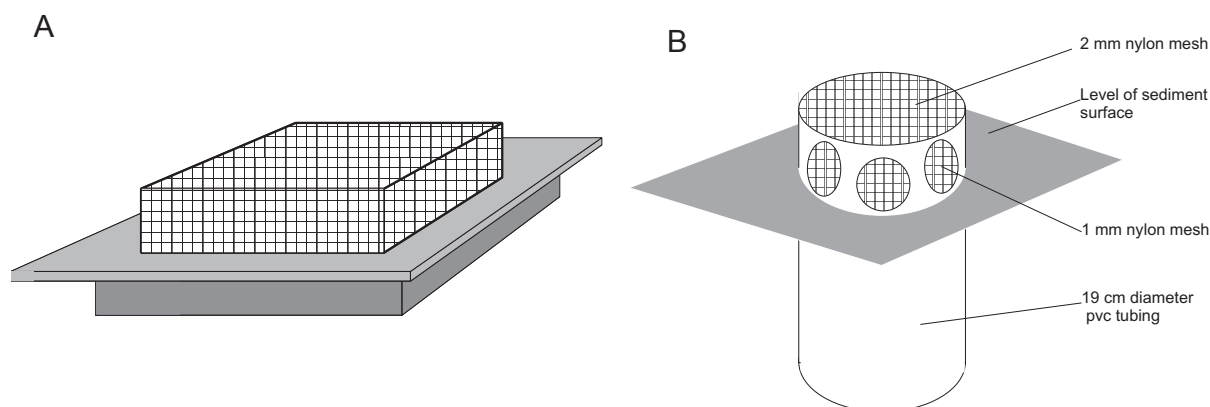
19 cm diameter pvc tubing

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

bird exclosure). The control for this plot was an untreated (but marked) plot (Re: reference).

Enclosure (En) of crabs could occur by 2 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 had only settled 2 weeks before, were very small and probably consumed only small amounts of the large (3-4 mm) *M. balthica* -spat (see the results of the size selection experiment). Therefore, we consider low numbers of juvenile crabs (less than an 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 *M. balthica* was 200 to 10 000 m^{-2} (Chapter 2) and epibenthic predators reached densities up to 10 m^{-2}, the size of the plots was chosen as 1x1 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 *M. balthica* . 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 maintainance of cages difficult, only 1 experiment with the less vulnerable Bi and Re treatment was carried out in winter (series 2000-0).

The 'exclosure' experiments were carried out in 5 consecutive series, 4 between March and October and 1 in winter only examining bird predation on 1+ *M. balthica* (Table 2). Each time, we placed all treatments at 8-10 locations (Figure 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).

For the 1999-1 series, the locations were chosen in duplicate at 4 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 4 tidal levels. The locations for series 2000-1 and 2000-2 were chosen randomly within the map area of Figure 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 *M. balthica* 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 cm^2 from each plot; these samples were pooled in the field and sieved over 1 mm. For series 1999-1 and 2000-1, 1 core of 43 cm^2 was taken to sample spat <1 mm in the centre of the plot. This sample was sieved in the lab 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 *M. balthica* 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 *M. balthica* were added to small Ex and Co-treatments with 1 mm mesh (Figure 2B) (no En and Bi treatment were applied). Further, 100 *M. balthica* were added to a further untreated Re plot and an untouched plot (Un) was sampled at the end of the experiments. All plots had an area of 283 cm^2. Before adding the bivalves to the plots, the original 0-group *M. balthica* 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 *M. balthica* that were transplanted into the plots, were collected at a common source location at mid tide level, 1 day earlier (Figure 1B). They were stored overnight in 4 cm of sediment in an aquarium with running water. 2 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 6 locations (Figure 1B). The second experiment started on 27 September 2000 and ended on 8 November 2000 (42 days). The animals were transplanted to 5 different locations (Figure 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 exclosure experiment samples, but only the 0-group and not older shellfish were examined.

Statistical analysis of caging experiments

Densities and lengths in the exclosure and transplantation experiments were examined in a 3-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.

RESULTS

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 constants (King 1995). No shrimp <10 mm were caught, while no shrimps longer
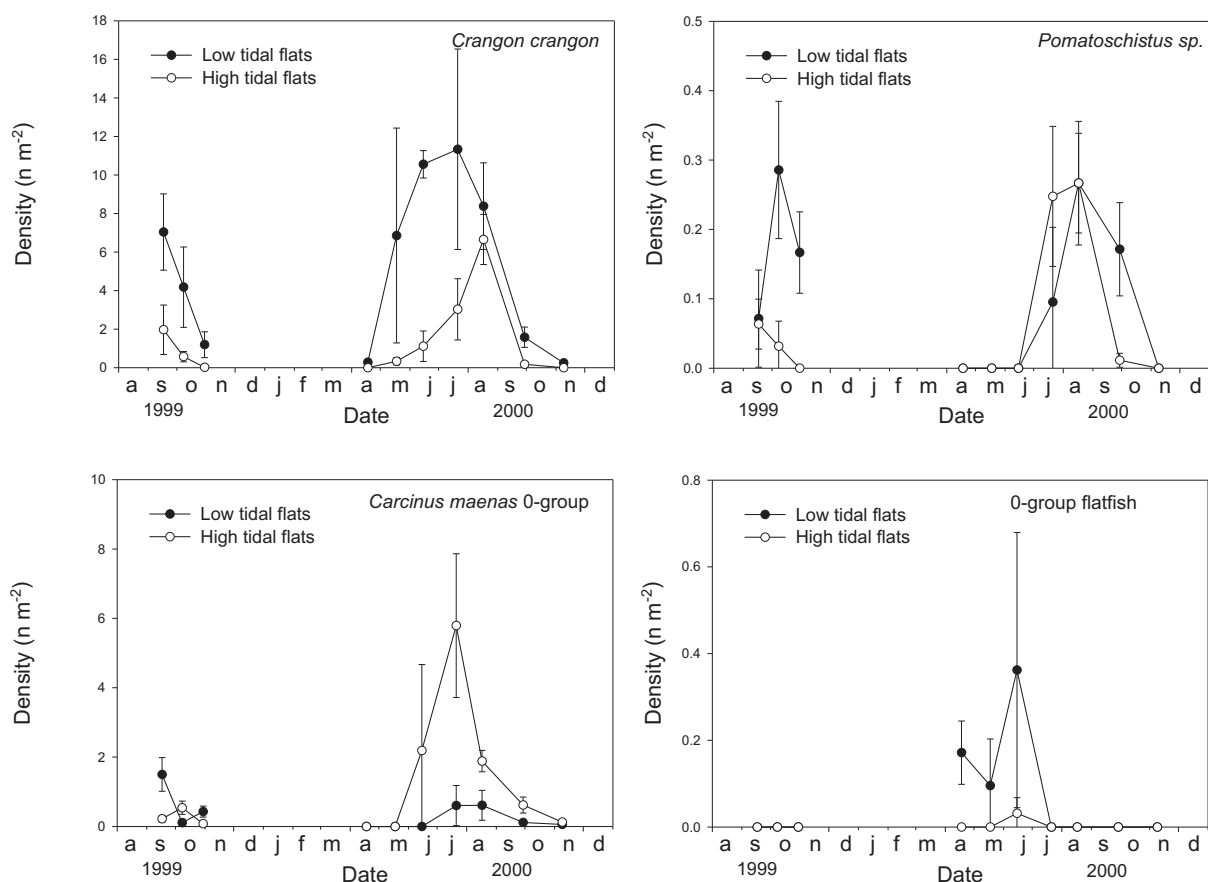

Figure 3. Estimates of densities of 4 predators (±95% confidence intervals) on low and high tidal flats of the Groninger Wad from September 1999 to November 2000. Sampling was carried out at high tide on the tidal flats with a pushnet. Notice the different scalings on the density-axis.

than 22 mm passed through the mesh (A=0.68, B=11, R^2=0.89, p = 0.000). No crabs <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 <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. Figure 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 *Pomatoschistus 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, Figure 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

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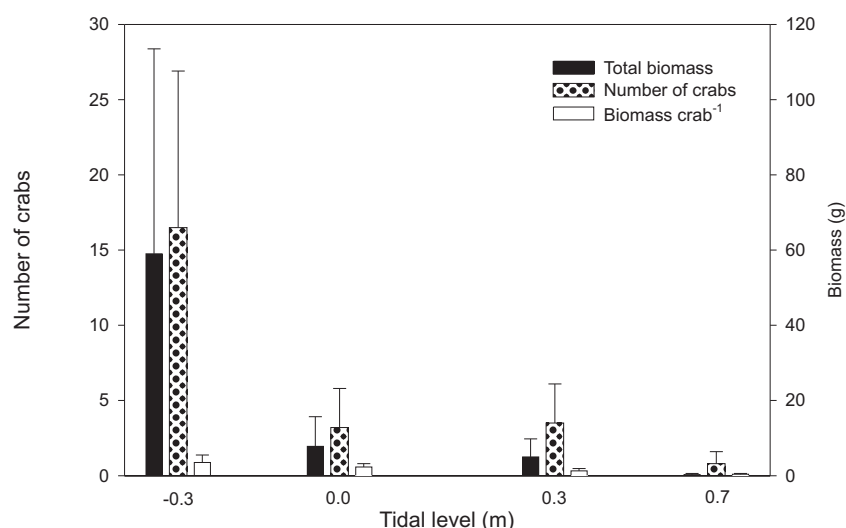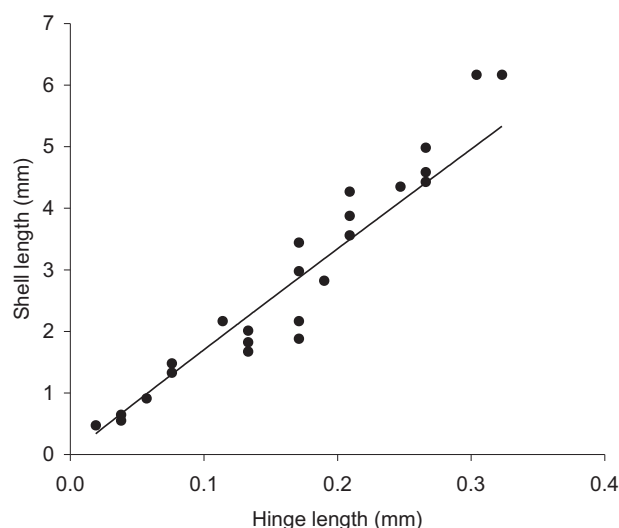

Figure 5. Calibration of shell length on hinge plus top-width for juvenile *Macoma balthica*. n = 25, R^2 = 0.93, p = 0.000.

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 5.1±2.0 mm on the high flats (t-test, p = 0.000). *Crangon* on the low tidal flats measured 25.2±4.7 mm and 18.8±9.1 mm on the high flats (t-test, p = 0.000).

Adult *Carcinus* were most abundant in both numbers and biomass in the lowest pitfall (–0.3 m above MTL) (Figure 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 & Koks 1999). Their spatial distribution was not recorded.

Stomach contents of epibenthic predators

The number of animals of which the stomach content was examined per month and the number of *M. balthica* 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 *M. balthica*-remains were found in fish stomachs. In total, 38 fragments of *M. balthica* shells were found in 338 examined stomachs. In 0-group *Carcinus* on average 0.20 *M. balthica* was found. Both *Crangon* and adult *Carcinus* stomachs contained on average 0.10 *M. balthica* per stomach.

Calibration showed that there is a significant relation between shell-length and hinge + top length of juvenile *M. balthica* (2-7 mm) (Figure 5): L=16.0 x H$^{0.97}$ in which L = shell

Table 3. Juvenile *Macoma balthica* in the stomachs of *Crangon crangon* and *Carcinus maenas* (juveniles and adults) on the tidal flats of the Groninger Wad. The average number *of M. balthica* per stomach is given.

Date	*Crangon*		*Carcinus* 0-group		*Carcinus* adult	
	n	*Macoma* predator^{-1}	n	*Macoma* predator^{-1}	n	*Macoma* 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	
N	222	0.10	68	0.20	15	0.10

Figure 6. Length-frequency distribution of *Macoma balthica* shell length on the tidal flats of the Groninger Wad on 7 July 1999 (white bars) and as found in stomach contents of *Crangon 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*.
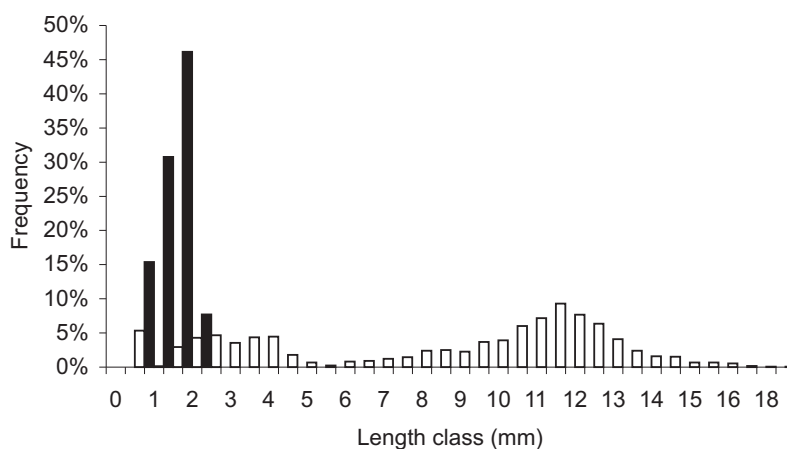
length and H is hinge width (n=25, R^2=0.93, p = 0.000). We found 13 measurable hinges in the stomachs of *Crangon* and only 2 in 0-group *Carcinus* (both 1.9 mm shell length). All eaten *M. balthica* were <2.5 mm, while length of the whole population on 7 July 1999 ranged from 0.5 to 17 mm (Figure 6). Stomachs of flatfish and gobies contained no bivalve shells, but did contain up to 50 1-mm pieces of bivalve siphons.

Figure 7. Length-frequency distribution of the average number of *Macoma balthica* eaten per experiment by the crab *Carcinus maenas* (A), *Crangon crangon* (B) and by juvenile flatfish and the goby *Pomatoschistus microps* (C) in laboratory size-selection experiments. Five shellfish were offered per size class, to 6 size-classes of crabs, 3 size classes of shrimps and 3 fish species (for predator sizes and fish species see legends in graph).
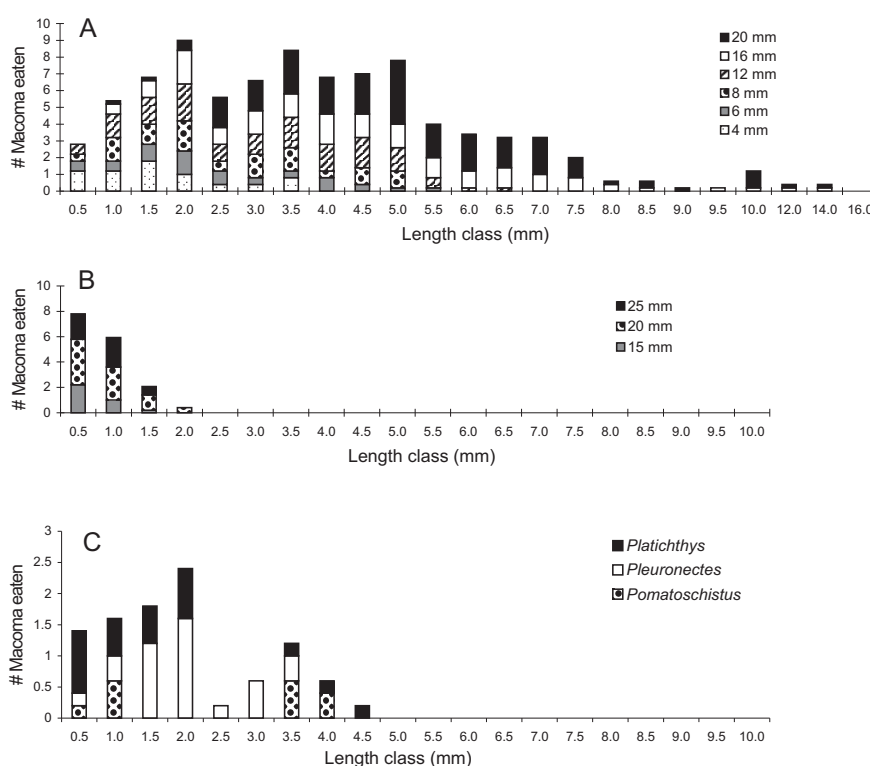
Size selection by epibenthic predators: laboratory experiments

Carcinus mainly consumed *M. balthica* <5 mm, but eaten *M. balthica* ranged from 0.5 to 14 mm in length (Figure 7A). The size class most consumed in the crab experiments was 2.0 mm. The largest *M. balthica* 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 *M. balthica*-size class most consumed and the carapace width of the crab was: *M. balthica*-size = 0.21x 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 *M. balthica* and 20 mm crabs positively selected for 5 mm *M. balthica* (Table 4). Significantly negative E'-values, indicating rejection, were found for large *M. balthica* for all sizes of crabs and for the smallest *M. balthica* in 16 and 20 mm wide crabs. *Crangon* only ate *M. balthica* <2.5 mm (Figure 7B). The smallest size class (<0.5 mm) was most consumed. 15 and 20-mm shrimp showed a significant positive selection for *M. balthica* <1.5 mm (Table 4). All fish species consumed only few shellfish in the experiments and only ate *M. balthica* <5 mm.

Growth of epibenthic predators in relation to growth of 0-group *M. balthica* in the field

Figure 8 shows the growth of crabs and *M. balthica* in the field from June to November. *M. balthica* size was estimated from Re treatments in the exclosure studies and from a survey of 57 stations on the Groninger Wad in 1998 (Chapter 2). From the actual size of 0-group *Carcinus* from the field and the relation between crab size and preferred *M.*

Figure 8. Size of 0-group *Carcinus maenas* (2000) and 0-group *Macoma balthica* (1998, 1999 & 2000). The size of *M. balthica* 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 *M. balthica* length was approximately equal, while later *M. balthica* quickly outgrew the preference of the crabs.
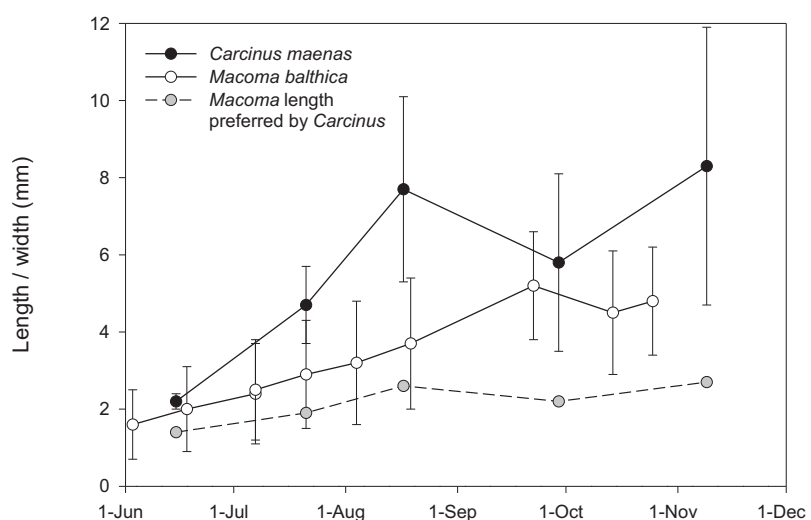
Table 4. Size selection by predators eating *Macoma balthica* in laboratory experiments. The Electivity index (E') per predator species per *M. balthica* length class is given. Positive E'-values indicate a preference, negative E'-values indicate rejection. Bold E'-values are significantly different from zero (t-test, p<0.05).

Species	Carcinus	Carcinus	Carcinus	Carcinus	Carcinus	Carcinus	Crangon	Crangon	Crangon	Pleuronectes	Platichthys	Pomatoschistus
	4	6	8	12	16	20	15	20	25	45	75	45
Length class												
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**						

balthica size in the lab size selection experiment, we calculated the preferred size of *M. balthica* for each date for which we knew *Carcinus* size (Figure 8).

Exclosure studies

0-GROUP MACOMA BALTHICA

There was a significant effect of treatment on the density of 0-group *M. balthica* (Table 5). Density of the 0-group was very high in the Ex-treatment, while it was low in the Co and En treatment (Figure 9A). Thus, epibenthic predators consumed a lot of 0-group *M. balthica* . 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 *M. balthica* in the low intertidal than in the high intertidal. 0-group *M. balthica* was significantly larger in the high intertidal, there was no effect of treatment (Figure 9B, Table 5).

1+GROUP MACOMA BALTHICA

Density of older *M. balthica* was not affected by the treatments (Figure 9C & Table 5). There was however a significant interaction between tidal level and treatment, as the density of 1+ *M. balthica* 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 (Figure 9D, Table 5).

The average number (± SE) of large crabs *Carcinus maenas* in the treatments, at low tide, was 0 (±0) in Ex (by definition), 1.4 (±0.5) in En, 0.2 (±0.1) in Co, 0 (±0) in Re and 0.2 (±0.2) in Bi at the end of the experiment. The average number of 0-group crabs *Carcinus maenas* was 5.7 (±2.8) in Ex, 6.3 (±3.1) in En, 4.6 (±3.2) in Co, 1.6 (±0.6) in Re and 1.6 (±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 Figure 3 and Figure 4 as a measure of predation pressure.

At the end of the experiment, in some of the Ex and Co cages there were several cm 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.

Table 5. Exclosure experiments, 3-factor ANOVA-tables. Density and length for 0-group and 1+group *Macoma balthica*.

Source	Df	Mean Square	F-Ratio	P-Value
Density 0-group *Macoma balthica* (SQRT-transformation)				
Season	1	30719	33.64	0.0000
Tidal level	1	11625	12.69	0.0006
Treatment	4	5224	4.61	0.0019
Tidal level x treatment	4	59992	6.54	0.0001
Residual	96	916		
Total (corrected)	106			
Length 0-group *Macoma balthica*				
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 x treatment	4	0.67	0.74	0.5677
Residual	62	0.90		
Total (corrected)	72			
Density 1+group *Macoma balthica* (SQRT-transformation)				
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 x treatment	4	130.6	4.28	0.0030
Residual	105	30.5		
Total (corrected)	116			
Length 1-group *Macoma balthica*				
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 x treatment	4	0.4	0.85	0.4963
Residual	97	0.5		
Total (corrected)	107			

Table 6. 2-Factor ANOVA tables of the transplantation experiment. Density and length for 0-group *Macoma balthica*.

| Source	Df	Mean Square	F-Ratio	P-Value
Density 0-group *Macoma balthica* (SQRT-transformation)				
Abundance	1	4854	45.59	0.0000
Treatment	3	2025	18.89	0.0000
Tidal level x abundance	3	436	4.09	0.0140
Residual	34	106712		
Total (corrected)	41			
Length 0-group *Macoma balthica*				
Abundance	1	1.5	4.4	0.0469
Treatment	3	0.8	2.3	0.0979
Tidal level x abundance	3	2.1	5.9	0.0033
Residual	26	0.3		
Total (corrected)	33			
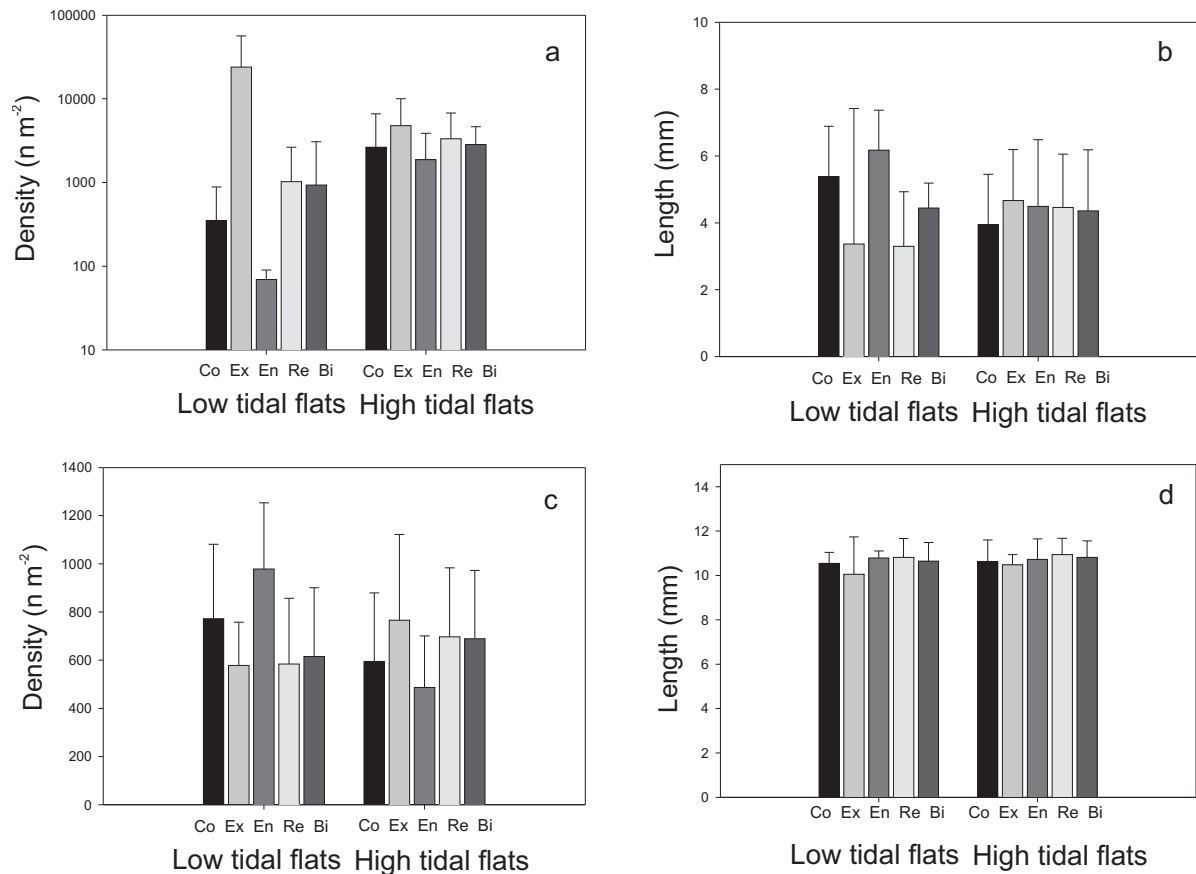
Figure 9. Exclosure experiment. Density (a), length (b) of 0-group and density (c) and length (d) 1+group *Macoma balthica* (+SD) in the 5 different treatments at 2 tidal levels in the exclosure experiment. Co: Procedural control epibenthos exclosure , Ex: Exclosure epibenthos, En: Enclosure epibenthos, Re: marked but otherwise untreated, Bi: Birds exclosure. Low tidal flats: below 0.2 m above MTL, High tidal flats: above 0.3 m above MTL.
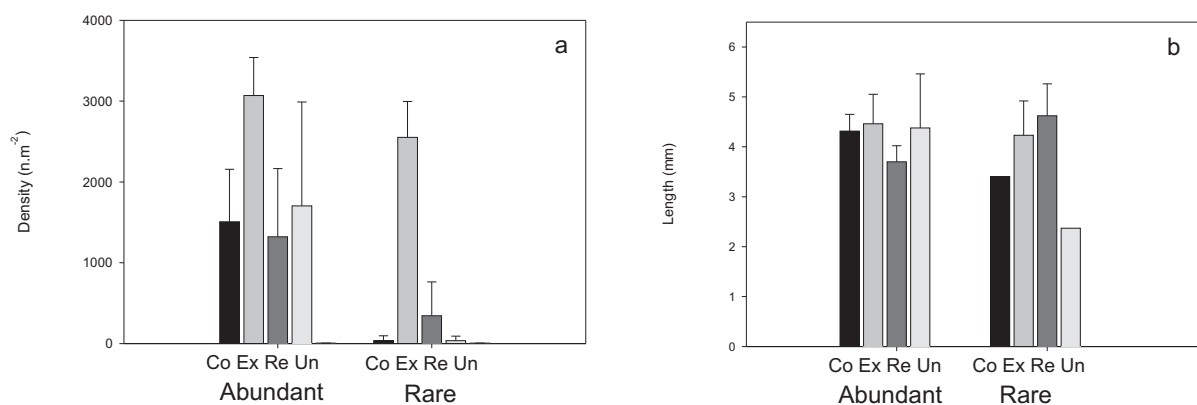

Figure 10. Transplantation experiment. Density (a) and length (b) of 0-group *Macoma balthica* (+SD) in the 4 different treatments at locations where 0-group *M. balthica* was originally abundant and rare, respectively. Co: procedural control, with open sides 100 *M. balthica* added, Ex: exclosure of predators, 100 *M. balthica* added, Re: only marked with bamboo sticks 100 *M. balthica* added, Un: untreated, ambient density sample, no *M. balthica* added or removed.

Transplantation experiment

At all high intertidal locations, 0-group *M. balthica* were abundant. At 2 low intertidal locations, the 0-group was absent, while at 1 low intertidal location the 0-group was abundant. The density of 0-group *M. balthica* was strongly affected by both the treatment and the original abundance (Figure 10A, Table 6). The density in Ex was much higher than in Co and Re, thus predation pressure on 0-group *M. balthica* 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 & Figure 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 *M. balthica* was abundant, while the effect was the other way round on locations where *M. balthica* was rare.

Discussion

This study evaluates the effect of interaction between predation and tidal level on the abundance of *Macoma balthica*. The epibenthic predators *Crangon crangon*, adult *Carcinus 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 *M. balthica* remains. All epibenthic predators selected for small (generally <5 mm), 0-group *M. balthica*. 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 <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 *M. balthica* grow during the summer. From a comparison of growth rates of crabs and shellfish in the field, we can conclude that most *M. balthica* outgrow predation by *Carcinus* 0-group within their first summer. Although *Carcinus* grew faster

than *M. balthica* , it did not grow fast enough to keep its preferred size up with actual *M. balthica* size. Shrimps did not eat any *M. balthica* >2.5 mm in the laboratory experiments and >3.0 mm in the field. As mean *M. balthica* length reached 3 mm in August (Figure 8), shrimp predation becomes probably less important after August, although there were still smaller *M. balthica* after August and *M. balthica* was found in *Crangon* stomachs in September (Table 4).

Our conclusions on the exclosure experiments are somewhat hampered by the problems with enclosing crabs and the loss of some cages. We made a somewhat arbitrary distinction between successful exclosures 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 *M. balthica* 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 exclosure and transplantation studies, only densities of 0-group, and not the older, *M. balthica* 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 exclosure experiments.

We found no effect of bird predation on densities of 0- and 1+group *M. balthica* . However, from many studies it is obvious that shorebirds eat large *M. balthica* (Hulscher 1982; Zwarts & 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 exclosure studies (Sewell 1996) or that the experiments had a too small spatial and temporal scale (Van der Meer *et al*. 2001a). In the study area and period, the oystercatcher *Ostralegus haematopus* was the most abundant shorebird, with on average 2500 birds roosting in the area at high tide during the whole year (De Jong & Koks 1999). This would result in about 1.2 foraging birds ha^{-1} at low tide. Hulscher (1982) calculated that an oystercatcher foraging on *M. balthica* only, eats 499 *M. balthica* low tide^{-1}, thus almost 1000 d^{-1}, in our case this equals 0.12 *M. balthica* m^{-2} d^{-1}. Hence, in our longest experiments (105 days) a difference of about 13.5 *M. balthica* m^{-2} can be expected between controls and bird exclosures (if oystercatchers eat *M. balthica* only and if no other species takes *M. balthica*). As the standard deviation within treatments was many times this value (Figure 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, Figure 9) suggests increased survival of adult *M. balthica* in the low intertidal and reduced survival in the high intertidal under epibenthic predation, which is unexpected and cannot be explained.

Consumption by predators

Table 7 gives an order-of -magnitude calculation of the consumption and the resulting mortality of 0-group *M. balthica* 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 & Rosenberg 1984; del Norte-Campus & Temming 1994e). The estimated mortality values (Z) are 0.0091 d^{-1} for low tidal flats and 0.0008 d^{-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 (Chapter 2) for low and high tidal flats were 0.0107 and 0.0017 respectively. *Crangon* and 0-group *Carcinus* predation can explain 85% of the Z on the low tidal flats and 49% on the high

Table 7. Order of magnitude calculation of the consumption of 0-group *Macoma balthica* by the epibenthic predators *Crangon crangon* and 0-group *Carcinus maenas* (± 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 & Teming (1994e) 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 m^{-2})	*Macoma balthica*	1022 ± 168	3329 ± 449
	Crangon crangon	4.9 ± 1.5	1.7 ± 0.9
	Carcinus maenas	0.6 ± 0.4	2.4 ± 1.7
Stomach content	*Crangon crangon*	0.12 ± 0.01	0.08 ± 0.01
(*Macoma* $stomach^{-1}$)	*Carcinus maenas*	0.28 ± 0.03	0.08 ± 0.01
Evacuation time (h)[*]	*Crangon crangon*	1.7	1.7
	Carcinus maenas	6.5	6.5
Consumption	*Crangon crangon*	8.70 ± 3.05	2.04 ± 1.19
(*Macoma* m^{-2} d^{-1})	*Carcinus maenas*	0.60 ± 0.45	0.70 ± 0.63
Calculated Z	due to *Crangon crangon*	0.0085 ± 0.0016	0.0006 ± 0.0003
(d^{-1})	due to *Carcinus maenas*	0.0006 ± 0.0003	0.0002 ± 0.0002
Total calculated Z		0.0091 ± 0.0020	0.0008 ± 0.0004
Average observed Z field 1998-2000		0.0107 ± 0.0042	0.0017 ± 0.0048
% Z explained by predation *Crangon* and 0-group *Carcinus*		85%	49%

tidal flats can be explained.

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

Thus, 49 to 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:

- underestimating predator density due to (large) predators fleeing in front of our net

- predation by adult *Carcinus* (on average 0.1 *M. balthica* $stomach^{-1}$, but no reliable density data available). From the pitfall data (Figure 4), a substantial predation pressure by large crabs is expected.

- predation by *Crangon* and *Carcinus* without ingestion of hard shell parts. As *M. balthica* 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 Chapter 5

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 & Rosenberg 1984) and in the northern German Wadden Sea at unknown temperatures (del Norte-Campus & Temming 1994e). 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 (Chapter 2).

General conclusions

We conclude that small *M. balthica* 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 *M. balthica* -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 *M. balthica* in tidal channels and the North Sea (Chapter 2) where aquatic predators are abundant, confirms this idea.

This study explains why juvenile *M. balthica* 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 exclosure 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 *M. balthica* were larger and had a better condition in the high intertidal too. This observation is surprising because the time available for feeding is longer is 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 & Green 1991). However, adult growth is usually fastest in the low intertidal (Harvey & Vincent 1990; Harvey & Vincent 1991; Beukema 1993a; Vincent *et al*. 1994). As we found no significant epibenthic or bird predation on 1+ *M. balthica* and growth was better, the high intertidal seems to remain the best location for *M. balthica* as they grow older. Nevertheless, Beukema (1993a) found higher mortality-values for adults living in the high than in the low intertidal.

CHAPTER 5

Predation of intertidal infauna on juveniles of the bivalve *Macoma balthica*

J.G. HIDDINK, R. TER HOFSTEDE & W.J. WOLFF

ABSTRACT

Juveniles of the bivalve *Macoma balthica* live on tidal flats in the Wadden Sea. This study examined the interaction of *M. balthica* with the infaunal polychaetes *Arenicola marina* and *Nereis diversicolor* and the gastropod *Retusa obtusa*. The distribution of *M. balthica* spat on the flats, shortly after settlement in April, showed a positive correlation with the *Arenicola* distribution and a negative correlation with *Nereis* distribution. There were no locations where *M. balthica* spat and *Retusa* occurred together. In August, *M. balthica* spat had grown too large for predation by intertidal infauna.

Small individuals of *M. balthica* spat were found in stomachs of *Arenicola* (0.14 worm^{-1}) and *Nereis* (0.05 worm^{-1}). Laboratory experiments showed that *Nereis* and *Retusa* could reduce *M. balthica* spat abundance, both in the absence and presence of sediment and alternative prey. *Arenicola* reduced the abundance of small *M. balthica* (<1 mm) in sediment without, but not with, alternative prey.

In field experiments, we manipulated the density of *Arenicola* in 0.25-1 m^2 plots and of *Nereis* in 0.03 m^2 cages and examined the effect on *M. balthica* density several weeks later. We found a significant negative relation between densities of polychaetes and *M. balthica* spat for both polychaete species in these experimental plots. Peculiarly, we found a significant positive relation between manipulated *Nereis* density and adult *M. balthica* density in the cages; we cannot explain this.

Consumption rates, calculated both from stomach contents and from field experiments, were 45 to 102 *M. balthica* m^{-2} d^{-1} for *Arenicola* and 5 to 116 *M. balthica* m^{-2} d^{-1} for *Nereis*. These values are higher than recorded consumption rates by epibenthic predators in the same area. Nevertheless, between-year differences in year-class strength could not be explained by differential abundance of these polychaetes.

In conclusion, *Arenicola* and *Nereis* had a negative effect on the abundance of *M. balthica* <1.5 mm, which was at least partly caused by direct consumption. *Retusa obtusa* can eat juvenile *M. balthica*, but probably did not so in the study area, because there were no locations where *Retusa* and *M. balthica* spat occurred together in the period that *M. balthica* was <2 mm.

INTRODUCTION

Juvenile shellfish such as *Macoma balthica, Cerastoderma edule* and *Mya arenaria* are <300 µm at settlement after a pelagic larval stage. These young macrobenthic animals thus belong to the meiobenthos and have to cope with other conditions than the older and larger stages. The effect of infaunal polychaetes on meiofaunal and juvenile macrofaunal abundance has been studied at many locations. Infaunal polychaetes had little effect in some studies (Reise 1979a; Kennedy 1993) and large impact in others (Commito 1982; Ambrose 1984a; Ambrose 1984b; Commito & Shrader 1985; Ronn *et al.* 1988; Desroy *et al.* 1998; Tita *et al.* 2000). Negative effects of polychaetes can be separated in direct effects due to predation and indirect effects due to disturbance. Deposit-feeding infauna usually ingests, moves and disturbs large amounts of sediment. The number of meiofaunal organisms that is killed by disturbance in these cases can be much higher than the number that is actually eaten (Tita *et al.* 2000).

Macoma balthica is one of the most common and widespread bivalves in the intertidal and subtidal Wadden Sea. *Macoma balthica* spawns in the end of March and April (Honkoop & Van der Meer 1997). The eggs and larvae are pelagic for a short period and then settle, mainly on the low tidal flats at a length of 190 µm to 300 µm (Günther 1991; Armonies & Hellwig-Armonies 1992). It can reach a length of 4-7 mm in September of its first year (Armonies 1996).

Two major groups of predators on *M. balthica* are generally acknowledged: wading birds (Hulscher 1982; Zwarts & Blomert 1992) and epibenthic organisms like shrimps, crabs and fish (Reise 1978; Van der Veer *et al.* 1998; Chapter 4). There are, however, also many indications of predation and/or disturbance by infaunal invertebrates on juvenile bivalves (Sarvala 1971; Reise 1979a; Ratcliffe *et al.* 1981; Berry 1988; Flach 1992a; Thiel & Reise 1993; Olafsson *et al.* 1994; Cummings *et al.* 1996). So far, effects of infaunal predation and disturbance on *M. balthica* in the Wadden Sea have not been examined quantitatively.

Infauna is generally very numerous. For example, the large deposit-feeding polychaete *Arenicola marina* may reach densities over 45 m^{-2} (Flach & De Bruin 1993) and the omnivorous scavenger *Nereis diversicolor* 400 m^{-2} (Essink *et al.* 1998a). In comparison, densities of the most abundant epibenthic predator, the shrimp *Crangon crangon* are generally smaller than 100 m^{-2} (Beukema 1992; Van der Veer *et al.* 1998), and average densities of waders are several orders of magnitude lower at about 1 per 10 000 m^2 (Zwarts & Wanink 1984). Since many species of infaunal animals are so numerous, even a low consumption per predator may heavily affect the abundance of *Macoma balthica*-spat, and thus the later year-class strength of adults.

The question we want to answer in this study is whether infauna affects densities of juvenile and adult *Macoma balthica*. The study was primarily aimed at the effects of

predation.

We examined the interaction of juvenile *M. balthica* with the lugworm *Arenicola marina*, the ragworm *Nereis diversicolor* and the gastropod *Retusa obtusa. Arenicola marina* is a large deposit-feeding polychaete that lives in U-shaped burrows in intertidal areas. On the head side of the burrow, surface sediment descends through a funnel and is ingested (Retraubun *et al.* 1996). A few hours after digestion, the sediment is deposited as a cast at the surface through the tail shaft. The worm ingests vast quantities of sediment every day. It is estimated that a large *Arenicola* may ingest 80 cm^3 of sand per day (Cadée 1976). *Arenicola* is known as a bioturbator, disturbing other infauna, like the amphipod *Corophium volutator* and small bivalves (Flach 1992a). Flach and Tamaki (2001) found a negative correlation between adult *Arenicola* and juvenile *M. balthica* density on tidal flats of the Wadden Sea. This correlation was strongest from July to September, suggesting that post-settlement processes cause this correlation.

Nereis diversicolor is an omnivorous scavenger. It lives in a burrow in the sediment, where it can use 3 different food-searching strategies (Tita *et al.* 2000). While deposit feeding, the worm swallows surface sediment unselectively, the largest part of the gut is filled with inorganic sediment. *Nereis* can also filter feed, by pumping water through a mucous web. This net-bag is swallowed with the trapped particles afterwards (Riisgard *et al.* 1992; Vedel *et al.* 1994). The third feeding mode is active hunting on meiofauna from the burrow. *Nereis* is known to prey on spat of the cockle *Cerastoderma edule* and *Macoma balthica* in both field and laboratory (Reise 1979a; Reise 1985; Ronn *et al.* 1988).

The small predatory gastropod *Retusa obtusa* (up to 6 mm shell length) lives in the top layer of the sediment. The main foods are the gastropod *Hydrobia ulvae* and Foraminifera. Prey is ingested whole (Stamm 1995). Mean shell length of ingested *Hydrobia* was 1.37 mm with a maximum of 1.9 mm in a study by Berry (1988). It can eat *M. balthica* in laboratory experiments (Ratcliffe *et al.* 1981).

As burying depth is positively related with *M. balthica* size, the adults are probably less vulnerable to sediment disturbance by infauna than the juveniles. Because infaunal predators are relatively small, it seems unlikely that the older *M. balthica*, which usually reach a shell length of 5 mm within 1 year, are vulnerable to infaunal predation.

The intertidal distribution of *M. balthica* was compared with the distribution and density of the predators to examine which species show overlapping distributions. The effect of these species on both 0-group and older *M. balthica* was studied with stomach content analysis and in laboratory and field experiments. From stomach content analysis and predator density manipulations predation/disturbance rates in the field were estimated. From these studies, we quantified the effect of these predators on the density and distribution of *M. balthica*.
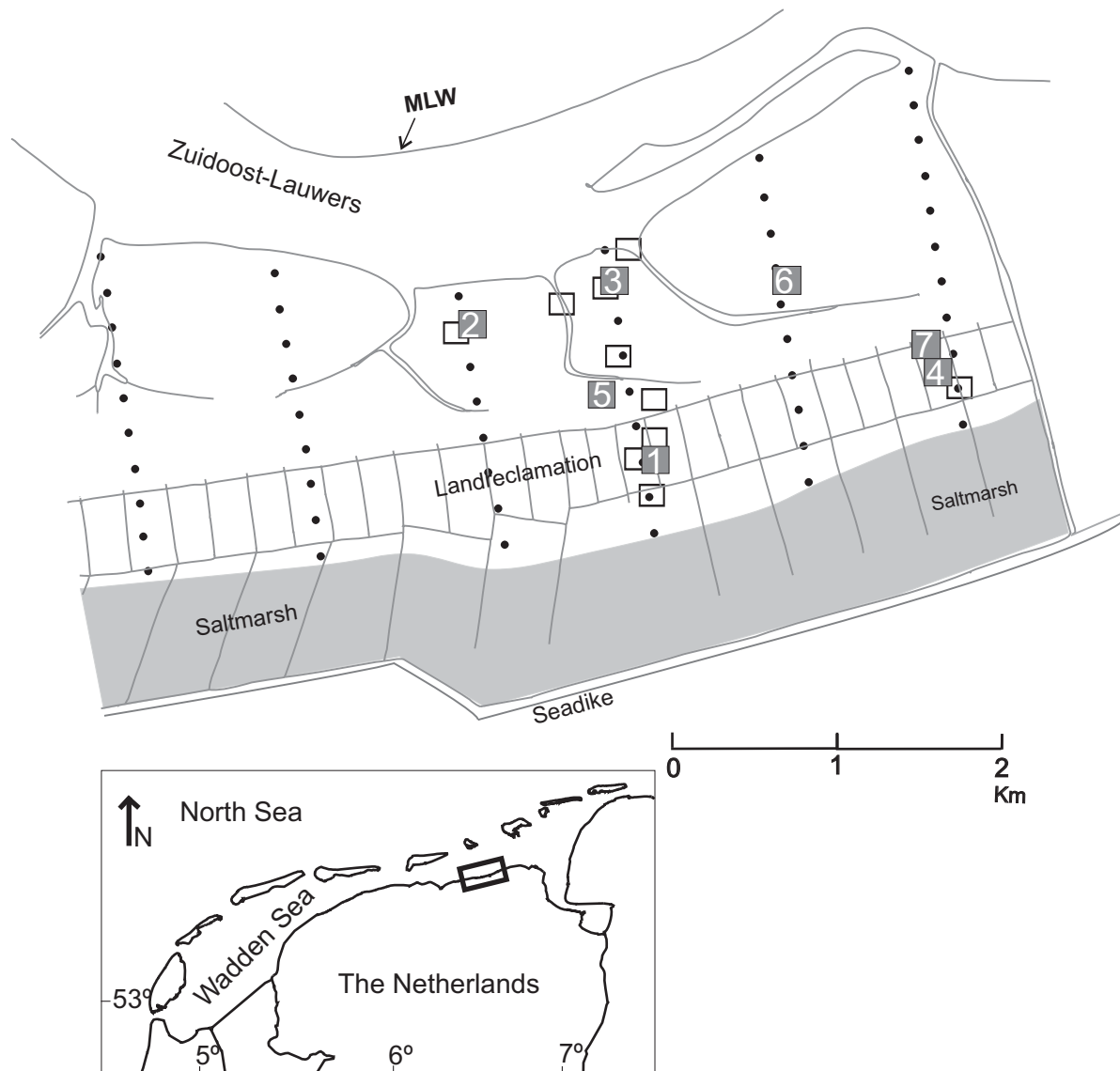
Figure 1. Map of the study area at the Groninger Wad, Eastern Dutch Wadden Sea. Locations of sample stations (●), locations where polychaetes for stomach content analyses were collected (□) and enclosure experiments with location number (▣) (see Table 2).

METHODS

Study area

Our study was carried out at the Groninger Wad, which is part of the Lauwers basin, in the eastern Dutch Wadden Sea (6° 31' E, 53° 26' N) (Figure 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); saltmarshes occur at the higher levels. Average high water (MHW) is at +1.0 m, mean low water (MLW) at –1.4 m NAP. At 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. The studied area (7.9 km^2) was enclosed by salt marsh at the south side, the shallow shipping gully to Noordpolderzijl at the eastern side, the deep (10 m) tidal channel Zuidoost-Lauwers at the northern side and partly by another shallow tidal channel on the western side.
Abundant species in the study area are the bivalves *Macoma balthica*, *Cerastoderma edule*, *Mya arenaria* and *Scrobicularia plana*, the gastropod *Hydrobia ulvae*, the polychaetes *Nereis diversicolor*, *Arenicola marina*, *Tharyx marioni*, *Heteromastus filiformis*, *Scoloplos armiger* and *Eteone longa* and the crustaceans *Crangon crangon* and *Carcinus maenas* (Tydeman 2000).

Collection of experimental animals

All animals for field and laboratory experiments were collected at the Groninger Wad. *M. balthica* -spat was retrieved from the top layer of the sediment, on locations where spat was abundant. The samples were sieved over 1000, 500, 300 and 125 µm and the fractions were sorted under binocular microscope. *M. balthica* was stored in sediment in a dish with a shallow layer of aerated seawater. The size range studied was 0.3 to 2 mm for 0-group and 5-20 mm for 1+ group *M. balthica*. *Nereis* and *Arenicola* were excavated with a spade and intact worms were picked out of the sediment by hand. The polychaetes were stored in the laboratory in buckets with a 10 cm layer of sediment from the field, placed in an aquarium with running seawater (S=30). *Retusa obtusa* was collected by sieving the upper sediment layer in the field over 1 mm. They were stored in the laboratory in small containers with a 2 cm layer of sediment from the field.

Field distribution

On 10-14 April and 23-25 August 2000 the density of *Macoma balthica*-spat, 1+ group *M. balthica* , *Nereis diversicolor*, *Arenicola marina* and *Retusa obtusa* was measured at 57 intertidal stations at the Groninger Wad (Figure 1). *M. balthica* spat was sampled in April by coring 5 times with a 4.6 cm^2 corer to a depth of 2 cm. Samples were sieved through 1000, 500, 300 and 125 µm mesh. The fractions were sorted at 6-25 x

magnification under a binocular dissecting microscope. *Nereis, Retusa* and 1+ *M. balthica* were sampled by coring 5 times with an 83 cm^2 corer to a depth of 15 cm in April and once with an 83 cm^2 corer to a depth of 15 cm in August. Samples were sieved over 1 mm and sorted in the laboratory. Per species, the number of individuals was counted. As *Nereis* was often broken, the number of heads per sample was counted. In August, the number of *M. balthica* spat was also counted in these samples (1 x 83 cm^2). All samples were stored at -25°C until sorting. The lugworm density was estimated from the number of casts on the sediment in a 0.5 x 0.5 m grid at 4 locations within 10 m of the station. According to Flach and Beukema (1994) (in March and August) and Farke *et al.* (1979) (in July) the number of casts underestimates the density of lugworms on average with 6%.

Stomach content analysis

The stomachs of 87 *Arenicola* (84±26 mm, 2.7±1.7 g wet weight, WW) and stomachs of 120 *Nereis* (55±13 mm) were examined for the presence of *M. balthica.* The polychaetes were collected on 15 June 1999, 23 June 1999, 8 July 1999, 26 April 2000, 4 May 2000, 16 May 2000, 25 May 2000 and 4 April 2001 on locations where juvenile *M. balthica* was present (Figure 1). At these locations, the density of the polychaetes and the bivalve was measured as described in the section 'field distribution'. Polychaetes were stored in 4% formalin in seawater until analysis in the laboratory. The polychaetes were cut open over their whole length and the gut content was rinsed into a petridish with water. The whole gut content was analysed under a binocular microscope at 10-40 x magnification. Only *M. balthica* that were presumed to be alive at the moment of ingestion were counted. While old shells are white, fresh shells are usually translucent with the 2 valves still attached, sometimes with flesh still inside. All *M. balthica* were measured with a calibrated micrometer eyepiece.

 GUT THROUGHPUT TIME
The stomachs of *Nereis* and *Arenicola* are filled and emptied with sediment several times a day. To calculate daily predation rates from stomach contents, we need to know the time that it takes prey (and sediment) to reach the anus from the mouth (the gut throughput time, GTT) (Plante & Mayer 1996). Cadée (1976) studied the faeces production of *Arenicola marina* in the Wadden Sea under similar temperature conditions as on the Groninger Wad. An average *Arenicola* produced 11.0 to 12.8 ml of faeces per day, or 0.45 to 0.53 ml h^{-1} (egestion rate ER). If the volume of sediment in the gut of the worm is known, the throughput time of the sediment can be calculated. The ingestion and egestion rates in lugworms are almost equal, as only a small fraction of the ingested material is digested (Plante & Mayer 1996).
Arenicola was collected on the tidal flats of the Groninger Wad; we used animals from the same locations and dates as for stomach content analysis. Before processing, the length and WW (after blotting on paper for 10 s) of the animal were measured (79±25 mm, 2.22±1.32 g WW, n = 42). The polychaetes were cut open over the whole length

Table 1. Laboratory experiments on the effect of polychaete and *Retusa* predation on juvenile *Macoma balthica*. In experiments where sediment from the field was used, an unknown number of *M. balthica* were present in this sediment and no *M. balthica* were added.

Predator	Experiment type	Sediment	# Predators	Container	*Macoma* start	Duration (days)	n predator	n control
Arenicola marina	Azoic sediment	Azoic	1	15 x 10 x 13 cm	100	20	6	9
Arenicola marina	Alternative prey	Field	1	15 x 10 x 13 cm	Unknown	13	4	4
Arenicola marina	Alternative prey	Field	2	15 x 10 x 13 cm	Unknown	14	6	4
Arenicola marina	Alternative prey	Field	2	15 x 10 x 13 cm	Unknown	14	6	4
Nereis diversicolor	No sediment	None	2	Petridish 9 cm	20	3	10	10
Nereis diversicolor	Azoic sediment	Azoic	2	Petridish 9 cm	20	3	10	10
Nereis diversicolor	Alternative prey	Field	2	Petridish 9 cm	Unknown	5	5	5
Nereis diversicolor	Alternative prey	Field	2	Petridish 9 cm	Unknown	7	5	5
Nereis diversicolor	Alternative prey	Field	2	Petridish 9 cm	Unknown	6	8	8
Retusa obtusa	No sediment	None	5	Petridish 9 cm	20	3	10	10
Retusa obtusa	Azoic sediment	Azoic	5	Petridish 9 cm	20	3	10	10
Retusa obtusa	Alternative prey	Field	5	Petridish 9 cm	Unknown	5	5	5

and the gut content was rinsed out with water into a 10 ml cylinder with 0.1 ml scaling. The sample was left to set for 30 s. GTT was calculated from the estimated average volume and literature values of ER (Cadée 1976) as: GTT (h) = gut capacity (cm^3) / ER ($cm^3 h^{-1}$).

We estimated the GTT of deposit-feeding *Nereis diversicolor* in an experiment where we fed the worm sand that was coloured with methylene blue and enriched with dead microalgae (Instant Algae, Reed Mariculture). Sixteen containers were filled with sediment on the tidal flats. *Nereis* was collected and 3 of them were allowed to bury in each of the containers directly after collection (61±16 mm, n=58). Containers were transported to the laboratory and stored in an aquarium with running seawater in a climate room at 10 or 15°C. They were left to acclimate for 1 week. The sediment from the field (with all natural food sources) provided food for the worms in this period. At the start of the experiment, a 1 mm layer of the enriched blue sediment was spread over the sediment of all containers. For the first 8 h, we sampled 1 container each hour. After 8 h, we sampled 1 container every 2 h. The last samples were taken after 24 h. When a container was sampled, the *Nereis* was sieved out over 1 mm and killed by a short immersion in 70% ethanol. Using this method, the worms stopped moving within a few seconds without ejection of gut contents. The length of the worm was measured to the nearest mm and was then cut in 2 mm pieces, starting at the tail. We measured at what distance from the head (in mm) coloured sediment was found in the guts and calculated this distance as a percentage of the total length. The experiment was carried out at 10 (n=34) and 15°C (n=25) (normal water and sediment temperatures in April and June) to examine the effect of temperature on the turnover rate. The filling of *Nereis* was calculated as the average of all samples in percentages per h, without non-feeding and thus empty animals and without animals that had already filled completely with blue sediment.

Laboratory experiments

All laboratory experiments were executed in a climate room with a 16/8 h day/night cycle at 10°C and S=30.

In a pilot experiment, 5 *Nereis* were added to a 15 (l) x 10 (w) x 13 (h) cm container with a layer of sand and 100 0-group *M. balthica* for 24 h. 4 *Arenicola* were put in a bucket (201 cm^2) with a 10 cm thick layer of sediment for 68 h. After this period the stomachs were examined for the presence of 0-group *M. balthica* as described above. Other laboratory experiments with *Nereis* and *Retusa* were executed in 9 cm diameter 1 cm high petridishes. Experiments with *Arenicola* were performed in plastic containers with dimensions 15 (l) x 10 (w) x 13 (h) cm that were filled with a 7 cm layer of sediment and submerged in an aquarium with running seawater. In all experiments, we used 0-group *M. balthica* that were retained on a 300 μm sieve and passed through a 1 mm sieve at the start of the experiment (shell length between 400 and 1400 μm). We performed 3 types of laboratory experiments. Table 1 provides details on the number of replicates and duration of the laboratory experiments. Generally, the duration of experiments with *Arenicola* was longer than for *Nereis* and *Retusa*, because the experimental units with *Arenicola* contained much more sediment since lugworms need a thick layer to show their natural burrowing behaviour and cannot forage otherwise. As the amount of sediment was much higher, we expected a smaller effect

Table 2. Field density manipulation experiments. The densities A*renicola marina* and *Nereis diversicolor* were manipulated, all treatments in duplicate. The number of removed *Arenicola* (stabbed to death) was not known exactly and indicated as negative numbers added. For location numbers see Figure 1.

| Location		1	2 & 3	4[a]	4[a]	5	6	7
Species		*Arenicola marina*				*Nereis diversicolor*		
Type		Plot	Plot	Plot	Plot	Cage	Cage	Cage
Date Start		22-Jun-00	04-Apr-01	01-May-01	01-May-01	26-May-00	19-Apr-01	03-May-01
End		28-Jul-00	17-Apr-01	30-May-01	28-Jun-01	08-Jun-00	03-May-01	14-Jun-01
Duration (days)		36	13	29	58	13	14	42
Plot size (m^2)		0.25	1	0.5	0.5	0.03	0.03	0.03
Macoma age sampled		0-grp	0-grp & adults	0-grp	Adults	0-grp & adults	0-grp & adults	0-grp & adults
Natural # of worms in plot		5	15	5	5	4	7	8
N		8	10	11	11	8	12	12
Manipulation	a	-2	-15	-5	-5	0	0	0
(# added,	b	0	0	0	0	10	10	10
treatments in	c	5	15	8	8	20	20	25
duplicate)	d	10	30	16	16	50	30	40
	e		45	24	24		40	55
	f			50	50		50	70

[a] One experiment sampled twice
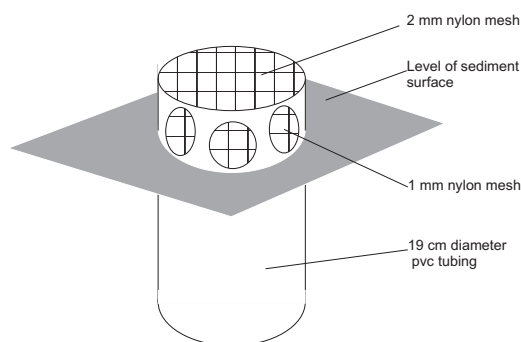
Figure 2. Construction of the enclosure cage used in the *Nereis diversicolor* density manipulation experiments.

of *Arenicola* and therefore duration of experiments was longer. For the same reason, the experimental densities were higher for *Arenicola* than for *Nereis* and *Retusa* experiments (Table 1).

The 'no-sediment' experiments indicate whether the predators are able and willing to eat or kill *M. balthica.* 20 *M. balthica* and 2 *Nereis* or 5 *Retusa* were put in a petridish with seawater but without sediment. In controls, no predator was added. This experiment could not be performed with *Arenicola* because this polychaete cannot show its natural foraging behaviour (ingesting sediment) without sediment. The number of remaining live *M. balthica* was counted after 3 days.

In the 'azoic sediment' experiment, we examine whether the predators kill *M. balthica* if both prey and predator are buried in the sediment. Experiments with 2 *Nereis* or 5 *Retusa* were done in a 0.5 cm layer of azoic sediment (<125 µm, without organic material, incinerated at 550°C for 2 h) with seawater . In controls, no predator was added. 20 *M. balthica* were added to each petridish at the start of the experiment and the number of remaining live *M. balthica* was counted after 3 days. 'Azoic sediment' experiments with *Arenicola* were performed in plastic containers, which were filled with 7 cm of azoic (all fauna killed by heating to 100°C for 3 h) sediment, which was enriched with dead microalgae (Instant Algae, Reed Mariculture) to stimulate foraging. 100 *M. balthica* were added to each container. The containers were submerged in an aquarium with running seawater. After 20 days, the whole content of each container was sieved over a 1000 and 300 µm and the number of live *M. balthica* per fraction was counted under the binocular microscope at 10 x magnification.

In an 'alternative prey' experiment, we examined whether the predators do kill *M. balthica* in sediment that contains abundant alternative prey, like diatoms, nematodes and Foraminiferans. The containers were filled with sediment from the field, from locations where *M. balthica* was abundant (25 ml of sediment for *Nereis* and *Retusa* (4 mm thick), a 7 cm thick layer for *Arenicola*). This sediment already contained *M. balthica* -spat (in the size range of 300 to 1000 µm) and alternative prey; no *M. balthica* was added to the sediment afterwards. For *Nereis* and *Arenicola*, 3 of these experiments were conducted, for *Retusa* one (Table 1). As the locations where and time when the sediment was collected varied between experiments, there was a large variation in the number of *M. balthica* present at the start of the experiments. The duration of these experiments varied from 5 to 14 days and was longer for *Arenicola* because the sediment volume was larger in their experimental units. Samples were treated as described for the other experiments.

Arenicola often died or came out of the sediment during the experiments; these

treatments were discarded and caused the unbalanced design of some experiments in Table 1.

Field experiments

In the field experiments, we tried to estimate the impact of *Nereis* and *Arenicola* on the density of 0-group and older *Macoma balthica*. Therefore, we manipulated the density of *Arenicola* and *Nereis* by adding animals to experimental plots on the tidal flats or killing animals in these plots. We examined the effect on the number of *M. balthica* after 2 weeks to 2 months. We assumed that the number of *M. balthica* at the start of the experiment was similar in the plots. Table 2 gives an overview of the locations (see also Figure 1), period, duration and the applied manipulation (number of polychaetes added) per experiment. We did 3 consecutive experiments for both *Arenicola* and *Nereis,* but we sampled the third *Arenicola* experiment twice, once for juvenile and once for adult *M. balthica.* The second *Arenicola* experiment (location 2&3) was executed at 2 locations simultaneously and analysed as one experiment.

*A*RENICOLA MARINA

If a lugworm is dug from the sediment and laid down at another location (to experimentally increase densities), it buries itself at that location. Flach (1992a) showed that increased densities of lugworms in experimental plots slowly decrease towards the natural densities, but that differences in densities between treatments remain apparent for months. Densities of *Arenicola* could be reduced by stabbing with a spade on the presumed location of the worm in the sediment, between the cast and the funnel. We tried to do this without strongly disturbing the ambient sediment. Plot sizes in the experiments were 0.25 (0.5 x 0.5 m), 0.5 (0.7 x 0.7m) and 1 (1 x 1) m^2. In general, we added between –5 (removal) and 50 lugworms per plot, all treatments in duplicate, aiming at experimental densities between 0 and 60 m^{-2}. Table 2 gives the number of worms that was added per plot. During the experiment, the number of casts in each plot was counted at least twice and the average was used as the lugworm abundance. Only casts of adult *Arenicola* (casts at least 2 cm wide) were counted. The experiments lasted between 13 and 58 days. At the end of the experiment, in 2 experiments the density of 0-group *M. balthica* was determined (location 1&4), in 1 experiment only the density of older *M. balthica* was estimated (location 4) and in 1 experiment, the density of both adults and juveniles was determined (location 2&3, Table 2). In the first experiment, the whole top layer (3 cm, 0.25 m^2) of the sediment was sieved over a 1 mm sieve. In the other 2 experiments, 0-group *M. balthica* was sampled by coring 10 and 16 times with a 4.5 cm^2 corer, scattered over the whole plot. Samples were sieved through 1000, 500, 300 and 125 µm mesh. The fractions were sorted at 6-25 x magnification under a binocular dissecting microscope. Adult *M. balthica* was sampled in the second and fourth experiment, by coring 5 and 9 times with an 83 cm^2 corer and sieving over 1 mm. All samples were stored at -25°C until sorting.

NEREIS DIVERSICOLOR

Nereis diversicolor is a motile worm that can and does leave its burrow. The worms were, therefore, enclosed in a cage in density manipulation experiments. The cage was a 19 cm diameter 50 cm long diameter PVC tube and had 5 8 cm diameter holes in the sides, which were covered with 1 mm mesh nylon (Figure 2). The top of the cage, which was difficult to reach for *Nereis*, was covered with 2 mm nylon mesh. The cages were pushed into the sediment until the lower side of the side holes was at the sediment level. No *Nereis* was killed in the experimental plots, as this was not possible without severe sediment disturbance. We used 8 to 12 cages per experiment, to which between 0 to 70 *Nereis* were added, each treatment in duplicate (see Table 2).
At the end of the experiment, the top layer of the sediment was removed to 2 cm depth and collected in a plastic bag to count juvenile *M. balthica.* The rest of the sediment was removed to a depth of 20 cm and sieved over 1 mm to count *Nereis* and adult *M. balthica.* We took care to add up the numbers of *Nereis* and *M. balthica* from the 2 different samples. Samples were treated as in the lugworm experiment.

Statistical analysis

The distribution of *M. balthica* was compared with the distribution of the polychaetes and *Retusa* with a correlation of the densities at the 57 sampled stations. For normally distributed data, we used the Pearson's correlation. If the densities were not normally distributed, we used a Spearman's rank correlation.
The laboratory experiments were analysed with an ANOVA or 2 factor-ANOVA (Type III), with the factors predators presence and sediment presence or experiment number (only if applicable) and their interaction.
We analysed the density manipulation experiments with a General Linear Model (GLM) (type III) (Crawley 1993) in which experiment number was used as a categorical factor and polychaete density as a quantitative factor. In the GLM we only give the interaction term in the final model if is it was significant.

RESULTS

Field distribution

Figure 3 presents the spatial distribution and density of 0-group and 1+ *Macoma balthica, Arenicola marina, Nereis diversicolor, and Retusa obtusa* in April and August 2000. In April, *M. balthica*-spat reached densities over 10 000 m^{-2}. Nearly all 0-group *M. balthica* were found in the 125 µm fraction and thus passed through the 300 µm sieve. They were concentrated in the low sandy area close to the main tidal channel. Their distribution overlapped with that of *Arenicola* (density 0-30 m^{-2} at locations where 0-

group *M. balthica* occurred, Pearson's correlation coefficient=0.404, p = 0.002) and to a lesser extent with the distribution of *Nereis* (0-700 m^{-2} at locations where *M. balthica* occurred, although their densities correlated negatively, Pearson's correlation coefficient=-0.331, p = 0.012). *Retusa obtusa* was rare in April (0-120 m^{-2}) and concentrated at the border of the former landreclamation works. There were no stations where both *Retusa* and *M. balthica* were present (Spearman's rank correlation coefficient = –0.313, p = 0.018).

In August, most 0-group *M. balthica* were present at stations adjoining the saltmarsh and landreclamation works. The highest *M. balthica* density that was found was 6506 ind m^{-2}. They had a mean length of 4.2 ± 1.3 mm. There was a negative correlation between the numbers of *M. balthica* and *Arenicola* (Pearson's correlation coefficient=-0.277, p = 0.037), but still there were many stations where both *M. balthica* and *Arenicola* were common. There was a significant positive correlation between the number of *M. balthica* and *Nereis* in August (Pearson's correlation coefficient=0.384, p = 0.003). *Retusa* density did increase to maximal 1084 ind m^{-2} in August. There were many stations with *M. balthica* and without *Retusa* and there was no significant correlation between the densities of *Retusa* and 0-group *M. balthica* (Pearson's correlation coefficient=0.080 p = 0.55).

There was a significant positive correlation between 1+ *M. balthica* and *Retusa* density in April 2000 (Pearson's correlation coefficient=0.360 p = 0.006) and a significant positive relation with *Retusa* density in August 2000 (Pearson's correlation coefficient=0.389 p = 0.003). Other correlations were not significant.

Stomach content analysis

Figure 4 gives the length-frequency distribution of *M. balthica* found in polychaete stomachs from the field. We found 0.14±0.51(SD) *M. balthica* per *Arenicola* stomach (12 *M. balthica* found in 87 stomachs). These *M. balthica* were between 0.19 and 0.92 mm long with an average of 0.41 mm. In the stomach of *Nereis*, 0.05±0.26 *M. balthica* was found (7 *M. balthica* found in 120 stomachs). These *M. balthica* were between 0.21 and 1.5 mm long with an average of 0.59 mm.

Preliminary experiments showed that 43% of *M. balthica* between 0.5 and 1 mm died when submerged in fluids from the intestine of lugworms.

The average size of *Arenicola marina* examined for the volume of the stomach contents was 79±25 mm length and 2.22±1.32 g WW. Cadée (1976) used lugworms with wet weights between 1 and 9 g and found that the faeces production doubled in this weight range. The volume of sediment in the intestine of the lugworms was 0.57±0.54 ml. Cadée (1976) found that an average *Arenicola* produced 11.0 to 12.8 ml of faeces per day. Thus, at a faeces production of 12 ml per day this means that the complete stomach content is replaced 21.6 times per day and that the gut throughput time (GTT) is 66 minutes.

Nereis diversicolor filled its stomach with a rate of 15% (±14) h^{-1}. There was no significant difference between the filling rate at 10 and 15°C (t-test, p = 0.48). The 15%
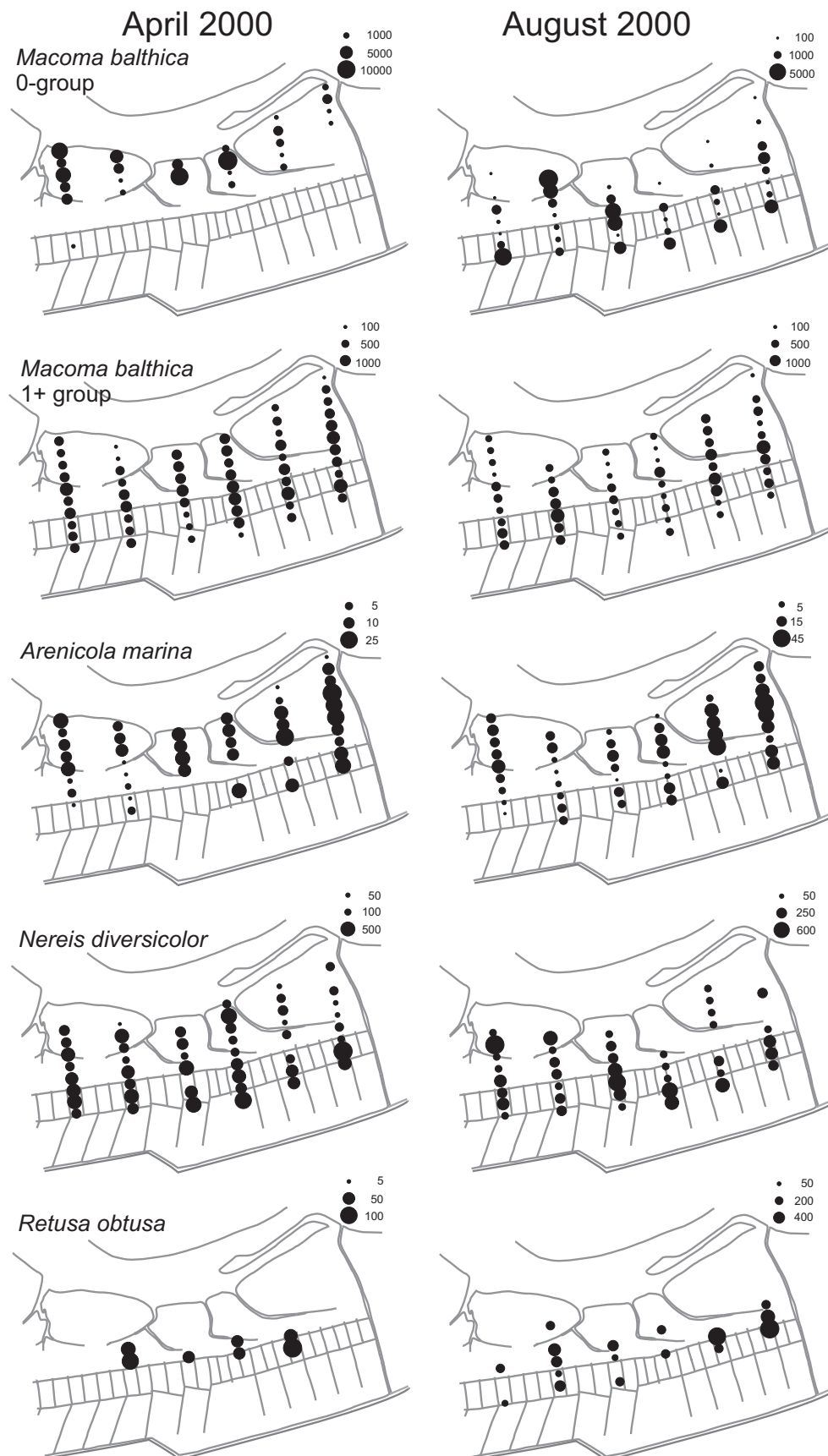
Figure 3. Distribution patterns of 0-group and 1+ *Macoma balthica, Arenicola marina, Nereis diversicolor* and *Retusa obtusa* (ind m^{-2}) in April and August 2000 at the Groninger Wad. See Figure 1 for the locations of the sample stations.

filling per h of the stomach equals 3.6 fillings per day and a GTT time of 6.7 h. Table 3 gives an order-of-magnitude calculation of the effect of *Arenicola* and *Nereis* predation on the *M. balthica* -spat mortality in the field, at the locations where the polychaetes were collected. Although the consumption per worm is much lower for *Nereis* (0.2 *M. balthica* d^{-1}) than for *Arenicola* (3.0 *M. balthica* d^{-1}), the mortality caused by both species is approximately equal (0.3-0.4% per day) because *Nereis* densities in the field were much higher.

Laboratory experiments

In 25 examined *Nereis* from the pilot experiments, we found 8 *M. balthica* , which measured 0.97±0.35 mm with a range of 0.60-1.50 mm. Out of 4 examined *Arenicola* from the pilot experiments, 1 contained 1 *M. balthica* of 0.57 mm.

NEREIS DIVERSICOLOR

No sediment & azoic sediment. The number of surviving *M. balthica* was significantly lower in treatments *Nereis* was present (Figure 5). There was no difference in the number of surviving *M. balthica* with and without sediment in the absence of *Nereis*, but in the presence of *Nereis* the
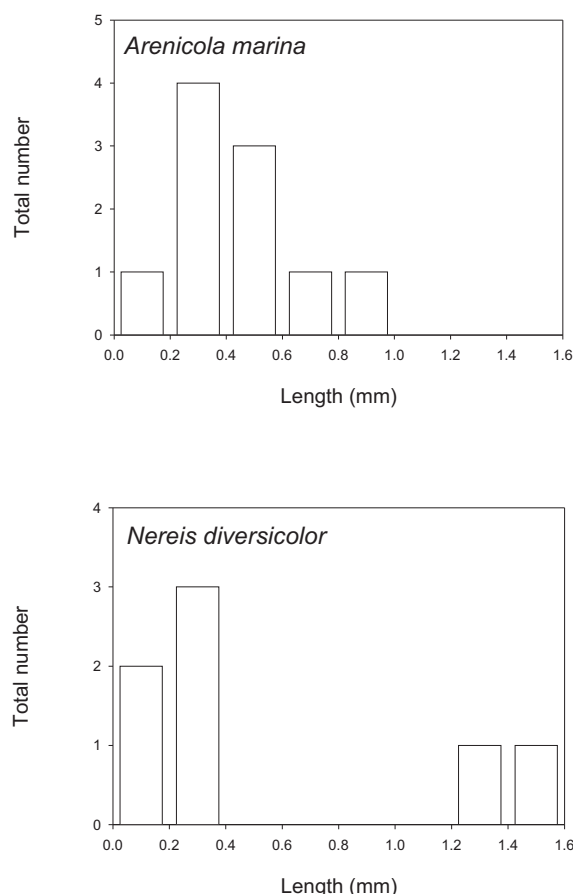
Figure 4. Length-frequency distribution of *Macoma balthica*, found in the stomachs of *Arenicola marina* and (bottom) *Nereis diversicolor.*

Table 3. *Macoma balthica* in the stomach contents (±95% confidence intervals) of *Arenicola marina* and *Nereis diversicolor*. From stomach contents, gut throughput times (GTT) and density in the field, mortality rates of *M. balthica* were calculated. All values are average from April to June.

Species	Arenicola marina	Nereis diversicolor
N	87	120
# *Macoma balthica* worm^{-1}	0.14 ± 0.11	0.05 ± 0.05
GTT (h)	1.1	6.7
Consumption worm^{-1} d^{-1}	3.0 ± 2.3	0.2 ± 1.0
Density worm (n m^{-2})	24 ± 6.2	272 ± 116.5
Consumption m^{-2} d^{-1}	71 ± 73	53 ± 408
Density *Macoma balthica* (n m^{-2})	17064 ± 11225	18458 ± 11780
% *Macoma balthica* consumed d^{-1}	0.4% ± 0.2%	0.3% ± 1.3%

number of surviving *M. balthica* was significantly higher in the presence of sediment (Table 4A).

Alternative prey. Experiments with sediment from the field, which contained *M. balthica* and many other meiofaunal organisms, showed that the number of surviving *M. balthica* was significantly lower in the presence of *Nereis* than without these polychaetes (Table 5A, Figure 6).

RETUSA OBTUSA

No sediment & azoic sediment. The number of surviving *M. balthica* was significantly lower in treatments where *Retusa* was present than in no-predator treatments (Figure 5). There was no effect of sediment presence on the number of surviving *M. balthica* in the presence of *Retusa* (Table 4B).

Alternative prey. *Retusa obtusa* did eat *M. balthica* in the presence of alternative prey (Figure 7). The number of surviving *M. balthica* at the end of the experiment was significantly lower in the presence of *Retusa* (ANOVA, df = 9, F-ratio = 5.79, p = 0.043).

Table 4. 2 factor-ANOVA table. Effect of Nereis *diversicolor* and *Retusa obtusa* on the number of surviving *Macoma balthica*, with and without sediment in the laboratory experiment.

A. *Nereis diversicolor*

Source	Df	MS	F-ratio	p-value
Nereis presence	1	371.6	19.91	0.0001
Sediment presence	1	113.2	6.07	0.0186
Nereis x Sediment	1	223.5	11.97	0.0014
Residual	37	18.7		
Total	40			

B. *Retusa obtusa*

Source	Df	MS	F-ratio	p-value
Retusa presence	1	153.3	10.15	0.0029
Sediment presence	1	0.48	0.03	0.8589
Retusa x Sediment	1	13.0	0.86	0.3586
Residual	37	15.1		
Total	40			

Table 5. 2 factor-ANOVA table. Effect of *Nereis diversicolor* and *Arenicola marina* on the number of surviving *Macoma balthica* in sediment from the field (with alternative prey) in the laboratory.

A: *Nereis diversicolor*

Source	Df	MS	F-ratio	p-value
Experiment number	2	64677.0	120.06	0.0000
Nereis presence	1	4120.6	7.65	0.0098
Nereis presence x experiment	2	321.5	0.60	0.5572
Residual	29	539.7		
Total	34			

B: *Arenicola marina*

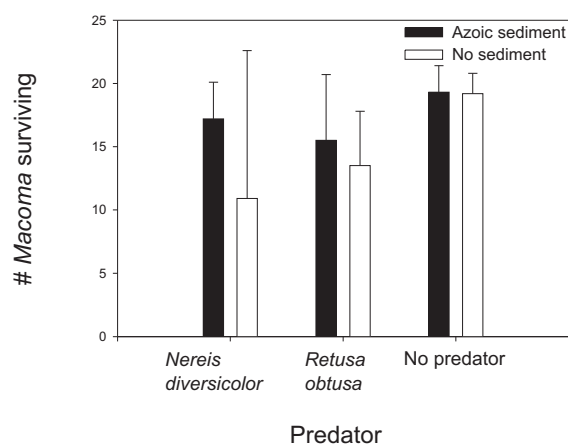| Source	Df	MS	F-ratio	p-value
Experiment number	2	27468	30.07	0.0000
Arenicola presence	1	3281	3.59	0.0713
Arenicola presence x experiment	2	6992	7.65	0.0030
Residual	22	913		
Total	27			

Figure 5. Number of surviving 0-group *Macoma balthica* (+SD) in laboratory predation experiments with *Nereis diversicolor and Retusa obtusa*, with and without sediment. All experiments started with 20 *M. balthica.*
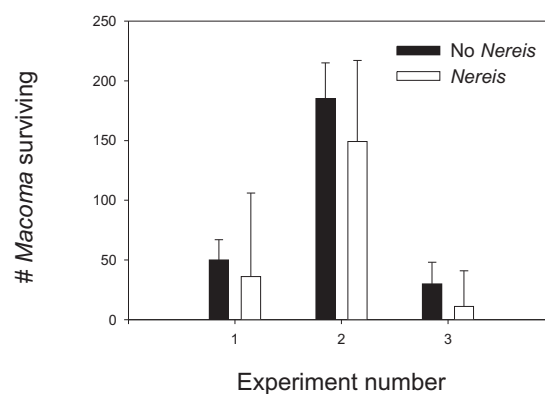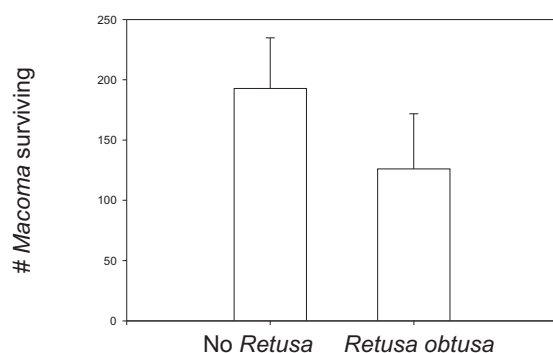

Figure 6. Number of surviving 0-group *Macoma balthica* (+SD) in 3 laboratory predation experiments with and without *Nereis diversicolor,* in natural sediment (with alternative prey present). The initial number of *M. balthica* in the sediment varied between experiments and was unknown.

Figure 7. Number of surviving 0-group *Macoma balthica* (+SD) in laboratory predation experiments with and without *Retusa obtusa*, in natural sediment (with alternative prey present). The initial number of *M. balthica* in the sediment varied between experiments and was unknown.
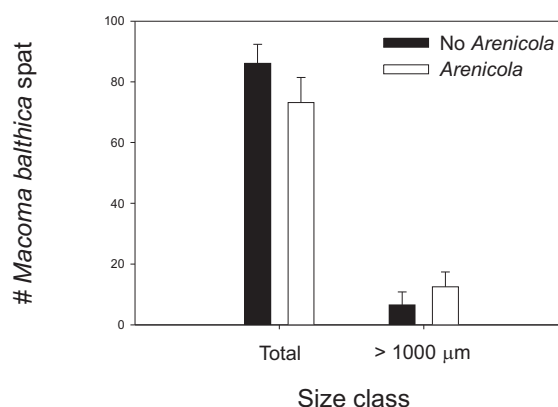
Figure 8. Number of surviving *Macoma balthica* (+SD) in laboratory predation experiments with and without *Arenicola marina* in azoic sediment. The experiment started with 100 *M. balthica.*

ARENICOLA MARINA

In the absence of *Arenicola*, an anoxic layer of sediment was usually present below the sediment surface, while this layer was never present with *Arenicola*.

Azoic sediment. *Arenicola* decreased the number of juvenile *Macoma balthica* in

laboratory experiments in the presence of azoic sediment without other prey (ANOVA, df = 14, F-ratio = 12.11, p = 0.004) (Figure 8). The number of juvenile *M. balthica* retained on the 1 mm sieve (at the start of the experiment all *M. balthica* could pass through this sieve), however, was significantly higher in the presence of *Arenicola* (ANOVA, df = 14, F-ratio = 6.27, p = 0.026).

Alternative prey. *Arenicola* did not have a significant effect on 0-group *M. balthica* abundance in experiments with sediment from the field containing alternative prey (Figure 9, Table 5B).

In these experiments, there was no effect of lugworm presence on the size of *M. balthica*. As the number of *M. balthica* at the start of the experiment was unknown and probably different in each container, large variations in these numbers may have affected the outcome of this experiment.

Field experiments

In the *Arenicola* density manipulation experiments many *Nereis* (in ambient densities) were present in the plots, while in the *Nereis* density manipulation experiments no adult and only few juvenile *Arenicola* were present in the cages.

ARENICOLA MARINA

Manipulated lugworm density ranged from 2 to 54 m^{-2}. There was a significant negative effect of *Arenicola* abundance on the density of 0-group *Macoma balthica* (Table 6, Figure 10), while there was no effect on the number of 1+*M. balthica* (Table 6, Figure 11). It is remarkable though, that there was a significant positive relation between the number of lugworms and adult *M. balthica* in the first experiment (linear regression, p = 0.044, R^2=0.37, *M. balthica* = 5.99 *Arenicola* + 265).

NEREIS DIVERSICOLOR

Density of *Nereis* was manipulated successfully. Densities in the cages ranged from 100 to 2200 m^{-2}. In the third experiment, at location 7, 4 out of 12 cages accidentally enclosed crabs with a carapace width of more than 15 mm. In this experiment, both

Figure 9. Number of surviving *Macoma balthica* (+SD) in 3 laboratory predation experiments with *Arenicola marina*, in sediment with alternative prey. The initial number of *M. balthica* in the sediment varied between experiments and was unknown.
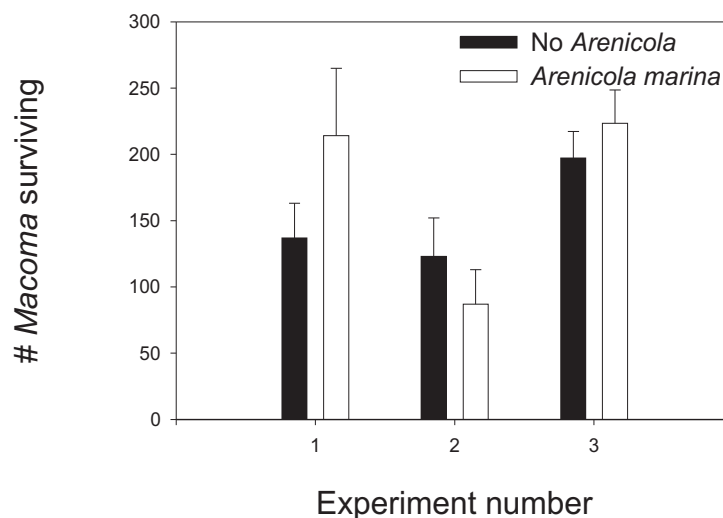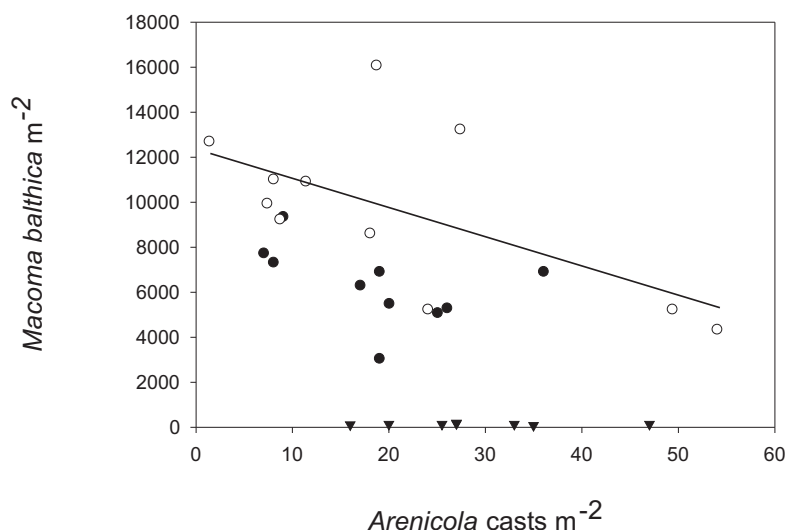
Figure 10. The relation between the number of *Arenicola marina* and 0-group *Macoma balthica* in 3 density manipulation experiments in the field.▼ Location 1,● location 2&3, ○ location 4. Significant regression lines are drawn.

Nereis and *Carcinus* had an effect on the 0-group *M. balthica* densities, according to the formula:

M. balthica = 48705 - 11 x # *Nereis* - 326 x # *Carcinus* (Multiple regression, p = 0.0167, R^2=0.64). Thus, during the 42 d study period, 1 crab ate the same amount of *M. balthica* as (326/11=) 28 *Nereis*. There was a significant negative effect of *Nereis* abundance on the density of 0-group *Macoma balthica* (Table 7, Figure 12). In this analysis, the second experiment (at location 7) is divided in the treatments with and without crabs and thereby analysed separately. There was a significant positive effect of *Nereis* density on the number of 1+ *M. balthica* (Figure 13, Table 7), but there was no significant effect of experiment number and crab presence.

By dividing the slope of the regression line (relation number of worms with number of *M. balthica*) by the duration of the experiment for the significant experiments, it is possible to estimate the consumption worm^{-1} d^{-1}. This is necessary to be able to estimate the consumption/disturbance rates, because the duration of the experiments was not equal. Table 8 shows that 1 *Arenicola* killed 4.24 *M. balthica* per d in the third experiment. 1 *Nereis* consumed 0.02 *M. balthica* d^{-1} in the first and 0.30 d^{-1} in the third

Table 6. GLM table. Density manipulation experiments with *Arenicola marina* in the field, effect on the number of surviving 0-group and adult *Macoma balthica*.

0-group *Macoma balthica*, R^2=0.80

Source	Df	MS	F-ratio	p-value
Experiment	2	1.64E8	35.93	0.0000
Arenicola density	1	0.47E8	10.44	0.0034
Residual	25	0.04E8		
Total	28			

Adult *Macoma balthica* R^2=0.76

Source	Df	MS	F-ratio	p-value
Experiment	1	907163	58.93	0.0000
Arenicola density	1	1388	0.09	0.7674
Residual	18	15393		
Total	20			

Figure 11. The relation between the number of *Arenicola marina* and 1+group *Macoma balthica* in 2 density manipulation experiments in the field. ● Location 2&3, ○ location 4. Only significant regression lines are drawn.
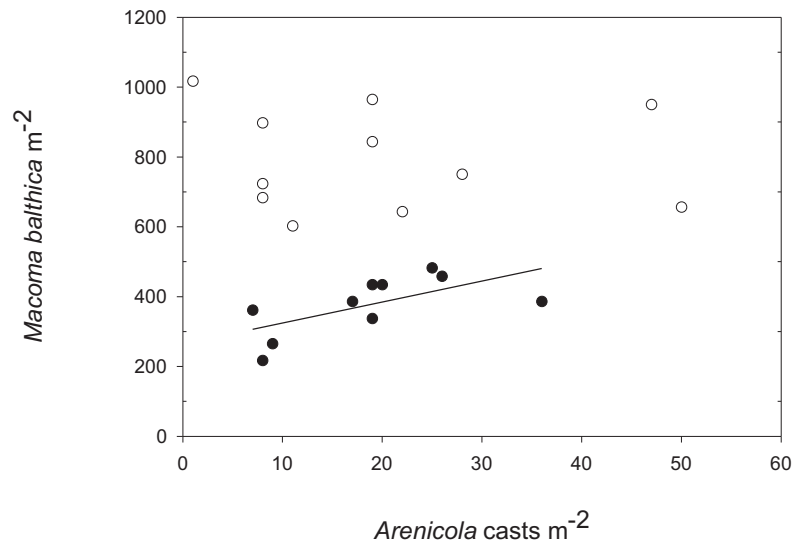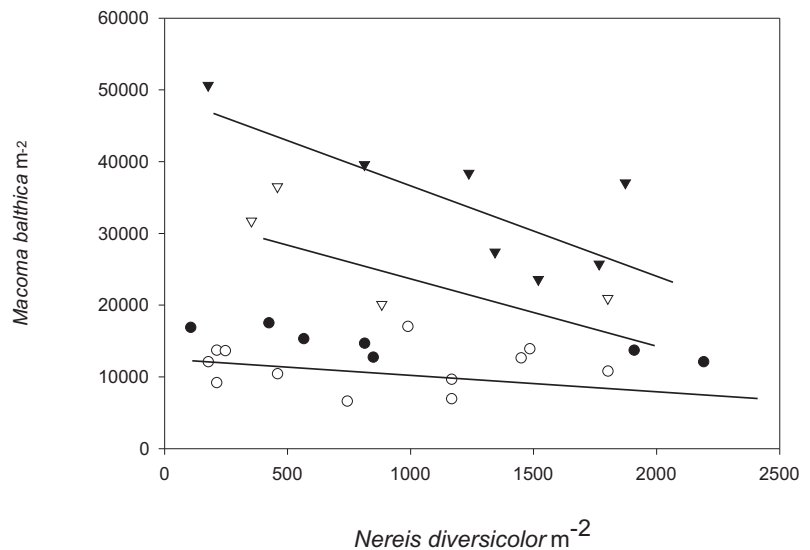
Figure 12. The relation between the number of *Nereis diversicolor* and 0-group *Macoma balthica* in 3 density manipulation experiments in the field. ● Location 5, ○ location 6, ▼ location 7 without crabs, ▽ location 7 with crabs. Only significant regression lines are drawn.

Figure 13. The relation between the number of Nereis *diversicolor* and 1+group *Macoma balthica* in 3 density manipulation experiments in the field. ● Location 5, ▼ location 6, ○ location 7. Only significant regression lines are drawn.
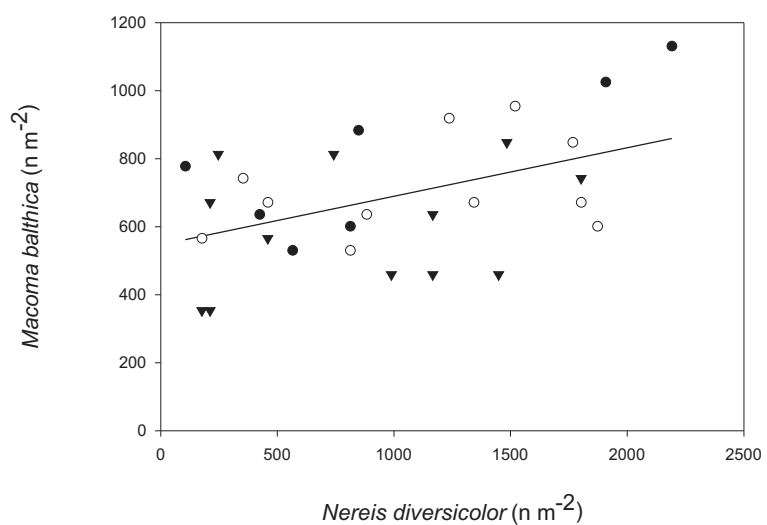
Table 7. GLM table. Density manipulation experiments with *Nereis diversicolor* in the field, effect on the number of surviving juvenile and adult *Macoma balthica.*

0-group *Macoma balthica*, R^2=0.87

Source	Df	MS	F-ratio	p-value
Experiment	3	1.27E6	56.28	0.000
Nereis density	1	116596	5.15	0.032
Residual	25	22642		
Total	29			

Adult *Macoma balthica* R^2=0.36

Source	Df	MS	F-ratio	p-value
Experiment	3	38.8008	1.80	0.1737
Nereis density	1	149.011	6.90	0.0145
Residual	25	21.6034		
Total	29			

experiment, in treatments without crabs.

DISCUSSION

In the period that *M. balthica* is <1.5 mm, there is a negative effect of *Nereis* presence on the abundance of 0-group *M. balthica* in field and laboratory experiments. A negative effect of *Arenicola* was found in the field, but not in all laboratory experiments. As juvenile *M. balthica* was found in the stomach contents of both polychaetes in the field and laboratory, polychaete predation on *M. balthica* is a mechanism that can at least partly explain these density reductions. Above 1.5 mm shell length, the bivalves reached a size refuge. In stomach contents of *Nereis* in both laboratory and field, we never found a *M. balthica* >1.5 mm. The largest *M. balthica* found in *Arenicola* was 0.92 mm. *Arenicola* even had a positive effect on 0-group *M. balthica* >1 mm in 1 of the laboratory experiments. This suggests that the presence of *Arenicola* increases the growth rate of 0-group *M. balthica* , through a so far unknown mechanism. *Arenicola* is probably not a real *predator* on *M. balthica* , as predation supposes an

Table 8. Relation between the number of polychaetes and *Macoma balthica*-spat in the density manipulation experiments in the field with *Arenicola marina* and *Nereis diversicolor.* 'Slope' is the slope of the regression line, which describes the relation between the number of *M. balthica* , and the number of polychaetes. By dividing this slope by the duration of the experiment, the number of *M. balthica* that was eaten (or disturbed) per polychaete per day was calculated (only for the significant relations).

Location	Species	p-value	R^2	Slope	*Macoma* predator^{-1} day^{-1}
1	*Arenicola marina*	0.65	0.00	-0.92	
2 & 3	*Arenicola marina*	0.07	0.36	-117	
4	*Arenicola marina*	0.03	0.41	-123	4.24
5	*Nereis diversicolor*	0.03	0.64	-0.23	0.02
6	*Nereis diversicolor*	0.95	0.00	-0.10	
7	*Nereis diversicolor*	0.04	0.59	-12.6	0.30
7	*Nereis diversicolor* with crabs	0.24	0.57	-9.3	

active and selective searching for prey. This is not the case for *Arenicola*, which feeds on sediment in bulk and ingests the *M. balthica* -spat, which have the same size as the sand grains. It does not matter whether *M. balthica* dies after active selection or after bulk feeding on sediment, it dies anyway. *Retusa* ate *M. balthica* -spat in laboratory experiments, both with and without sediment, but the number of *M. balthica* eaten by 1 *Retusa* was low. As there was no overlap in the distribution of *Retusa* and *M. balthica* -spat in April, *Retusa* cannot be predator on *M. balthica* -spat in the field. In August, there was overlap in distribution and *Retusa* densities had increased. Since *Retusa* swallows its prey whole (Stamm 1995) and the largest *Hydrobia ulvae* that have been recorded in *Retusa* stomachs measured 1.9 mm (Berry 1988), we expect no predation on *M. balthica* >2 mm. Therefore, *M. balthica* was too large (4.2 mm) for *Retusa* predation in August.

The magnitude of consumption was comparable in field experiments and stomach content analysis for both *Arenicola* and *Nereis*. For *Arenicola*, from stomach content analysis, we expect a consumption of 71 *M. balthica* m^{-2} d^{-1} at the average density of 24 *Arenicola* m^{-2} (Table 3). From field experiments, we expect a consumption of 102 *M. balthica* m^{-2} d^{-1} at this lugworm density. For *Nereis*, from stomach content analysis, we expect a consumption of 53 *M. balthica* m^{-2} d^{-1} at the average density of 272 *Nereis* m^{-2} (Table 3). From field experiments, we expect a consumption of 5 to 116 *M. balthica* m^{-2} d^{-1} at this ragworm density (Table 8).

In some of the experiments (especially in the field), the effects of predation/ingestion and disturbance could not be viewed separately from each other. The sediment reworking activities of some infaunal invertebrates, like the lugworm (Flach 1992a) may cause disturbance or death of *M. balthica* and other small benthos (Hunt & Scheibling 1997). As *M. balthica* is very mobile during its early life history (Armonies 1994b), disturbance may stimulate the small benthos to migrate away from locations with many polychaetes (Flach & De Bruin 1994). This increased migration can possibly explain the reduced number of *M. balthica* in the experiments with *Arenicola*, a very active bioturbator, as *M. balthica* was not enclosed in cages in these experiments. However, as calculated above, the stomach contents of *Arenicola* can explain 70% of the disappearance of *M. balthica* in field experiments and therefore killing by ingestion seems to be the major cause of mortality by lugworms.
As *Macoma balthica* spat can stand burial in anoxic sediment for 10 days without mortality (Elmgren *et al.* 1986), we do not expect that burial by *Arenicola* casts had any adverse effects on *M. balthica* spat.

Other authors have also described the adverse effects of polychaetes on juvenile bivalves. Flach (1992a) manipulated *Arenicola* densities in the field and found a negative correlation between densities of bivalve-spat (*Cerastoderma edule, Macoma balthica, Angulus tenuis, Mya arenaria, Ensis* spec.) and lugworm densities, although the numerical effects were much smaller than in the current study. Flach assumed that disturbance (especially by the funnels) was the mechanism explaining reduced

densities. The priapulid *Halicryptus spinulosus* reduced the number of settling *M. balthica* postlarvae in the Baltic. As no *M. balthica* was found in the guts of *Halicryptus*, this effect was probably due to disturbance (Aarnio *et al*. 1998).

We found an unexpected significant positive relation between *Nereis* and 1+group *M. balthica* abundance in field experiments. As these experiments were conducted in cages that did not allow migration of adults in and out of the experimental plots (mesh maximal 2x2 mm), this effect cannot be explained by selective im- or emigration. Therefore, the lower densities of large *M. balthica* at low experimental *Nereis* densities and vice versa must be explained by a higher mortality at low *Nereis* abundance, for which we know no mechanism. The 2 highest points in Figure 13 play a major role in causing the positive relation between *M. balthica* and *Nereis* densities. Without these 2 data points, no relation between *Nereis* and adult *M. balthica* density exists. Therefore, we believe this relation to be a Type I error (though with a very low probability, p = 0.0087).

From field experiments, it also became clear that polychaetes were not the only factor affecting *M. balthica* -spat densities. For example, in the third *Nereis*-enclosure experiment, *Nereis* and crabs inside the cages consumed significant numbers of *M. balthica.* Since the density outside the cages (319-391 m^{-2}) where all predators where present, was lower than inside the cages where crabs and *Nereis* were present (593-1433 m^{-2}), there were other factors, besides crabs and *Nereis*, that caused a reduction in spat densities that we did not cover in this experiment.

In many other studies, crustacean predation is considered very important for bivalve spat abundance (Van der Veer *et al*. 1998; Strasser & Günther 2001; Chapter 4). Combined, the shore crab *Carcinus maenas* and the brown shrimp *Crangon crangon* consumed 7.3 *M. balthica* m^{-2} d^{-1} on the low tidal flats and 2.7 *M. balthica* m^{-2} d^{-1} on the high tidal flats at the Groninger Wad (Chapter 4), while polychaete consumption can be higher than 100 m^{-2} d^{-1} (Table 3). A further indication of the importance of polychaete predation comes from the field experiments: in the enclosure experiment 1 small crab consumed the same amount of bivalves as 28 *Nereis*. The ratio of the densities of these 2 species was however more like 1/175, showing the numerical importance of *Nereis* predation. Thus, the number of *M. balthica* killed by polychaetes seems to be higher than the number eaten by epibenthic crustaceans, especially in the period that the spat is <1 mm (Strasser *et al*. 2001).

Year-class-strength of *M. balthica* is determined somewhere between the egg stage in early spring and the post-settlement stage next August (Honkoop *et al*. 1998). Egg production and shrimp predation can explain a portion of the year to year variability in *M. balthica* recruitment (Beukema *et al*. 1998). Based on the current study, it can be hypothesised that polychaetes play a larger role in determining the year-class strength of *M. balthica* than the epibenthos, as they consume large amounts of bivalves shortly after settlement.

Average densities per year from the long term-monitoring of the macrobenthos on 5 stations on the Groninger Wad by RIKZ (Essink 1978; Essink *et al*. 1998b) were used

to examine the effect of *Nereis* (1969 to 1999) and *Arenicola* (1976 to 1999) on the abundance *M. balthica* -spat. Our experiments showed that polychaetes affect *M. balthica* -spat in spring, but in the monitoring study spat was not present in the spring samples. Therefore, the density of *M. balthica* -spat in summer and/or autumn (August-November) was related to polychaete-density in spring of the same year (between February and May). A prerequisite for a between-year correlation between the densities of *M. balthica* and the polychaetes is that there was variation in the densities of both *M. balthica* and the polychaetes. As the densities and standard deviations of the average densities per year were 622±667 for *M. balthica* -spat, 278±165 for *Nereis* and 33±35 for *Arenicola*, there was a large enough variation in densities between years. Nevertheless, we found no relation between the densities of *M. balthica* and *Arenicola* or *Nereis* (Spearman's rank correlations, *M. balthica-Arenicola*=0.083, p = 0.706, n=31, *M. balthica-Nereis*=0.001, p = 0.994, n=24). Therefore, although the polychaetes consume large quantities of *M. balthica* -spat, polychaete density does not seem to be a major factor determining spat density in autumn.

In the calculation of predation rates from the stomach contents of *Arenicola* and *Nereis* the GTT used were important. For *Arenicola* the GTT of 66 min we calculated was longer than GTT of 15 and 63 minutes as calculated by Kermack (1955) and Plante and Mayer (1994), but very similar to values of 1 to 1.5 h calculated by Plante and Mayer (1996). Thus, an underestimation of predation pressure is more likely than an overestimation. The GTT of 6.7 h we used in our calculations for *Nereis*, is a bit shorter than the value found by Masson *et al.* (1995) (75% of the gut of emptied after 8 h) and may have led to an overestimation of predation pressure.

We can draw the general conclusions that both *Arenicola marina* and *Nereis diversicolor* cause a reduction in *Macoma balthica*-spat abundance. Effects on densities in the field were expected from stomach contents analysis and were shown in enclosure experiments. Nevertheless, the polychaetes were no important factor determining the year-class-strength of *M. balthica. Retusa* was no significant predator, because in early spring there is no overlap in distribution with *M. balthica* -spat, while later in the year *M. balthica* probably outgrows *Retusa* mouth size.
Similar effects of polychaetes can be expected for other bivalve-species with small benthic spat, like *Mya arenaria* and *Cerastoderma edule*. We did not find these bivalves in the stomachs of the polychaetes, but this was probably because settlement of these species occurs later in the season. *Retusa*-impact on these species may be larger because due to the later settlement, periods of spat- and *Retusa*-abundance match better than for *M. balthica.*

The importance of polychaetes for *Macoma balthica* spat abundance probably depends on the examined scale. In the intertidal polychaetes seem to be important predators on *M. balthica* spat. However, *Arenicola marina* and *Nereis diversicolor* are rare or absent in the subtidal Wadden Sea and coastal North Sea (Dekker & De Bruin 1998; Holtmann *et al.* 1998) while *M. balthica* -spat is also very rare at these locations

(Chapter 2). Therefore, we hypothesise that *M. balthica* spat lives in the intertidal despite the presence of polychaete predators. The impact of worms in the intertidal is probably much lower than the potential predation pressure of epibenthic crabs and shrimps in the subtidal.

CHAPTER 6

Can predation and migration risk explain the mortality of *Macoma balthica* on tidal flats?

J.G. HIDDINK

ABSTRACT

On the tidal flats of the Wadden Sea, many predators consume the bivalve *Macoma balthica*. Another important mortality causing factor is the migration to and from the high tidal flat nurseries. This study evaluates if *M. balthica* mortality as observed on tidal flats can be explained from consumption by predators and migration risk, by means of a model based on empirical data. Density was modelled as a function of settlement density, predation and migration mortality only.

A model that included predators for which detailed knowledge on consumption and size-selection was available could explain the mortality pattern in time, but underestimated mortality rate by a factor 1.5. An extended model that included higher densities of some of the predators, additional predator species, starvation, and death due to parasitism could explain all observed mortality.

INTRODUCTION

According to Werner and Gilliam (1984) an animal should try to minimise its mortality to growth ratio. If another habitat shows lower mortality or higher growth rates, it may be profitable to migrate to the other habitat, provided that migration costs are not too high.

When trying to understand under what circumstances migrations are profitable, it is required to know what causes mortality. Only when the mortality can be explained from consumption by known predators and other factors, the adaptive value of migrations can be understood.

M. balthica is a small bivalve found in coastal areas in temperate and arctic regions of the Northern Hemisphere (Beukema & 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 *M. balthica* settles in May at a size of 300 ìm in the low intertidal. Subsequently, these animals migrate to the high intertidal in June, where they stay until winter. In winter, juvenile *M. balthica* (5 mm) migrate back to the low intertidal and the North Sea (Beukema & De Vlas 1989; Chapter 2).

Predators on *Macoma balthica* include the brown shrimp *Crangon crangon*, the shore crab *Carcinus maenas*, gobies (*Pomatoschistus* sp.) and flatfish (*Pleuronectes platessa, Platichthys flesus*) (Chapter 4), the polychaetes *Nereis diversicolor* and *Arenicola marina* (Chapter 5), and several species of shorebirds (Hulscher 1982; Zwarts & Blomert 1992). During the spring and winter migration of *M. balthica* mortality is much higher than outside these periods, possibly due to increased predation on migrating *M. balthica* (Chapter 3) and because *M. balthica* end up at unsuitable locations.

In this chapter I will examine whether observed mortality of *Macoma balthica* at the Groninger Wad can be explained from consumption rates of predators and the additional mortality caused by the migration. The mortality observed on the tidal flats was compared with the mortality that could be calculated based on empirical predation rates and migration mortality values derived from earlier chapters (Chapter 2, 4 and 5) and literature values.

METHODS

Mortality of *Macoma balthica* at the Groninger Wad

Mortality of the 1998 and 1999-yearclass was estimated from repeated sampling of 57 stations at the tidal flats of the Groninger Wad. The location of sampling stations, dates

and methods are described in detail in Chapter 2.

Construction strategy and general model structure

I constructed an age-structured model that calculates the density of a *Macoma balthica*-yearclass, per 1 mm length-category, from age 0 (April of their first year) for a period of 5 years. *M. balthica* grow from 1 length class to the next and density is a function of mortality by predation and migrations only. In the model, the migration pattern as observed in the field was evaluated. *M. balthica* settled at the low tidal flats in April and migrated to the high tidal flats in May. Here they lived until January, when they migrated back to the low intertidal.

 All parameter values, predator densities and *M. balthica* settling density were derived empirically from field and laboratory studies (Chapter 2, 4 and 5). Field studies were carried out at the tidal flats of the Groninger Wad in the Dutch Wadden Sea from 1998 to 2001 and data from all 4 years were used to construct the model. The model was partitioned in low (below 0.25 m NAP, Dutch Ordinance level, close to mean tidal level) and high (above 0.25 m NAP) tidal flats, which had different predator densities and predation rates. For factors that were not studied on the Groninger Wad, literature values were used from tidal flat areas as close as possible and always in the Wadden Sea.

Description of the model

GROWTH - In the model, *M. balthica* settled in April at age 0 in the 0.5 mm length class at a density of 10000 m^{-2}. *M. balthica* grew from size class to size class according to a seasonalised Von Bertalanffy growth curve with K=0.75 and L$_{\infty}$=17.5 mm, both derived from a Ford-Walford-plot (King 1995) of field length data. Monthly growth rates were adjusted by a factor (which can be interpreted as the result of food-availability and temperature), to generate the observed seasonal growth; juvenile *M. balthica* grow from April to October, while 1+ animals show high growth rates from April to July. This factor was adjusted per month to fit the length-age curve that was generated by the model, to lengths of the 1998-yearclass on the Groninger Wad.
Preliminary tests of the model showed that size-selection by high densities of epibenthic predators could increase mean shell-length of the population by maximally 1 mm at a length of 14 mm. Because this deviation is smaller than between-year differences in the field, I assumed it was safe to use length data from the field, which are somewhat changed by size-selective predation, to fit growth rates for the model.

PREDATION - Predators considered in this study are the brown shrimp *Crangon crangon* L., 0-group and older (1+ group) shore crabs *Carcinus maenas* (L.), the ragworm *Nereis diversicolor* (Müller), the lugworm *Arenicola marina* (L.) and the oystercatcher *Haematopus ostralegus* L..

Table 1. Shape (Holling I, II or III), parameter values and fit of the regression of the functional responses for all predators. The FR describes the relation between *Macoma balthica* density (n m^{-2}) and number of *M. balthica* consumed per predator per month.

Species	Tidal level	FR Type	R^2	N	a	b	c
Crangon crangon	Low	II	0.65	8	0.301	0.001	
Crangon crangon	High	III	0.72	4	130	0.002	10926
Carcinus maenas 0- & 1-group	Low	II	0.28	4	0.250	0.0015	
Carcinus maenas 0- & 1-group	High	II	0.08	6	0.108	0.0015	
Haematopus ostralegus	Both	II	0.37	24	650	0.016	
Arenicola marina	Both	I	0.01	8	0.00526		
Nereis diversicolor	Both	I	0.21	7	0.00047		

PREDATOR DENSITIES - Densities of shrimps, crabs and polychaetes were determined on the tidal flats of the Groninger Wad between 1998 and 2001 (Chapter 4 and 5). All densities were calculated separately for the low and high tidal flats (Figure 1). I used average densities per month; missing data were linearly interpolated. In the model, equal predator densities were used for each of the 5 years examined.

Densities of *Haematopus* foraging on the tidal flats were calculated from high tide counts by De Jong and Koks (1999), a method justified by Yates and Goss-Custard (1991). I assumed that *Haematopus* roosting at the saltmarsh at high tide foraged in an area of 20 km^2 at low tide, which includes 7 km^2 of my study area. Spatial distribution of waders is primarily governed by food abundance in the high intertidal, but is limited by emersion time in the low intertidal (Wolff *et al.* 1975). For simplicity reasons, it was assumed that the predation pressure on *M. balthica* by *Haematopus* on the low and high tidal flats was proportional to the exposure time (ratio low to high = 3.1 / 9.8 h per tidal cycle).

FUNCTIONAL RESPONSES AND SIZE-SELECTION - The relation between the density of *M. balthica* in the suitable size range and predator consumption was described by a functional response (FR) that was fitted with a regression through empirical data. Whenever possible, separate FR's were fitted for low- and high-tidal-flat-predators. The FRs-fitted had a Holling type I ($y = ax$), Holling type II ($y = ax/(1+bx)$) or Holling type III ($y = a/(1+\exp(-b(x-c)))$) –shape, where y is predator consumption (prey per predator per month), x = *M. balthica* density (n m^{-2}) and a, b and c are parameters (Holling 1965). The Holling-type curve that showed the best fit with empirical data was selected for the final FR.

The deposit-feeding polychaetes probably feed on *M. balthica* -spat in numbers proportional to the amount of sediment they process. Therefore, and because field observations showed considerable scatter, I assume a linear relation (Type I) between *M. balthica* -density and intake rate (Figure 1). The parameter value a (# *M. balthica* eaten worm^{-1} month^{-1} *M. balthica* $^{-1}$ m^{-2}) was calculated from the average number of *M. balthica* per examined stomach of *Nereis* and *Arenicola* and the gut-throughput-time (Chapter 5).

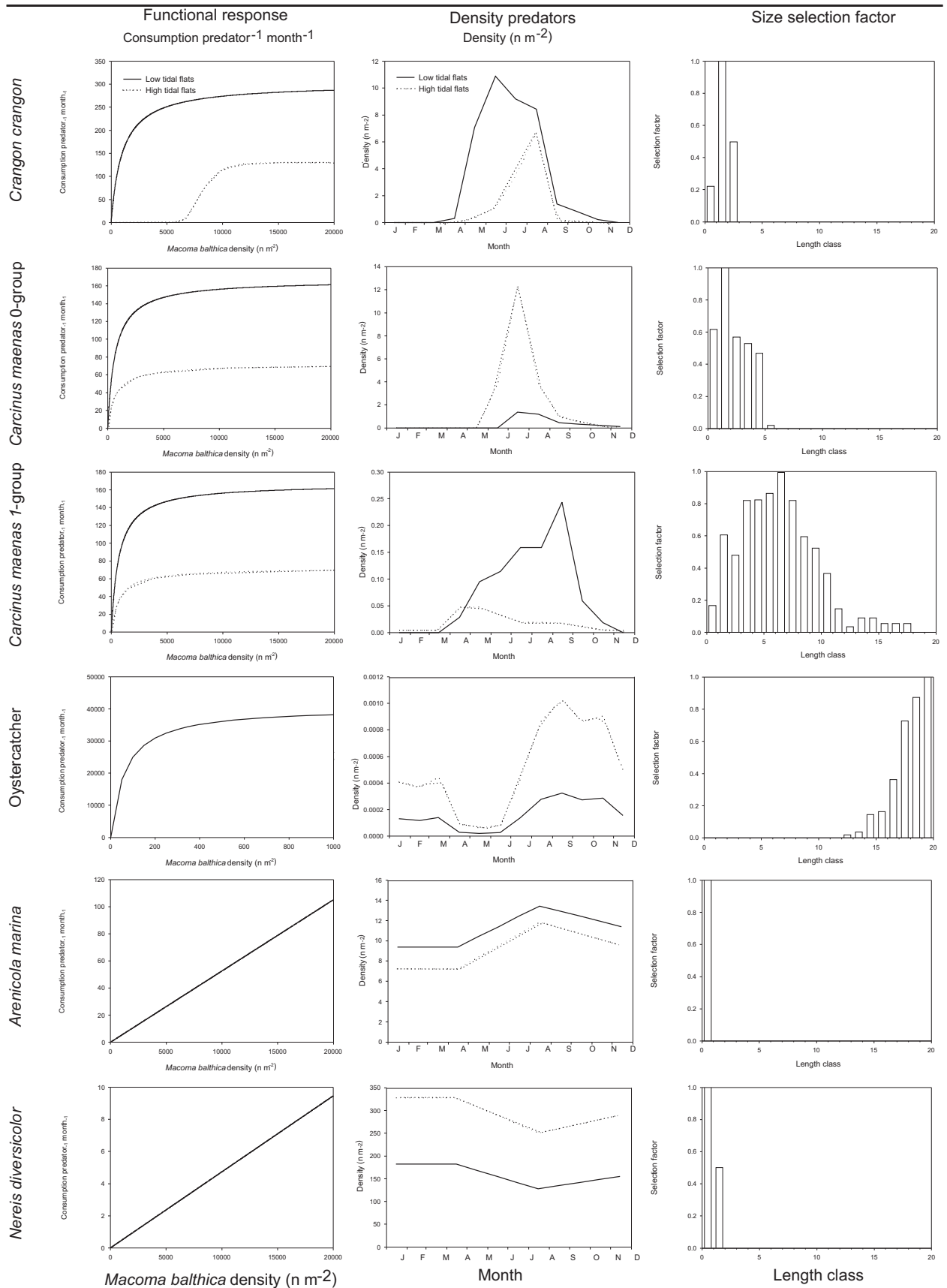*M. balthica* consumption as a function of density was never measured for *Haematopus*.

Figure 1. Functional responses, density and size-selection of all predators. Note the different x-axis scaling for *Haematopus* FR. For *Crangon crangon* and *Carcinus maenas* 0 and 1+ group, a different FR was used for the low and high tidal flats.

From available data on intake rates and densities of *M. balthica* (Hulscher 1982; Bunskoeke *et al.* 1996; Ens unpublished data), a Type II FR-curve was constructed. The effect of temperature on predation rates of predators was ignored, because knowledge on the relation between temperature and predation rates is scarce for most predators. Furthermore, the short yearly predation period of most predators on *M. balthica* would results in only minor effects of temperature on predation rates.

SIZE-SELECTION - For each predator species, a size-selection factor between 0 and 1 was assigned per *M. balthica* length category, based on laboratory size-selection experiments (Chapter 4), stomach content analysis (Chapter 4 and 5) and on literature values for *Haematopus* (Hulscher 1982). The maximum selection value was set at 1. A 0-selection value indicates that the size class was rejected, a 1 indicates strong preference for this size class.

CALCULATION OF CONSUMPTION - The number of consumed *M. balthica* per predator and per time step (1 month) was calculated from the overlap of the size distribution of the *M. balthica* population and the size-selection factors, *M. balthica* density and the FR. First, densities per size class were multiplied with the selection factors to calculate a total density that is corrected for the size selection: the density perceived by the predator. From this density, the number of consumed *M. balthica* was calculated from the FR. This number was partitioned over the different *M. balthica* size classes according to the density x size-selection ratios.

Parasite infestation

On tidal flats in the Dutch Wadden Sea, *Parvatrema affinis* only occurred in the high intertidal and only in animals >9 mm. More than 30% of the large *M. balthica* on high tidal flats may be infected (Hulscher 1973; Swennen & Ching 1974). Because infection increase rates per month were needed for the calculations, lengths were recalculated to ages, using the Von Bertalanffy-growth curve. The slope of the parasite incidence against age (in months) was used as the monthly parasite increase rate (1.03%, R^2=0.76), for animals above 9 mm (the intersection with the x-axis) on the high tidal flats. In the model, infected animals cannot loose their infection and suffer no additional mortality (but can be eaten by predators). As *M. balthica* cannot reproduce due to parasitic castration (Lauckner 1983; Pekkarinen 1987), the animals are dead from a fitness point of view.

Migration mortality

Migrations are dangerous for *M. balthica* because predation during pelagic drifting is higher than when staying buried (Chapter 3). From a field study, the additional mortality due to the spring migration was estimated at 13% and at 24% due to the winter migration, assuming that the whole population drifted and that a only fraction of the

animals really relocated (Chapter 2). As the energetic costs of forming a byssus thread are very small (Chapter 3), these costs were not incorporated in this study.

Fit of the models on empirical data

The fit of the mortality rates predicted by the models on the mortality rates of the 1998 and 1999 yearclass at the Groninger Wad was determined with a Pearson correlation. Mortality rates were calculated for 5 periods (spring migration, first summer, winter migration, second year and third year (not for the 1999 yearclass)) as described in Chapter 2 for both yearclasses and both models. A high correlation coefficient indicates that the model predicts periods with high and low mortality rates well.
The principal axis was estimated, and provided a single axis, which represents the relation between mortality rates in the models and the 1998 and 1999-yearclass (Sokal & Rohlf 1990). This method was used because the 2 mortality rates were both measured with error and therefore a regression analysis was not feasible. If the slope of the principal axis is 1, the model predicts the exact value of the mortality right.

Results

Input

The data used as input for the simple model is summarised in Figure 1 and Table 1. Some of the FR-curves showed a rather poor fit with the field data, especially those for the polychaetes and crabs. Predation rates of *Crangon* and *Carcinus* on the low tidal flats were higher than those at he high flats at equal *M. balthica* density because individuals were bigger and immersion times were longer (Figure 1). For 1+ *Carcinus* no data to fit a FR were available, therefore the 0-group FR was also used for the 1+ group.

Fit of the simple model to empirical data

The simple model underestimated the mortality in the field by a factor 1.5, but correctly predicted periods with low and high mortality rates (Figure 2, Table 2). Nevertheless, the simple model predicted a constant population size (no mortality), in the period September to January at age 0, while mortality in the field was high.

Extended model

Apparently, certain predator groups or processes were overlooked or parameter values and predator densities were underestimated. Hence, an extended model was constructed by including extra factors that were possibly important for *M. balthica* mortality.

- SHRIMPS AND CRABS that escape in front of the net during sampling may have caused an underestimation of the densities. Further, shrimps and crabs are more active and abundant at night (Ansell *et al.* 1999), while I sampled in daytime. In the extended model densities 50% above the measured values were used.

- SHELDUCK (TADORNA TADORNA) may predate on small (1.5-6.5 mm) *M. balthica* in large quantities and was added as a predator to the extended model. I assumed a type III FR with a=6.10^5, b=0.1 and c=1000. The shelduck could not be included in the simple model because there are no detailed records on the size-selection and FR of the shelduck.

- OTHER WADERS than *Haematopus* (e.g. knot *Calidris canutus* and dunlin *Calidris alpina*) feed on smaller size classes of *M. balthica.* In the extended model *Haematopus* was replaced by a general bird species with twice *Haematopus* densities, the same FR and a flat size-selection from 5.5 to 19.5 mm

- MORTALITY DUE TO PARASITE INFECTION. From data on the periwinkle (*Littorina*) is appears that trematode infected molluscs suffer higher mortality than non-infected animals (Lauckner 1986), which is also likely for *M. balthica* (Lauckner 1983). A 10% additional mortality of infected animals per month was used in the extended model.

- MORTALITY DUE TO STARVATION. *M. balthica* with a body mass index of less than 6 mg cm^{-3} die. As approximately 10% of the *M. balthica* are just above 6 mg cm^{-3} in the growing season (Hiddink, unpublished results), it seems reasonable to suppose that some of these animals die during periods with low food supply. Therefore, an additional 10% mortality per month was imposed in the months without growth, November and December.

- A HIGHER MIGRATION MORTALITY. The additional mortality values due to migration, that
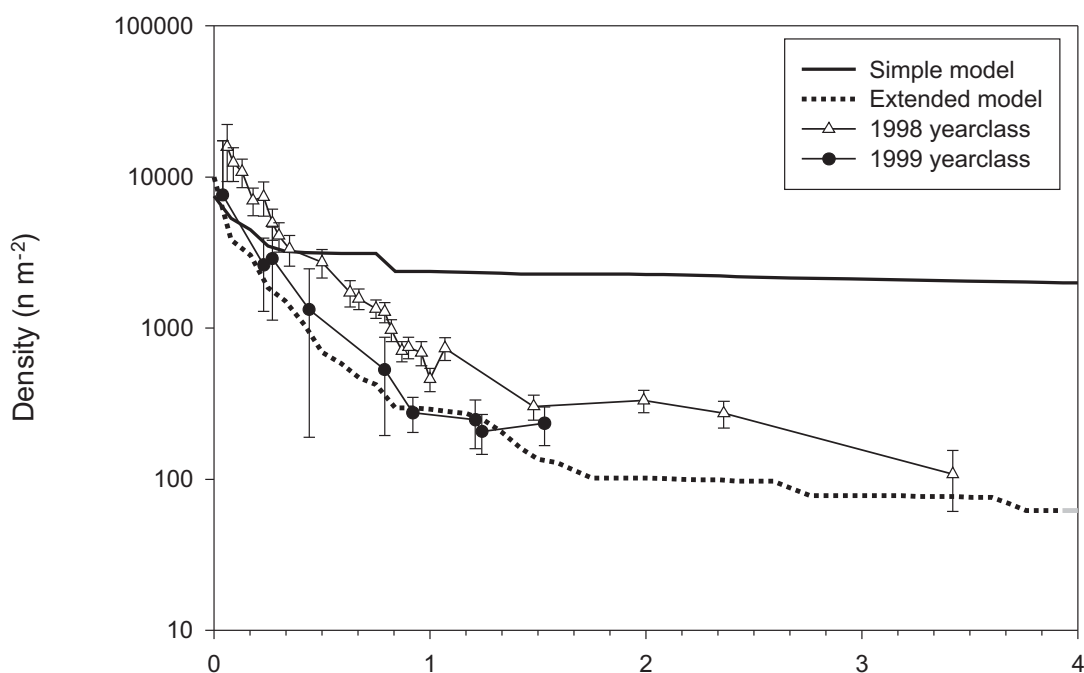

Figure 2. *Macoma balthica* density over time (±95% confidence interval), for the 1998 and 1999 yearclass at the Groninger Wad and for 2 versions of the model (simple and extended).

Table 2. Correlation between predicted (models) and observed mortality rates for *Macoma balthica* on tidal flats. The principal axis describes the relation between observed and predicted mortality rates, where y is the observed mortality on the tidal flats and x is the mortality predicted by the models.

		Simple model	Extended model
1998 yearclass	Pearson correlation	0.943	0.917
	p-value	0.016	0.028
	N	5	5
	Principal axis	y= -0.03 + 1.55 x	y = -0.0019 + 0.68 x
1999 yearclass	Pearson correlation	0.961	0.884
	p-value	0.039	0.116
	n	4	4
	Principal axis	y = -0.0024 + 1.71 x	y = -0.0001 + 0.84 x

were used in the simple model are minimum estimates, stemming from the assumption that all *M. balthica* migrated, but that not all *M. balthica* relocated during migration periods. If it is assumed that only the relocating animals migrated and therefore suffer additional mortality (the maximal estimate), the risk of migration would be much higher. Intermediate values of 53% for the spring migration and 30 % for the winter migration were used.

The extended model slightly overestimated the mortality of the 1998 and 1999 yearclass in the field (Figure 2, Table 2). Therefore, I conclude that the missing mortality in the simple model may be explained by 1 or more of the factors added to the extended model.

DISCUSSION

The simple model does not fully explain mortality as observed on the Groninger Wad. The mortality was in particularly underestimated during the period from September to January during their first year. After the age of 1.5 years, the slope of log-density against time (the mortality rate) is approximately equal for the 1998-year-class and the simple or the extended model (Figure 2). Therefore, after this age the predators that were included in the simple model may explain mortality as observed on the tidal flats. The high correlation coefficients in Table 2 show that, for both the simple and the extended model, the ratio of the mortality rates for the examined periods was estimated quite accurate. Therefore, it is likely that that the factors causing mortality on tidal flats are included in the models, but that the exact impact of these factors was over- or underestimated.

It should be kept in mind that an underestimation of mortality due to known factors is much more likely than an overestimation. It is much more likely that a predator eating *M. balthica* is missed than that the predation pressure of a predator that does hardly eat *M. balthica* is overestimated.

The extended model could explain all mortality, but as factors assumed to have caused the mortality, but have not been studied in enough detail were included, few conclusions can be drawn from this fit. Nevertheless, it is likely that the factor(s) causing missing mortality is among the factors included in the extended model (underestimation of epibenthic predator densities, shelduck predation, other important *M. balthica* eating waders aside *Haematopus*, starvation in winter, mortality caused by parasites). Of these, underestimation of shrimp densities, shelduck predation and parasite induced death are best established by studies.

It is likely that predation pressure by shrimps in the simple model was underestimated. Sampling was carried out in daytime with a 0.5 m wide pushnet (Chapter 4). Large shrimps, which probably eat more than small shrimps, could escape relatively easy in front of the net. Further, Ansell et al. (1999) found that shrimp and crab abundance was higher at night than in daytime.

Shelduck predation on *M. balthica* surely exists; in England 10.6% of the stomachs of shelducks contained small *M. balthica* , which constituted 7.3% of the volume (Olney 1965). Also, Goethe (1961) found small *M. balthica* in shelduck stomachs and Poutsma (1969) found *M. balthica* shell fragments in the faeces of shelduck on the Groninger Wad. As the numbers of shelducks on high tide roosts near the Groninger Wad from September to November were high (1000-7000, De Jong & Koks 1999), the shelduck may contribute to the observed mortality in autumn. The dunlin *Calidris alpina* is also abundant on the Groninger Wad (1000-9000, De Jong & Koks 1999) and does feed on *M. balthica* (Senner *et al.* 1989; Durell & Kelly 1990). The knot *Calidris canutus*, which prefers medium sized *M. balthica* as food source (Zwarts & Blomert 1992), is relatively rare on the Groninger Wad (De Jong & Koks 1999).

As already mentioned in the results, *Parvatrema* infection of *M. balthica* probably results in increased mortality rates and may be important in explaining the underestimation of mortality rates in the simple model.

In conclusion, the larger part of the mortality of *Macoma balthica* at the Groninger Wad can be explained from the simple model, which only included factors for which detailed information was available (predation and migration risk). If other predators and processes, for which less detailed information is available, are included in the extended model, all *M. balthica* mortality could be explained.

CHAPTER 7

Adaptive value of migrations and nursery use for an intertidal bivalve

J.G. HIDDINK

ABSTRACT

Ontogenetic niche changes (migrations) are worthwhile when there exist spatial differences that are age or size-selective. In the Wadden Sea, juveniles of the bivalve *Macoma balthica* use nurseries in the high intertidal, while adults are more abundant in the low intertidal. Therefore, a *M. balthica* individual has to migrate twice, from the primary settlement locations (low) to the high-level nursery (spring migration) and back to the low intertidal at an age of 9 months (winter migration).

This study evaluates by means of a model based on empirical data, under what conditions the costs of migration (increased mortality) are traded-off against an increased reproductive output (RO). Density was modelled as a function of predation and migration mortality. From density, the RO over a period of 5 years was calculated, assuming that parasitised animals do not reproduce.

RO was maximised for *M. balthica* that settle in the high intertidal and migrate to low tidal flats at an age of approximately 9 months. Shrimp predation makes living on the low tidal flats unfavourable for small *M. balthica.* Parasitation by the trematode *Parvatrema affinis* makes it beneficial for *M. balthica* to leave the high tidal flats around the age of 1 year. Of other examined predators (crabs, birds and polychaetes), some did affect the RO, but none of them had an effect on the migration moment that maximises RO, because spatial differences in predation pressure were not large enough to trade off migration costs.

In conclusion, migrations of *M. balthica* to and from nurseries on high tidal flats of the Wadden Sea may be seen as an adaptation to avoid shrimp predation on the juveniles and parasite infection of the adults. Although the costs of the migration are large, fitness is increased due to the migration because it is traded off by an increased RO.

INTRODUCTION

Nurseries, where juveniles are abundant, while adults are scarce, are found throughout the animal kingdom. Very clear examples of differential habitat use can be found in many metamorphosing animals, such as insects and amphibians with an aquatic larval stage. Other examples are found in the marine environment. Juvenile plaice *Pleuronectes platessa* live on tidal flats and in other shallow coastal areas, while adults live in deeper waters (Wennhage & Pihl 2001). Juvenile shore crabs *Carcinus maenas* live concentrated in the highest intertidal, while adults are most abundant in the low intertidal and subtidal (Klein Breteler 1976). As nurseries are spatially separated from the locations where the adults live, nursery-use implies that migrations have to be undertaken.

If a nursery is defined by the differential distribution of juveniles and adults, nurseries do not need to be adaptive. Passive dislocations usually affect small animals stronger than larger animals and therefore may 'sort' animals to size-groups. Examples of this kind of 'nurseries' may be found in marine high-energy environments, like sandy beaches or sandy tidal flats (Emerson & Grant 1991).

Change of living area by migration is adaptive when the benefits of the migration (the difference in survival or energy balance between 2 areas) are larger than the costs of the migration (energetic costs or number of animals dying due to the migration). Therefore, the animals have to trade off the short-term costs of migration against the possible long-term benefits in terms of increased reproductive output, if the costs of migration are constant. The moment in the life cycle that is optimal to change habitat, is the moment when growth or survival in the first habitat becomes lower than in the second habitat (Werner & Gilliam 1984).

This study examines the adaptive value of migrations and nursery use for the bivalve *Macoma balthica* (L.). *M. balthica* is a small bivalve found in coastal areas in temperate and arctic regions of the Northern Hemisphere (Beukema & 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 *M. balthica* settles in May at a size of 300 ìm in the low intertidal. Subsequently, these animals migrate to the high intertidal in June, where they stay until winter. In winter, juvenile *M. balthica* (5 mm) migrate back to the low intertidal and the North Sea (Beukema & De Vlas 1989; Chapter 2).

Migration occurs via byssus drifting, where increased drag on byssus threads decreases sinking rates (Sigurdsson *et al.* 1976; Sörlin 1988). Sinking rates depend on shell size and thread length and can be up to 5 times lower for small bivalves with a byssus thread compared to small bivalves without (Sörlin 1988; Beukema and De Vlas 1989). For departure from the sediment surface, current velocities of 0.1 cm.s^{-1} can be

sufficient (Lane *et al*. 1985). Mortality is higher during migration periods (Chapter 2), possibly due to fish predation on byssus-drifting *M. balthica* (Chapter 3).

A factor may stimulate nursery use if a) it acts size- or age-selective and if b) it is not homogeneously distributed over the low and high tidal flats. Site- and size-selective predation was found for epibenthic predators (Chapter 4), polychaetes (Chapter 5), waders (Hulscher 1982) and parasites (Hulscher 1973; Swennen & Ching 1974; Lim & Green 1991)

Beukema (1993a) proposed that the nursery use of *M. balthica* , with a spring and winter migration, was an adaptation to 1) avoid epibenthic predation on juveniles, 2) avoid disturbance of the juveniles 3) avoid parasitation and bird predation on the adults, and 4) find the best growing conditions for both adults and juveniles. Migrants should trade-off increased survival and growth on the long term (because the migration enables using predation refuges, which are different for juveniles and adults), against reduced survival on the short term because of the losses caused by the migration.

The aim of this study is to determine if nursery use of *Macoma balthica* is adaptive. Can the above mentioned factors explain nursery use of *M. balthica* and which specific factors cause nursery use? Moreover, what is the optimal timing for migration to and from the nurseries? These questions were answered by construction of a model that calculates fitness for *M. balthica* for different migration strategies as a function of the above mentioned factors. The model was used to examine if *M. balthica* can maximise survival by timely migrations between low and high tidal flats.

METHODS

Construction strategy and general model structure

I constructed an age-structured model that calculates the density of a *Macoma balthica*-yearclass, per 1 mm length-category, from age 0 (April of their first year) for a period of 5 years. *M. balthica* grow from 1 length class to the next and density is a function of mortality by predation and migrations only. All *M. balthica* live either on the low or on the high tidal flats during a time step (a month). They can migrate to the other location in the next month.

All parameter values, predator densities and *M. balthica* settling density were derived empirically from field and laboratory studies (Chapter 2 to 5). Chapter 6 describes the model in detail; I used both the simple and the extended model described in that chapter.

The difference with Chapter 6 is that in the current chapter the effect of different migration strategies on the fitness of *M. balthica* was evaluated. Therefore, *M. balthica* could migrate between the low and high tidal flats during each month. In the model calculations at the migration from low to high tidal flats, the *M. balthica* suffer the additional spring migration mortality (13%), while at migrations from high to low, they

suffer the additional winter migration mortality (24%).

Fitness measure

Fitness was defined as the total reproductive output (RO) of the population during 5 years. In the model, every *M. balthica* shows the same behaviour and therefore the RO is likewise an individual fitness measure. *M. balthica* generally starts reproducing at age 2 (Beukema *et al.* 2001). Few *M. balthica* reach an age of more than 5 years in the field (and in the model) and for practical reasons, RO was calculated only for these 5 years. RO was calculated from the number of uninfected animals alive in March for the 4 reproductive years and as fecundity correlates linearly with age (Beukema *et al.* 2001), this number was multiplied by the age of the animals.

RESULTS

Fitness as a function of migration date in the simple model

Survival from month to month - From the simple model, I calculated the survival from one month to the next (Figure 1). Below age 1, survival of *M. balthica* is much lower (especially in the low intertidal) than above age 1. Survival is highest in the high intertidal before age 1 and survival is higher in the low intertidal after age 1.

FITNESS AS A FUNCTION OF MIGRATION DATE FOR THE 'WINTER' MIGRATION FROM HIGH TO LOW TIDAL FLATS- In Figure 2 the cost of migration is incorporated in calculations of reproductive output for different moments of migration from the high to the low tidal flats ('winter migration'), assuming primary settlement on the high intertidal. The moment for migration that results in the highest RO lies a bit before age 1. This coincides with the moment at which the winter migration was observed in the field.
All factors included in the simple model were varied between zero (species or process not present in model) and 200% of the observed value. If the shape of the curve that describes the RO as a function of migration date, changes upon changing the input factor, this factor affects the migration moment that results in the highest RO. If however only the level and not the shape of the curve changes, the factor does affect the final RO but not the optimal moment to migrate.
Only the abundance of shrimps, migration risk, growth rate and parasite infection rates affect the shape of the curves to an extent that the best moment to migrate changes (Figure 3). If there are no shrimps (0%), the highest RO is reached when *M. balthica* immediately migrates to the low intertidal after settlement, while when there are many shrimps (>25% of observed density) a migration to the low intertidal within the first 5 months decreases the RO (Figure 3D). If there are no parasites, leaving the high tidal flats decreases RO, but if parasite infection rates become above 80% of the calculated
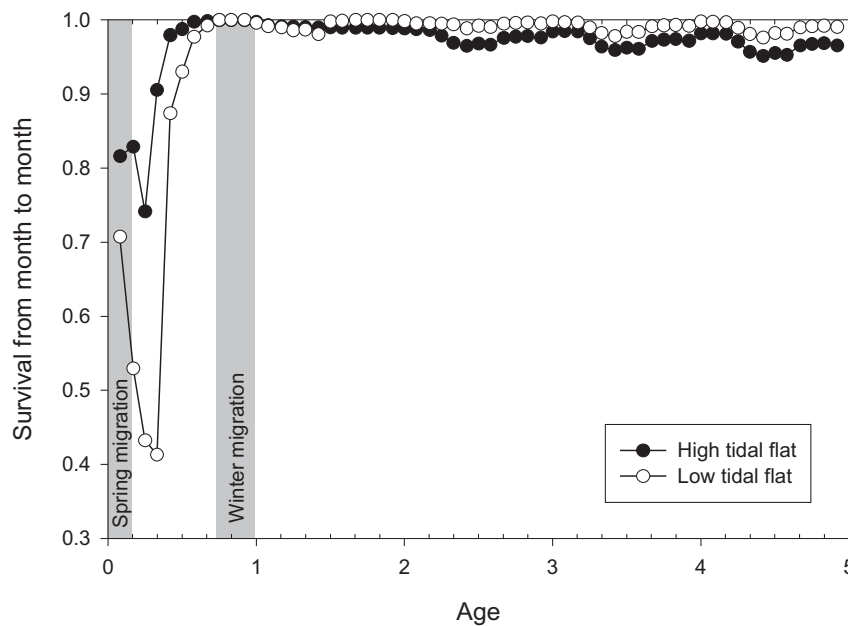
Figure 1. *Macoma balthica*. Survival (ratio next month to current month, minus parasite infected animals) at low and high tidal flats from the simple model calculations, without migration.

field value, a migration from the high to the low tidal flats after reaching age 1 increases RO (Figure 3I). If the migration risk is too high (less than 70% survival during migration), the migration does not increase the RO of the population. If migration survival is higher, the optimal moment to migrate is determined by shrimps and parasites around age 1 (Figure 3G). Finally, in populations with a L_8 <14 mm, migrations do not optimise the RO (Figure 3H). Other predators like *Nereis* and *Carcinus* 0-group have a large effect on the RO, but not on migration moment giving the highest RO (Figure 3B & E). *Arenicola marina*, 1+group *Carcinus* and *Haematopus* do only have a small effect on the RO (Figure 3A, C & F).

Starting density (=density at settlement) has an effect on the RO at different migration dates (Figure 3J). At very high settlement densities (>59 000 m^{-2}), the RO output is highest when *M. balthica* does not migrate after primary settlement in the low intertidal (migration from high to low at age=0), at lower densities the RO is maximal when migrating around the age of 1 year.

FITNESS AS A FUNCTION OF MIGRATION DATE FOR THE 'SPRING' MIGRATION FROM LOW TO HIGH TIDAL FLATS - The optimal moment of migration from low to high tidal flats was only affected by shrimp abundance (Figure 4). Normal and high shrimp abundances make it necessary to leave the low intertidal as soon as possible, at low shrimp abundances the best strategy is to always stay in the low intertidal (migration from low to high as late as possible). At normal shrimp abundances, predation by shrimps in the low intertidal was so strong that the *M. balthica* population almost dies out when it stays in the low intertidal. Therefore, parasite infection rates, migration mortality and all other factors did not affect the fact that leaving the low intertidal as soon as possible maximises RO.
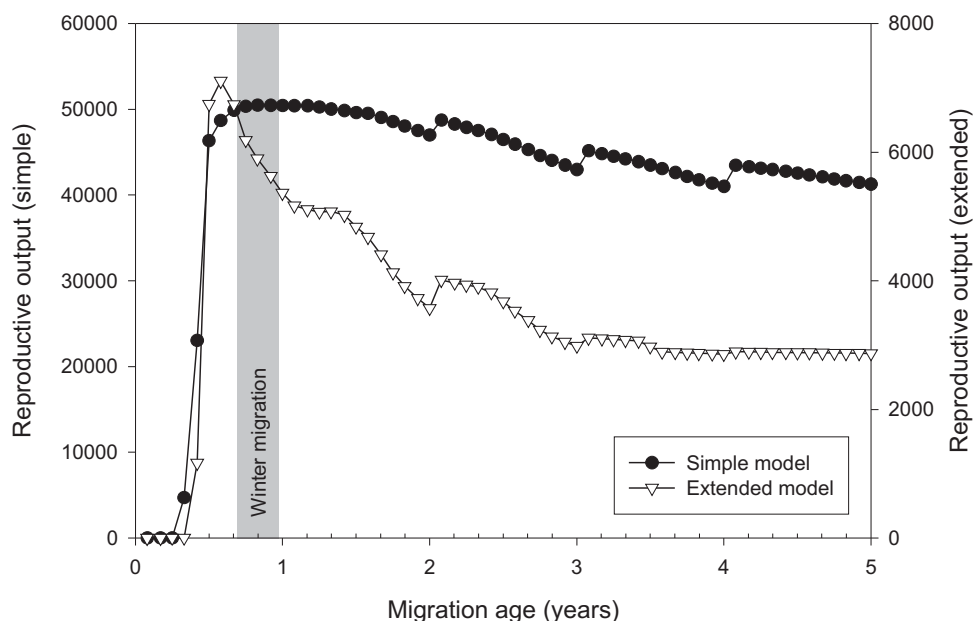
Figure 2. Reproductive output of a *Macoma balthica* population, calculated by the simple and the extended model, for *M. balthica* migrating from the high to the low tidal flats ('winter migration') at different ages. The first and last point on the time axis represent 'always low and 'always high' and therefore no migration. For the simple model the highest reproductive output is found for migration from the high to the low tidal flats that lies around age 1 (which is also the age at which the winter migration in the field was observed). For the extended model, this moment was somewhat earlier. The saw teeth in the curves are caused by the mortality caused by the migration (see Figure 3G). As in the simple model 76% of the population survives the winter migration, on the short term the population size is reduced by 24 % by the migration. Therefore, when migrating before the evaluation moments (March, reproduction) the population size is reduced as compared with migration directly after reproduction.

Fitness as a function of migration date in the extended model

The extended model showed similar responses to variations in predator densities and parasite abundance as the simple model. Shrimp predation remained the most important structuring factor; shrimp presence still makes an early migration to the high intertidal obligatory for small *M. balthica.* In the extended model parasites were not the only factor that made migration to the low tidal flats around age 1 profitable, because the increased wader and shelduck predation offers an extra reason to leave the high intertidal around age 1.

Nursery use and the best strategy

The above sections analysed the effect of spring and winter migration date separately, but in this paragraph the migrations are analysed together. The strategy that maximises RO of *M. balthica* is a migration to the high tidal flats as soon as possible after settlement and a migration back to the low tidal flats in January of their first winter
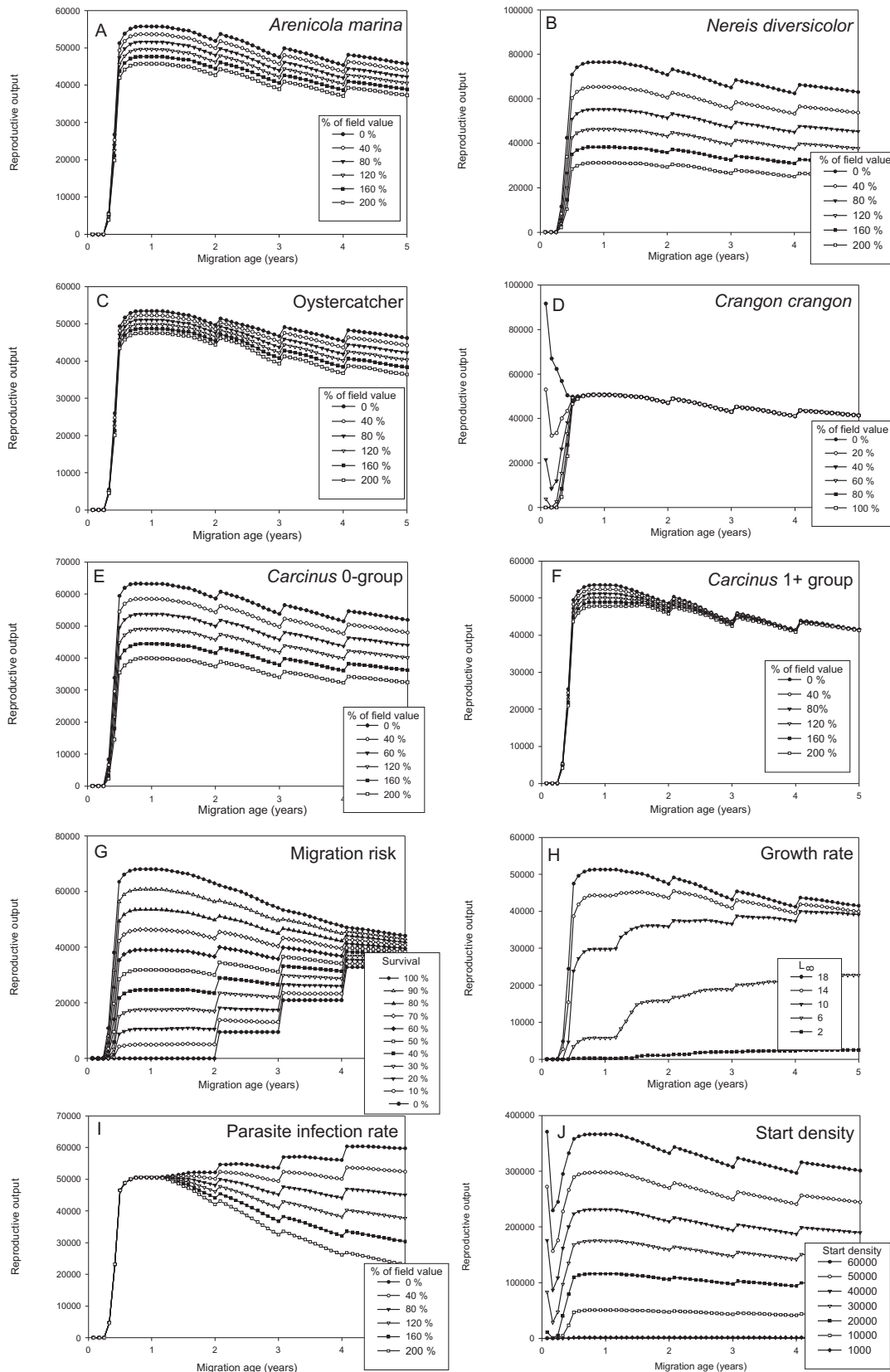
Figure 3. Reproductive output over 5 years of a *Macoma balthica* population (start density 10000 m^{-2}, except J), as a function of migration-age (migration from high to low tidal flats), for different predation, parasite infection and migration mortality rates. All values are given as a percentage of estimated field value, except for migration survival (% survival, field value 76%) and growth rate, where the L_{00} is given (field value 17.5 mm). The first and last point on the time axis represent 'always low' and 'always high' and therefore no migration.

(Figure 5). The RO of animals that initially settle in the low intertidal (54×10^3), as was observed in the Wadden Sea (Chapter 2) is lower than that of animals that initially settle in the high intertidal (63×10^3).

DISCUSSION

From the model calculations can be concluded that the spring and winter migrations of *Macoma balthica* serve as adaptations to avoid shrimp predation on spat and parasitation on large *M. balthica.* By leaving the low intertidal soon after settlement, *M. balthica* can increase the survival of small spat because shrimps are less abundant in the high intertidal. After *M. balthica* has outgrown the size range that is eaten by shrimps, it enters the size class that is vulnerable for infestation (and parasitic castration) by the parasitic trematode *Parvatrema affinis*, that is most common in the high intertidal. In the long run, the high mortality during the migration is outweighed by the increased reproductive output (RO) of longer living, not-infested animals. Although other predators do affect the RO of *M. balthica* , they do not have an effect on what migration strategy yields the highest RO. The model shows that the spring migration will be beneficial even if the mortality caused by the spring migration is very high (less than 10% survival). The winter migration is only worthwhile when migration causes an additional mortality smaller than 30%.

The last section of the Results–section shows that the migration strategy as observed on the Groninger Wad (settlement low, spring migration to high tidal flat, winter migration to low tidal flats) resulted in a lower RO than primary settlement in the high intertidal (and therefore without spring migration). Hence, the observed migration strategy does not maximise fitness. While primary settlement of *M. balthica* is found primarily in the low intertidal in the sheltered Wadden Sea (Günther 1991; Armonies 1996; Chapter 2), settlement was highest in the high intertidal in the highly dynamic
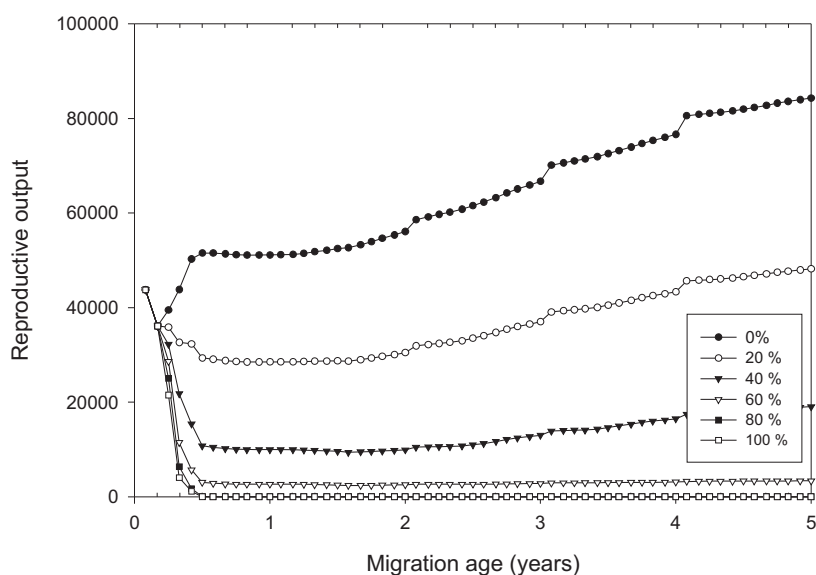

Figure 4. Reproductive output of *Macoma balthica* as a function of migration age (migration from low to high tidal flats) in the simple model, for different values of *Crangon crangon* predation pressure (100% is observed field density). The first and last point on the time axis represent 'always high' and 'always low' and therefore no migration.
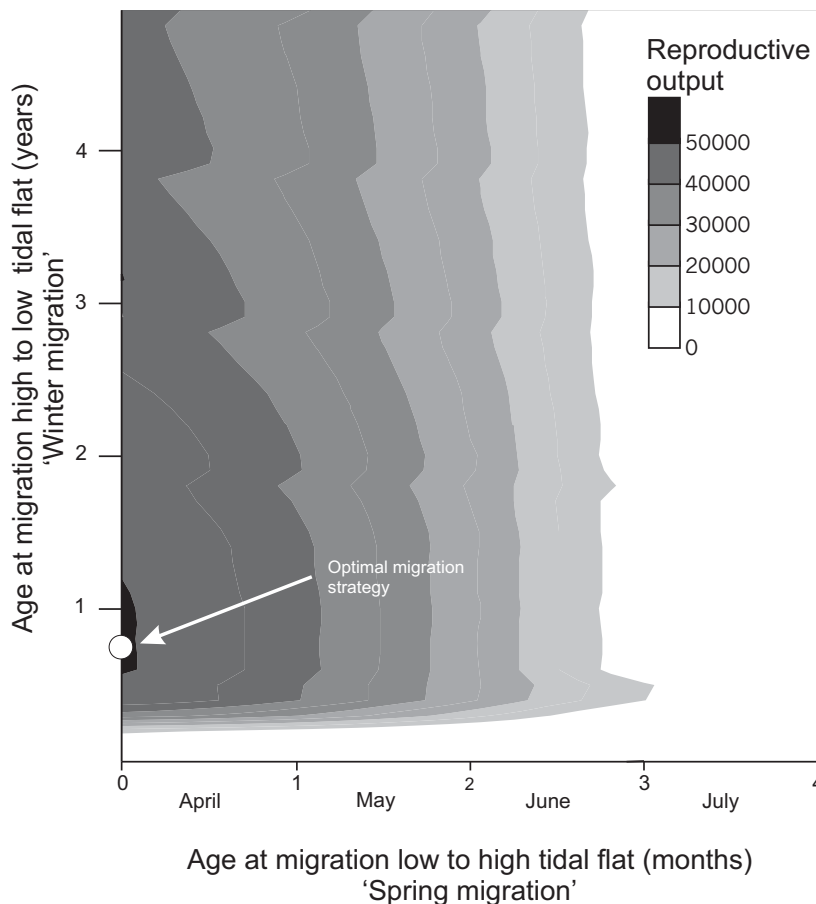
Figure 5. Contour plot of reproductive output (RO) of *Macoma balthica* as a function of spring and winter migration date. The highest RO is found after settlement in the high intertidal (age=0 months) and a subsequent migration to the low tidal flat in January of their first winter.

Westerschelde estuary (Bouma *et al.* 2001). Bouma *et al.* (2001) explain this pattern by showing that the location of primary *M. balthica* settlement is governed by local hydrodynamic conditions, implying that this location is not 'chosen' by *M. balthica.* Therefore, initial settlement in the low intertidal cannot be part of an adaptive strategy. However, given initial settlement in the low intertidal, the spring migration increases reproductive output, and, hence, is adaptive.

Beukema (1993a) showed that after mild winters with many shrimps and poor *M. balthica* recruitment, 0-group *M. balthica* was concentrated in the high intertidal, while after cold winters with few shrimps the majority of the abundant 0-group lived around mean tidal level. This shows that in years with few shrimps, spat can live at lower tidal levels (Beukema *et al.* 1998) and the spring migration is less obligate. This illustrates the importance of shrimps for nursery use of *M. balthica.* The change in distribution from the low to the high intertidal in spring can at least partly be explained by a migration (Chapter 2), but the above observation suggests that it can also be explained by direct effects of shrimps on low tidal levels (either predation or induced migration due to the presence of shrimps).

Freezing

M. balthica winter migration is triggered by low water temperatures, both in the field and the laboratory (Sörlin 1988; Chapter 2). Hence, it may be argued that migrations serve as a mechanism to avoid low temperatures in winter instead as an adaptive strategy to avoid shrimps and parasites. Temperatures are lower in the high intertidal in winter and it has been shown that some other benthic species experience higher mortality rates in the high intertidal during cold periods (Beukema 1985). In laboratory experiments, 50 % of the *M. balthica* died after exposure to –10°C for 1 day (Ibing & Theede 1975), but field studies showed that *M. balthica* is not sensitive to low winter temperatures in the Wadden Sea (Beukema 1985; Günther & Niesel 1999). Juvenile *M. balthica* is more sensitive to freezing than adults in the St. Lawrence estuary (Bourget 1983), but tolerates temperatures below –10°C, while adults can survive temperatures below –15°C. Summarising, avoiding low temperatures does not seem a probable reason for the winter migration of *M. balthica* in the Wadden Sea.

General conclusions

In conclusion, migrations of *M. balthica* on tidal flats of the Wadden Sea may be seen as an adaptation to avoid shrimp predation on juveniles and parasite infection of the adults. Although the risks of the migration are large, taking this risk increases fitness, because the migration risk is traded off against an increased RO. The migration cost is paid by the fraction of the animals that die/disappear during migration, while the surviving animals receive the benefits. Figure 2 shows that the differences in RO between migrating and non-migrating animals only become apparent after 2 years. It can therefore be predicted, also in accordance with life-history theory, that animals with a short life-expectancy (or with a higher predation risk during migration) should not migrate. This may explain the large remaining variation in the field, with many adult *M. balthica* living on the high tidal flats. Nevertheless, if the fitness of the majority of the animals is increased by the migration, the evolution of migration behaviour can be expected.

The migratory behaviour may explain why *M. balthica* is one of the most common macrozoobenthic species of the Wadden Sea. The use of a shrimp refuge by juveniles effectively prevents the complete recruitment failure so frequently observed in certain years in other bivalve species in the Wadden Sea (Beukema 1993a).

Therefore, both predation and parasitism may have been the driving forces in the evolution of the well-developed migratory abilities in *M. balthica.* However, some of the assumptions on which I based the calculations are not very well substantiated and need more study. In particular, the reason why juveniles are not infected with *Parvatrema* (or is it just not visible?) and why animals in the low intertidal are not infected should be studied. In my simple-model calculations, it was assumed that no extra mortality was caused by the parasites. This assumption is probably not right because 1) heavy infestation by trematode cercariae and metacercariae causes

damage to host tissues (Lauckner 1983) and 2) *Parvatrema* causes *M. balthica* to create crawling tracks (Swennen & Ching 1974), which in turn may increase shorebird predation (but see Mouritsen 1997). This will have led to an underestimation of infection rates, so the effect of *Parvatrema* on *M. balthica* fitness will probably even be larger.

This study explains the adaptive value of the differing distribution of *M. balthica* -age groups on the tidal flats, but *M. balthica* also occurs in the subtidal Wadden and North Sea. The absence of 0-group *M. balthica* from the subtidal as well as the winter migration to the North Sea (Chapter 2) may be explained in the same way (migration mortality, shrimp predation, parasite infestation) as on tidal flats. Although the polychaete *Nereis,* which eats much spat, is rare in the subtidal (Chapter 5), the predation pressure by shrimps is probably even higher than on the tidal flats because shrimps are larger and more abundant (Boddeke 1996; Hostens 2000). Therefore, the subtidal is probably a hostile environment for small *M. balthica*, while the absence of *Parvatrema* makes the subtidal attractive for adults. Therefore, it seems likely that for migrations, on a larger scale the same processes are important as on a tidal-flat scale.

ACKNOWLEDGEMENTS

CHAPTER 8

General Discussion

ASSUMPTIONS AND RELIABILITY OF DATA

Before formulating the major conclusions of my work, I will first discuss the reliability of my conclusions in earlier chapters. This section gives an overview of the vital assumptions and most important data that were used to reach these conclusions. It discusses how conclusions would change if data would change in the most likely direction.

Fieldwork in this thesis focused on the 1998 (Chapter 2), 1999 (Chapter 4) and 2000 (Chapter 4 and 5) yearclasses of *Macoma balthica* on the tidal flats of the Groninger Wad. The 1998, 1999 and 2000-year-classes rank as the 3rd, 13th and 27th strongest of all 32 years from 1969 to 2000 that were monitored on the Groninger Wad (RIKZ pers. comm.).There is no reason to assume that these yearclasses showed an exceptional behaviour in any way.

Chapter 2 draws conclusions based on the assumptions that the studied population is closed and that additional samples from the North Sea, tidal channels and tidal flats give representative estimates of *M. balthica* in the whole tidal basin of the Lauwers. The first assumption was necessary to be able to do any calculations at all, but there is no reason to assume it was violated to an extent that it would change conclusions. The reasons for this have already been discussed in Chapter 2. Although sampling was biased towards the spring and summer months, the number of additional samples from the North Sea and tidal channels was very large, leading to the conclusion that the second assumption probably is valid.

The additional mortality caused by the migration is very important when evaluating the adaptive value of migrations: if this cost of migration is too high, it will not be worth-

while (Chapter 7). In Chapter 2 this additional disappearance for the whole population during migration periods was calculated. In Chapter 6 and 7 I assumed that during migration periods all *M. balthica* migrated, but that only a fraction relocated. This results in an estimate of the minimum mortality percentage caused by the migration. If it is assumed that only the relocating animals migrated and therefore suffer additional mortality (the maximum estimate), the risk of migration would be much higher (53 instead of 13% for the spring migration and 79 instead of 24% for the winter migration). Figure 3G in Chapter 7 shows that under these values migrations will only decrease fitness and are therefore not adaptive. The distribution maps in Chapter 5, however, show that between April and August almost all 0-group *M. balthica* relocated in space, although not all 0-group *M. balthica* migrated from the low to the high intertidal. The rather homogeneous distribution of adult *M. balthica* on tidal flats (Chapter 5) suggests a large-scale redistribution and therefore that most *M. balthica* migrated during the winter migration period. Therefore, I conclude that my former figures are more likely to be right than the latter ones.

The infection rates of *Macoma balthica* with the trematode *Parvatrema affinis*, that were obtained from the literature (Hulscher 1973; Swennen & Ching 1974), are very important for the conclusions that were drawn in Chapter 7. The cited studies were not designed to examine the effect of tidal level on infection rates by *Parvatrema* and do not allow an estimation of mortality rates caused by *Parvatrema*. In my simple model (Chapter 6), I assumed no mortality due to *Parvatrema*. However, it is likely that the trematode causes mortality among infected *M. balthica* (Lauckner 1983; 1986), which will have led to an underestimation of infection rates. Therefore, the benefits of migration, due to avoiding *Parvatrema*-infection might be even larger than calculated in Chapter 7.

Chapter 6 showed that approximately two-third of the mortality of *Macoma balthica* on the Groninger Wad could be explained from predation by shrimps, crabs, polychaetes and the oystercatcher together with mortality caused by the migration. Therefore, it has to be concluded that some mortality causing factors were missed or underestimated. An extended model could completely explain the remaining mortality from predation by other bird species, an underestimation of shrimp and crab densities and mortality caused by parasites and starvation, but the parameterisation of the model is not reliable due to lack of data. As shrimps and crabs were sampled in daytime but are more active and abundant at night (Ansell *et al.* 1999), and because they were found to be important predators in daytime, an underestimation of their densities is particularly likely. Chapter 7 showed that the optimal migration strategy did not differ much between the simple and extended model, although birds were more important in the extended model in explaining the migration of *Macoma balthica*. Further research on factors causing *M. balthica* mortality may reveal whether birds are indeed more important as predators on *M. balthica* and may have a larger influence on *M. balthica* migration than can be calculated from the simple model.

Summarising, only the assumption about the fraction of migrating *M. balthica* and the calculated additional mortality rates resulting from this assumption, could form a major source of error for the conclusions drawn in the next section.

COSTS AND BENEFITS OF NURSERY USE AND MIGRATION OF *MACOMA BALTHICA*

My study was the first attempt to quantify the adaptive value of migrations of a marine infaunal invertebrate. My most important findings are that the migration costs for infaunal benthic animals can be quantified and are high, and that all benefits of migrations occur in relation to size-selective predators and parasites that were not homogeneously distributed in space.

M. balthica performs 3 ontogenetic niche shifts, of which I studied two. The first shift is from pelagic larvae to benthic postlarvae that settle on low tidal flats; this was not studied. The second shift is from the low to the high tidal flats (spring migration), while the third shift is back from the high to the low tidal flats (winter migration). In *Macoma balthica*, the last two niche shifts increase fitness (Chapter 7), even though migration is costly (Chapter 2 and 3).

Migration mortality

During migration periods, *Macoma balthica* suffered increased disappearance rates; additional to the normal mortality during the spring migration at least 13% and during the winter migration at least 24% of the population disappeared, during this period. Higher predation rates on migrating *M. balthica* by benthic and pelagic predators as compared to buried *M. balthica* and migrating *M. balthica* ending up in unsuitable locations may explain these higher disappearance rates.

Migration costs have to be considered when examining adaptive value of life histories. If not, the slightest differences in predation pressure or growth between locations may trigger migrations and one would not expect any sessile animals and plants to exist in this world. Figure 3G in Chapter 7 shows that if migration costs are neglected, the benefits of migration will be grossly overestimated.

Migration costs are a clear constraint on the evolution of migratory behaviour. If costs are too high, migratory behaviour can never evolve. In migratory species, one may expect adaptations that decrease the cost of migrations. Nightly migration (Chapter 3) and the existence of 3 colourmorphs in *Macoma balthica* may serve as adaptations to reduce migration costs (see text box). In the marine environment, possibly many benthic animals live in suboptimal locations because the cost of migration is too high, and primary settlement is dictated by hydrography.

Figure 1. Chlorophyll a content of the sediment (±SD) at the low and high tidal flats of the Groninger Wad in 1999, measured according to the method of Lorenzen (1967).
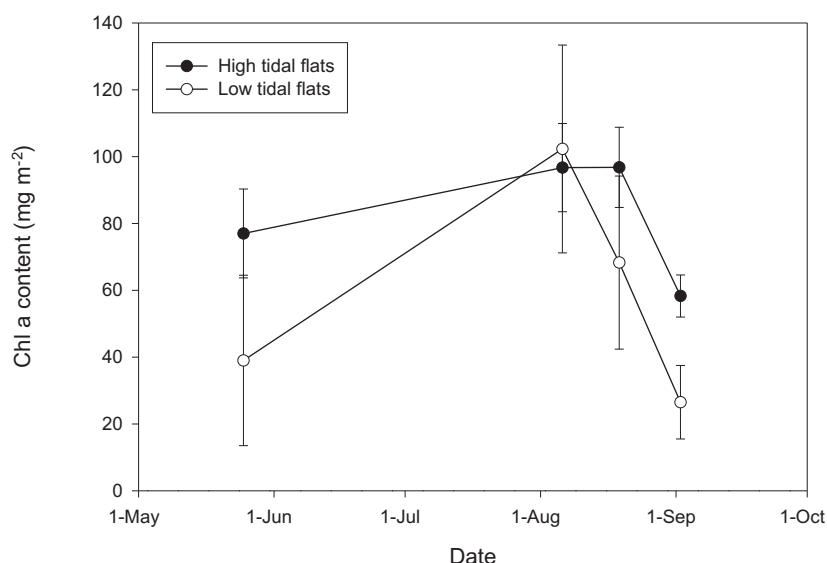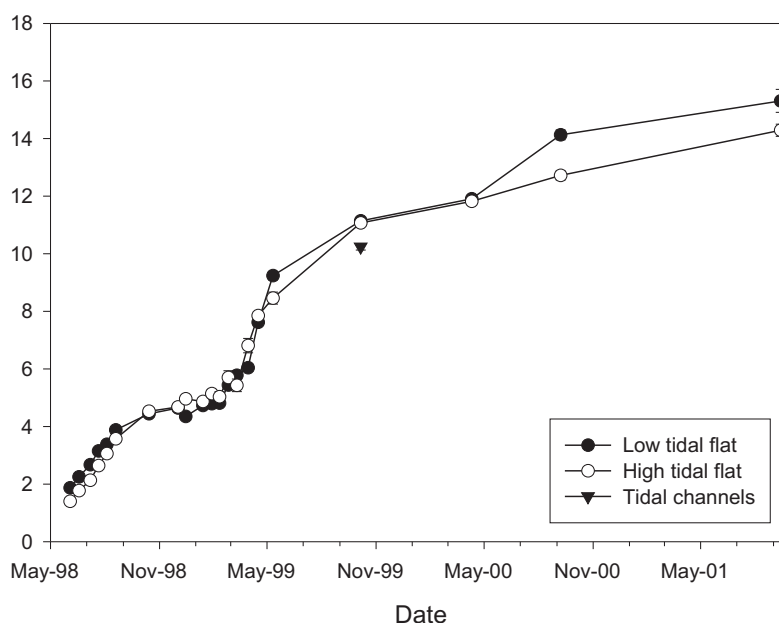

Figure 2. Length (±SE) of 1998-yearclass *Macoma balthica* at low tidal flats (n=32 per date), high tidal flats (n=25 per date), in a tidal channel (n=19) at the Groninger Wad.

The role of growth in nursery use of *Macoma balthica*

In Chapter 1 I explained that according to Werner and Gilliam (1984), animals should live at locations where they minimise their mortality to growth (μ/g) ratio. Growth rates of *Macoma balthica* probably depend on time available for foraging (immersion time), abundance of food (algae) and foraging mode (deposit or filter feeding). Immersion time is short on high tidal flats, but the light irradiance, and therefore primary production, is higher. Cadée and Hegeman (1977) found a linear correlation between primary production and tidal level on the Balgzand in the Dutch Wadden Sea. This may be the reason for higher biomasses of benthic diatoms at the high tidal flat on most dates (Figure 1). Figure 1 has to be interpreted with care, however, as biomass is the result of production and consumption. A high biomass may be interpreted as being the result

of a high primary productivity, but also as the result of absence of consumption. An analysis of growth data from the literature of *M. balthica* from 100 locations at different latitudes and tidal levels by Zwarts and Wanink (unpublished data) showed that there exists only a minor effect of tidal level on growth rate of *M. balthica* and that there exist an interaction between tidal level and latitude. In Europe, *M. balthica* grows faster at high tidal levels at low latitudes, while it grows faster at low tidal levels a high latitudes.

For *Macoma balthica* on the tidal flats of the Groninger Wad, there are only small differences in growth rate between the high and low tidal flats (Figure 2). Growth rates in exclosures, without siphon cropping and without predators inhibiting feeding, did also hardly differ between high and low tidal flats (Chapter 4). Therefore, the µ/g-ratio depends primarily on the mortality and a *M. balthica* in the Wadden Sea should minimise mortality.

Size-selection by predators and parasites that are limited in space

Almost all predators are size-selective. The upper limit of the prey size they consume is often limited by factors like gape width, claw strength and the risk of damage to the predator itself. The lower limit of prey size is often set by energetic constraints. The energetic value of the prey must of course be higher than the amount of energy needed to find, ingest and digest the prey and preferentially much higher. In waders, for small bivalve prey the ratio of the effort needed to handle and digest the prey, to the energetic content is lower than for large prey (Zwarts & Blomert 1992).

Epibenthic predation pressure (in particular by shrimps *Crangon crangon*) was highest on the low tidal flats. These animals only consumed small 0-group *M. balthica* and may therefore stimulate nursery use of *M. balthica.* I did not find an effect of bird or epibenthic predation on the densities of older *M. balthica.* Infaunal polychaete predators only consumed very small 0-group *Macoma balthica* and did affect spat densities on the tidal flats. As these polychaetes were distributed rather evenly over the tidal flats, they did not make migrations and nursery use of *M. balthica* worthwhile. Beukema (1993a) showed that in years after mild winters with many shrimps and poor *M. balthica* recruitment, 0-group *M. balthica* was concentrated in the high intertidal, while after cold winters with few shrimps the majority of the abundant 0-group lived around mean tidal level. Thus, in years with few shrimps, 0-group *M. balthica* can survive at lower tidal levels because the predation pressure by shrimps is lower. This observation stresses the importance of shrimps for recruitment of *M. balthica* (Beukema *et al.* 1998), but also shows that in years with few shrimps the spring migration is less obligate and spat can live at lower tidal levels. The change in distribution from the low to the high intertidal in spring can at least partly be explained by a migration (Chapter 2), but the above observation suggest that it can also explained by direct effects of shrimps at low tidal levels (either predation on non-migrating animals or induced migration due to the presence of shrimps).

***Macoma balthica* coloration and apostatic selection**

Three colourmorphs of *Macoma balthica* are distinguished: white, pink and yellow. These colours may have a genetic basis (Luttikhuizen pers comm) and correlate with shell morphology (Kafanov *et al.* 1999). The shell colour develops in autumn of their first year. The shell colour is not visible when *M. balthica* is buried in the sediment. Therefore, if shell colour has a function or adaptive value, this function must be expressed during the moments when *M. balthica* is not buried. *M. balthica* only comes out of the sediment when migrating. All three colourmorphs did migrate in the field (Chapter 2) and in the carousels (Chapter 3).
Edelaar (1998) suggested that the origin of these different colourmorphs may be found in apostatic (frequency dependent) selection by predators during the winter migration (Moment 1962; Owen & Whiteley 1988). If visually hunting predators have a search image of their prey, prey individuals will benefit from looking different from the search image (the rest of the population), e.g. because of a different colour (Bond & Kamil 1998). Examples of large variations in shell colour and pattern in bivalves, possibly related to predation, are found for some *Donax* species (Smith 1975; Owen & Whiteley 1986). Therefore, it seems possible that apostatic selection during the winter migration plays a role in the existence of three colourmorphs in *M. balthica.*

Parasites are generally less life-threatening for animals than predators. Nevertheless, parasites may be very important in the life history of animals (Hamilton 1980). There are few examples of size selection by parasites and the distribution of parasites does not seem to be restricted in space for many species. However, the lack of examples may be caused by the relatively low number of studies on parasites, compared to predation. The infection of *Macoma balthica* by the trematode parasite *Parvatrema affinis* is one of the few examples of a parasite that is both size-selective and spatially restricted.

ONTOGENETIC NICHE SHIFTS: THE SOLUTION FOR SIZE-SELECTIVE PREDATION?

Model calculations showed that the benefits of nursery use for *M. balthica* are larger than the costs of migration (Chapter 7). Fitness is highest for *M. balthica* that settle immediately in the high intertidal or migrate to the high tidal flat as soon as possible after settlement and that migrate back to the low tidal flats during their first winter. The main benefits of nursery use and migration are the avoidance of shrimp predation on juveniles in the low intertidal and the avoidance of parasite infection and bird predation of the adults in the high intertidal.

Chapter 7 shows that only factors that are both size-selective and spatially inhomogeneous can make nursery use worthwhile. In my *M. balthica* study, parasites and predation were the most important size-selective agents that were spatially variable, while in other organisms food abundance and temperature may be important. In general, any factor that has a size- or age-selective effect, is not spatially homogeneous and does affect growth or mortality (and therefore reproduction), may make migrations worthwhile. This condition may be general for all migrations in a spatially variable environment that is temporally constant or varying synchronously in time. If the environment does not change but the animal does (e.g. size, morphology or physiology), the interaction animal-state and environment can make that the habitat that offers the best conditions for the animal changes over time.

In conclusion, non-seasonal migrations should always be evaluated in terms of size- or age selectivity and spatial distribution of predators or parasites. Size-selectivity alone is not enough, there should also be a large spatial difference in predation pressure. For example, the strong size selection by polychaete worms (Chapter 5) alone was not enough to make migrations of *M. balthica* worthwhile (Chapter 7).

TESTING THE ADAPTIVE VALUE OF MIGRATIONS FOR *MACOMA BALTHICA*

The preceding sections of this chapter and Chapter 7 show that the migrations of *Macoma balthica* in the Wadden Sea may act as an adaptation to avoid shrimp predation on spat and parasite infestation of the adults. It has not been demonstrated that this behaviour has developed in response to shrimp predation and parasitism, however. This theory may be tested by comparing the migration behaviour in different populations with the presence of *Crangon* and *Parvatrema* at a larger geographical scale. If *M. balthica* performs no migrations in areas without *Crangon* and *Parvatrema,* this may be seen as a confirmation of the role of *Crangon* and *Parvatrema* in the causation of migratory behaviour of *Macoma balthica*.
An attempt to execute the proposed test by comparing the migratory behaviour of *Macoma balthica* from 5 areas between the White Sea and the Gironde in Europe was not successful, because the information on the migratory behaviour and nursery use of *M. balthica* and the occurrence of *Crangon* and *Parvatrema* were not extensive enough.

HOW DO OTHER JUVENILE BIVALVES COPE WITH EPIBENTHIC PREDATION?

The apparent obligatory nature of the spring migration of *M. balthica* -spat (no reproductive output for animals that stay in the low intertidal after settlement) poses the question why the spat of some other bivalve species in the Wadden Sea stays in the low intertidal (e.g. *Mya arenaria*, *Cerastoderma edule* and *Mytilus edulis*). Secondary dispersal by byssus drifting has been recorded for *Cerastoderma* (Armonies 1994b; Armonies 1996; De Montaudouin 1997) and *Mytilus* (De Blok & Tan-Maas 1977; Lane

et al. 1985), while *Mya* can be redistributed by bedload transport (Emerson & Grant 1991; Hunt & Mullineaux 2002), but none of these redistributions seems to be directed towards the high intertidal.

Cockles, however, settle in very high densities (Jensen 1992) that may protect the spat through swamping the predators. Figure 3 in Chapter 7 shows that for *M. balthica* this strategy may work for initial densities higher than 59 000 m^{-2}. *Mya arenaria* only shows recruitment in years when they outgrow shrimp and crab predation due to very extreme mismatch in timing between crustacean and bivalve settlement (Strasser & Günther 2001) and therefore pays the price of not migrating to the high intertidal in other years. *Mytilus* shows a migration from primary settlement sites on filamentous substrates to adult mussel beds where it may reach very high densities (Pulfrich 1996), which may provide a refuge from shrimp predation.

Summarising, *Cerastoderma* and *Mya* seem to have to endure the problem of shrimp predation in the low intertidal. This may explain why, compared to *M. balthica* , these species show a highly variable recruitment and many years with complete recruitment failure, while *M. balthica* shows a relatively constant recruitment between years (Beukema 1993a).

THE CONCENTRATION HYPOTHESIS: IS ADULT POPULATION SIZE LIMITED BY JUVENILE NURSERY SIZE?

Juvenile *M. balthica* live concentrated in a small area when young, while the adults are distributed much more homogeneously. Beverton (1995) formulated the concentration hypothesis based on the stock-recruitment relation and nursery use of plaice (*Pleuronectes platessa*). He observed that the adult stock for plaice, that uses coastal
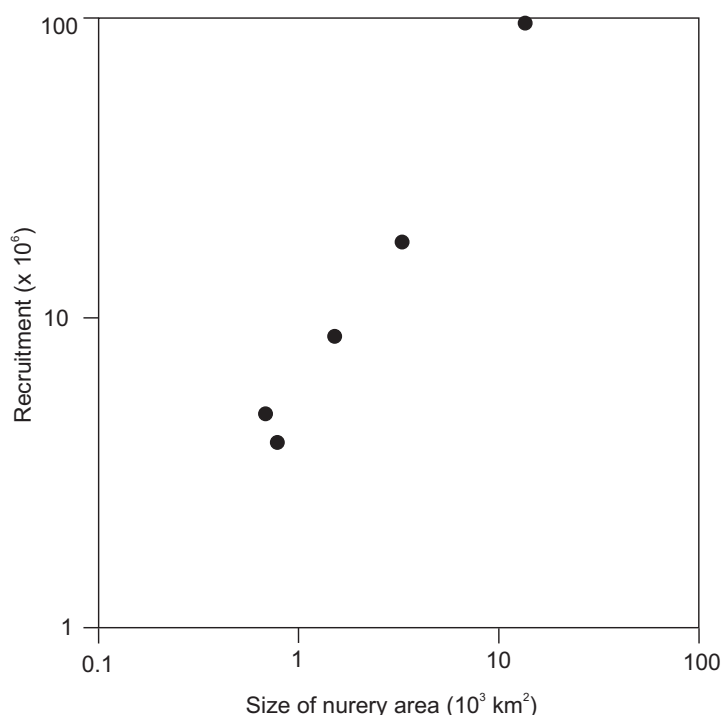

Figure 3. Relationship between estimates of geometric mean recruitment and the size of the nursery ground for *Solea solea* in the Northeast Atlantic (Gibson 1994).

nurseries, was relatively stable. He hypothesised that adult population size of plaice was regulated by the number of juveniles that fit in the nurseries due to density dependent processes. The hypothesis predicts a weak relation between stock and recruitment, relatively small deviations from the stock-recruitment (S/R) relation and mainly negative deviations from the S/R curve for species with strong concentration of the juveniles. The first two predictions seem to be supported by empirical evidence provided by fish stock monitoring (Iles & Beverton 2000).

Figure 3 indicates of the importance of nurseries for the adult population size of sole *Solea solea*. The graph shows that average recruitment of sole for different European populations is related to the nursery area available (Gibson 1994). At the same time, the figure shows that the nursery controls the adult population size in sole.
If the number of juveniles that fit in the nurseries is limited, due to density-dependent mortality, this implies that the adult stock size is limited by the size of the nursery. As *M. balthica* is a species that lives concentrated as juveniles, it seems very well possible that adult abundance is limited by the size of the nurseries. The S/R curve of *M. balthica* shows that there hardly exists any relation between adult stock size and subsequent recruitment (Honkoop *et al*. 1998). This suggests density-dependence in the nurseries. Density-dependent predation on *M. balthica* -spat by the shore crab *Carcinus maenas* was observed in Scottish estuaries (Richards *et al*. 2002). Adult abundance is limited by juvenile recruitment and there are no indications for post-recruitment density-dependence (Van der Meer *et al*. 2001b). Concluding, it seems plausible that the adult *M. balthica* stock size is limited by recruitment, which in turn is limited by nursery size.
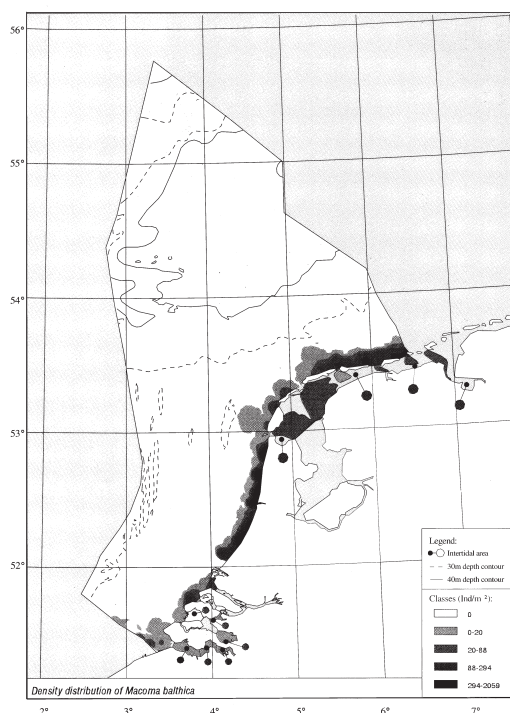
For *Macoma balthica*, the most suitable nursery areas are high and silty intertidal flats. In the Netherlands, these can be found mainly in the Delta area in Southwest of the Netherlands, in the Wadden Sea and in the Dollard (Ems estuary). However, large quantities of adult *M. balthica* are found along the Dutch coastal area, while adult *M. balthica* are less common north of the Frisian islands and rare outside the Delta area (Figure 4). From this map, one may, contrary to the concentration hypothesis, be tempted to conclude that the vicinity of nurseries does not affect adult *M. balthica* abundance in coastal areas and therefore that tidal flat nurseries are not important for *M. balthica* abundance. However, studies on the dispersal of the American jack-knife clam *Ensis*

Figure 4. Density and distribution of *Macoma balthica* on the Dutch continental shelf. From: Holtmann *et al.* (1996)

directus after introduction in Europe show that the population of this species could disperse 125 km with the residual current and 75 km against the residual current per year (Armonies 2001), probably through byssus drifting individuals. If byssus drifting *M. balthica* can disperse over similar distances, this implies that for *M. balthica* the coastal North Sea adults are well within the range that can be reached from the nurseries and that nurseries may be important.

HIGH TIDAL FLAT NURSERIES AND SEA LEVEL RISE

On the high tidal flats, small *M. balthica* are protected from predation by epibenthic crustaceans and therefore survival rates are much higher than on the low tidal flats. This means that high tidal flats are of disproportionate importance for the juveniles of *Macoma balthica* (Chapter 7). The major fraction of all *M. balthica* in the low intertidal, subtidal Wadden Sea and coast North Sea spend their juvenile phase in the high intertidal.

Seawalls or dikes generally set the upper limits of tidal flats and salt marshes in the Wadden Sea. In a natural system, sea level rise (due to climatic cycles, global warming or bottom subsidence) would result in an inland movement of tidal flats and saltmarshes and both low and high tidal flats could stay in existence in the Wadden Sea. In the current spatial layout of the Wadden Sea, however, the dikes limit any landward movement and saltmarshes and high tidal flats will be lost from the system in the case of sea level rise.

Increasing temperatures will probably also result in increased shrimp (*Crangon crangon*) and crab (*Carcinus maenas*) abundances and a better match between shrimp arrival and settlement of *M. balthica* (Beukema 1991; Beukema 1992; Beukema *et al*. 1998; Strasser & Günther 2001), although *Carcinus* will probably also suffer, as this species also use high intertidal nurseries (Klein Breteler 1976). Because of the loss of nurseries, through the loss of the high tidal flats, *M. balthica* abundance may drop sharply, not only in the intertidal but also in the coastal North Sea. So, global warming is expected to be detrimental for *M. balthica* in the Wadden Sea and other estuaries. Locally, e.g. in the Dutch Wadden Sea, gas extraction causing bottom subsidence will aggravate this situation. Maintaining brushwood groynes of the former land reclamation works on the mainland coast of the Wadden Sea may help to conserve high tidal flats and their nursery value at least temporarly.

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Summary

The adaptive value of migrations for the bivalve *Macoma balthica*

This thesis is about the movements of the coastal marine bivalve *Macoma balthica. M. balthica* migrates over several kilometres between nurseries at high tidal flats, where juveniles are found in high numbers, and the adult habitat on low-lying tidal flats. Most benthic species in the Wadden Sea have been caught in the water column; also, *Macoma balthica* has been frequently caught. Although *M. balthica* normally lives buried in the sediment, it can migrate over large distances (kilometres) via a long byssus thread, which is secreted into the water column. This thin mucous thread increases drag force on the animal and allows it to be transported over large distances by the current.

In the Wadden Sea, juvenile *M. balthica* is normally mainly found in the high intertidal (the nursery). Juveniles settle in the low intertidal in May at a size of 300 μm. Subsequently, they migrate to the high intertidal in June, where they stay until winter. In winter, juvenile *M. balthica* (5 mm) migrate back to the low intertidal and to the North Sea. Adults are much more widespread in distribution, occurring both in the low and high intertidal, as well as the subtidal of the Wadden Sea and adjacent North Sea. Since the locations where adults and juveniles live are spatially separated, *M. balthica* has to undertake migrations between these locations.

Migration may be profitable if another habitat has a higher quality than the current one. However, migration takes time, uses energy and the journey may be dangerous. Mortality and fecundity (and thus fitness) are likely to be affected by migration: by its energy cost, by its effect on food supply and predation rates and by its other dangers. Therefore, migration costs must be balanced by the benefits of living in a more

favourable environment. Thus, the decision of whether or not to migrate is a major component of a mobile organisms' life history strategy.

The quality of a location for an animal depends on the developmental stage of an animal. Due to ecological and physiological differences between juveniles and adults, they may prefer different habitats. Spatial variation in the environment may make costly migration worthwhile because of these different preferences of juveniles and adults.

The aim of this thesis is to determine why *M. balthica* migrates in the Wadden Sea; do these migration increase the fitness of *Macoma balthica*? To answer this question the costs and benefits of migrations and nursery use were assessed using laboratory and field experiments. The costs were sought in increased mortality during migrations, benefits were sought in differences in predation pressure and growth between the low and high tidal flats. Eventually, the costs and benefits of migration and nursery use were weighed in a model that calculates fitness of *M. balthica* as a function of migration strategy. The next paragraphs present the results of the different studies.

First, I describe the results of a study in which I estimated the costs of migration for *M. balthica*. Migration may increase mortality rates among *Macoma balthica* populations, e.g. because migrating *M. balthica* run a greater risk to be eaten by predators than buried *M. balthica*, or may end up at unsuitable locations. I examined if mortality rates of the *M. balthica* population were higher during migration periods than outside these periods. Hence, population development of the 1998-year-class of the bivalve *Macoma balthica* was studied by repeated sampling of 57 stations at a 7 km^2 tidal flat (Groninger Wad) area in the Lauwers tidal basin in the eastern Dutch Wadden Sea from May 1998 to August 2000. Additional data was collected by sampling a tidal channel close to the study area, and by collecting *M. balthica*-densities for the Lauwers tidal basin and adjacent North Sea from the literature. During both spring and winter migration, many animals disappeared from the tidal flat population. Partly this could be explained by normal mortality and by emigration to the subtidal channels and the North Sea. The rest of the disappearance was probably due to the increased mortality, associated with the risk of migration.

One mechanism that may explain the high number of disappearing animals is that predation by fish and crabs is higher when *M. balthica* is migrating through the water column than when it remains buried in the sediment. I examined if this mechanism can explain the increased mortality rates during migration periods. Migration was induced in a circular aquarium by generating a current. Without current, *M. balthica* remained buried in the sediment. Under illuminated conditions, relatively more migrating than buried *M. balthica* were consumed by predators, whereas there was no difference between predation rates on migrating and buried *M. balthica* under dark conditions.

Because of this light-dark difference in predation rates, I expected that the number of migrating *M. balthica* in the Wadden Sea would be larger at night than in daytime, either because they are avoiding predation or because in daytime many migrating *M. balthica* are eaten by predators. 1-group *M. balthica* was indeed much more abundant in nocturnal than in diurnal samples collected from the field. Furthermore, no *M. balthica* were found in the stomach contents of fishes collected during daylight hours of the migration period.

In conclusion, enhanced predation on drifting as compared to buried *M. balthica* may be the mechanism that explains enhanced mortality during migration in light and may explain why *M. balthica* mainly migrates at night in the field. As we found no *M. balthica* in stomachs of pelagic fish, we do not know whether predation on byssus-drifting *M. balthica* exists in the field.

The benefits of nursery use are probably found in spatial differences in the environment. I examined if differences in predation pressure between the low and high tidal flats by size-selective predators may be a reason for migrations and nursery use. Foraging time in the intertidal is limited by the tide. Shorebirds can only forage on exposed tidal flats. Therefore, predation pressure by birds on high tidal flats is probably higher than on low tidal flats. From earlier studies, it is known that shorebirds prefer large *Macoma balthica*. Marine predators, like shrimps, crabs and fish (the epibenthic predators) are only active at the tidal flats at high tide. In accordance with this, shrimps (*Crangon crangon*) were more abundant and larger on low than on high tidal flats. Crabs (*Carcinus maenas*) were more abundant on the high tidal flats, but were much larger on the low tidal flats. Size selection experiments and stomach content analysis showed that shrimps and crabs only consumed 0-group *M. balthica* smaller than 5 mm. From these findings, I expected a higher predation pressure on small *M. balthica* in the low intertidal, due to selective consumption of small *M. balthica* by epibenthic predators, and a higher predation pressure on large *M. balthica* in the high intertidal, due selective consumption of large *M. balthica* by birds. This would make nursery use and migrations of *M. balthica* beneficial. The hypothesis was tested in an exclosure experiment, where birds and epibenthic predators were selectively exclosed from experimental plots, at the low and high tidal flats. *Macoma balthica* density in plots without predation was compared with density in control areas with normal predation rates after several months. Bird predation had no significant effect on densities of large and small *M. balthica*. Densities of small *M. balthica* were higher in cages where epibenthic predators were excluded, compared to plots where these predators had normal access. This effect was, as expected, stronger in the low than in the high intertidal. Therefore, juvenile *M. balthica* can reduce epibenthic predation by living in the high intertidal.

Apart from birds and epibenthic predators, predation by polychaete worms may be important for the nursery use of *M. balthica* and was studied. Infaunal polychaetes reach much higher densities on tidal flats than epibenthic predators and birds. Therefore, a comparatively small *M. balthica*-consumption per polychaete may still negatively affect densities. Small *M. balthica* (<1.5 mm) were found in the stomach contents of the lugworm *Arenicola marina* and the ragworm *Nereis diversicolor*, showing that polychaetes really ingest small bivalves. Laboratory experiments showed that these polychaetes could reduce densities of small *M. balthica*. The impact of polychaete predation on *M. balthica* densities was examined in the field in an experiment where densities of polychaetes were manipulated. *Nereis* densities were experimentally increased in small cages (0.03 m^2), *Arenicola* densities were manipulated in 0.25 to 1 m^2 plots. The effect on densities of small and large *M. balthica* was examined after several weeks. These experiments showed that both polychaete species significantly negatively affected densities of very small 0-group *M. balthica*. Consumption rates, calculated from stomach contents and field experiments, were 45 to 102 *M. balthica* m^{-2} d^{-1} for *Arenicola* and 5 to 116 *M. balthica* m^{-2} d^{-1} for *Nereis*. These values are higher than consumption rates of shrimps and crabs in the same area. Nevertheless, between-year differences in year-class-strength could not be explained from the abundance of these polychaetes. Since both polychaete species were distributed rather homogeneously over the low and high tidal flats, the strongly size-selective predation by these species does not seem to provide an incentive for migration for *Macoma balthica*.

Besides predation, differences in growth rate between low and high tidal flats may be an incentive for migrations of *M. balthica.* For *Macoma balthica* on the tidal flats of the Groninger Wad, there are only small differences in shell-length and biomass between the low and high tidal flats. Growth rates in exclosures, without predators that crop siphons and inhibit feeding, did also hardly differ between high and low tidal flats. Therefore, differences in growth rate between low and high tidal flats are probably no major reason for the nursery use.

To determine to what extent the studied factors can explain the observed mortality, empirical predation rates from the Groninger Wad and literature values were combined in a model that calculated monthly mortality rates of the *Macoma balthica* population. The model showed that a large fraction of the mortality as observed on the Groninger Wad could be explained from predation by shrimps, small and larger crabs, polychaetes and oystercatchers.

All costs and benefits of migrations and nursery use for *Macoma balthica* were weighed against each other, in a model, to determine the effect of these migrations on the fitness of *M. balthica*. In the model, survival and reproduction was calculated for *M. balthica* living on the low and high tidal flats. Survival and reproduction were a function of mortality due to predation by shrimps, small and larger crabs, polychaetes and oystercatchers. Additional to these predators, the effect of the parasitic trematode *Parvatrema affinis* was added to the model. *Parvatrema* only infects *M. balthica* larger than 9 mm at high tidal flats. An infection by this parasite results in parasitic castration and therefore reduces the fitness of a *M. balthica* to zero.

I examined under what conditions the costs of migration are traded-off by an increased reproductive output and which settlement and migration strategy (location of settlement and timing of migrations) yielded the highest fitness. I examined all strategies that started with settlement at the low or high tidal flats, followed by an optional migration to the high tidal flats (if applicable) and subsequently an optional migration back to the low tidal flats. Therefore, the minimal number of migrations was zero (always high or low) and the maximal number of migrations to two (low-high-low). The factors responsible for the observed patterns were identified by varying the relative impact of each factor and examining the effect on the migration strategy that yielded the highest reproductive output.

Fitness was maximised for *M. balthica* that settle directly in the high intertidal and migrate to low tidal flats at an age of approximately nine months. High shrimp predation rates make living on the low tidal flats unfavourable for small *M. balthica*. Parasitation by the trematode *Parvatrema affinis* makes it beneficial for *M. balthica* to leave the high intertidal around the age of nine months. Of the other examined predators (crabs, birds and polychaetes), some did affect fitness, but none of them had an effect on the migration strategy that maximises fitness, because spatial differences in predation pressure of these species were not large enough to trade off migration costs.

In conclusion, migrations of *M. balthica* to and from nurseries on high tidal flats of the Wadden Sea may be seen as an adaptation to avoid shrimp predation on the juveniles and parasite infection of the adults. The migration increases fitness because the shrimp *Crangon crangon* and the parasite *Parvatrema affinis* are size selective and show a large difference in abundance on the low and high tidal flats. During its first year, *M. balthica* changes from a prey for shrimps, which can be avoided at the high tidal flats, into a host for *Parvatrema*, which can be avoided on the low tidal flats. Although the costs of migration are large, fitness is increased due to the migration because it is traded off by an increased reproductive output.

SAMENVATTING

Migraties en kinderkamergebruik van het nonnetje (*Macoma balthica* L.)

Dit proefschrift gaat over de migraties van het nonnetje (*Macoma balthica*), een tweekleppig schelpdier dat leeft op wadplaten en in kustzeëen. Normaal leeft *Macoma* ingegraven in het sediment, maar hij kan over grote afstanden (kilometers) migreren door gebruik te maken van een byssusdraad. Dit is een dunne slijmdraad die tientallen centimeters lang kan zijn. Deze draad verhoogt de weerstand in de stroming en zorgt er zo voor dat een *Macoma* over grote afstanden meegevoerd kan worden door de stroming.

In de Waddenzee leven jonge nonnetjes voornamelijk op het hoge, slikkige wad dat gedurende een getijdencyclus maar kort onder water staat Volwassen dieren leven meer verspreid over het wad en de kustzone van de Noordzee. Omdat de locaties waar de jonge en volwassen dieren leven ruimtelijk van elkaar gescheiden zijn, moet het nonnetje migreren. De larven, die in het water zweven, vestigen zich op het lage wad. Tijdens de voorjaarsmigratie, in mei en juni, migreren de jonge nonnetjes van minder dan één mm schelplengte naar het hoge wad. Ze gebruiken dit hoge wad als kinderkamer en groeien hier uit tot ongeveer vijf mm grote nonnetjes. Hier blijven ze tot de winter. Tijdens de wintermigratie, van december tot maart, migreren deze nonnetjes naar het lage wad, de geulen en naar de kustzone van de Noordzee.

Migraties kosten tijd en energie en kunnen gevaarlijk zijn. Kwaliteitsverschillen tussen locaties, zoals verschillen in voedselaanbod of predatiedruk, kunnen voor dieren een goede reden zijn om toch te migreren. Een dier moet de voordelen van een migratie afwegen tegen de nadelen, om te kunnen bepalen of een migratie zijn fitness (relatieve bijdrage aan volgende generaties) verhoogt. De kwaliteit van een locatie voor een dier is onder andere afhankelijk van het ontwikkelingsstadium van het dier zelf. Jonge

dieren stellen vaak andere eisen aan hun leefomgeving dan volwassen dieren, bijvoorbeeld omdat jongen kleiner en kwetsbaarder zijn of ander voedsel nodig hebben. Door de ontwikkeling van een dier in de tijd, zoals groei, kan het voordelig zijn om gedurende een bepaalde ontwikkelingsfase te migreren naar nieuwe locaties, die beter geschikt zijn voor het ontwikkelingsstadium waarin een dier zich dan bevindt.

Het doel van het onderzoek in dit proefschrift was om te bepalen waarom het nonnetje migreert in de Waddenzee. De centrale vraag was of deze migraties de fitness van het nonnetje verhogen. Om deze vraag te kunnen beantwoorden heb ik geprobeerd te bepalen wat de kosten en baten van de migratie voor het nonnetje zijn. De kosten van de migratie zijn gezocht in verhoogde sterfte tijdens de migratie. De baten zijn gezocht in verschillen in groei en predatiedruk tussen het lage en hoge wad. Deze onderwerpen zijn onderzocht door bemonsteringen en experimenten op het wad en in het laboratorium uit te voeren. Uiteindelijk zijn alle gegevens over de voor- en nadelen van migraties tegen elkaar afgewogen in een model om te bepalen of migraties de fitness van *Macoma* verhogen. In de volgende alinea's worden de resultaten van de verschillende onderzoeken besproken.

Allereerst beschrijf ik de resultaten van een onderzoek waarin ik de kosten van migratie voor het nonnetje onderzocht heb. De kosten van migratie heb ik gezocht in verhoogde sterfte tijdens de migratie. Migratie zou gevaarlijk kunnen zijn voor *Macoma*, bijvoorbeeld omdat ze een groter risico lopen om opgegeten te worden door vissen wanneer ze door de waterkolom migreren dan wanneer ze ingegraven leven. Verder kunnen ze op slechte plekken, zoals snelstromende geulen of kwelders, terechtkomen. Om te bepalen of migraties inderdaad gevaarlijk zijn, werd op het wad onderzocht of er gedurende de migratieperioden een hogere sterfte onder de *Macoma*-populatie is dan buiten deze perioden. Hiervoor werd de dichtheid van de 1998-jaarklasse (de nonnetjes die in 1998 geboren zijn) regelmatig bemonsterd tussen mei 1998 en augustus 2000, op 57 punten op het Groninger wad. Aanvullende gegevens werden verzameld door te monsteren in een grote geul bij het onderzoeksgebied (Lauwers) en door *Macoma*-dichtheden uit het stroomgebied van de Lauwers en de aangrenzende Noordzee te verzamelen uit de literatuur en gegevensbestanden van anderen. Er bleek inderdaad een veel groter aantal nonnetjes van de 1998-jaarklasse van het wad te verdwijnen tijdens de voorjaars- en de wintermigratie dan buiten deze perioden. Een klein deel van deze dieren migreerde naar de Noordzee en geulen, maar vergeleken met de dichtheden op het wad en de aantallen verdwenen dieren, waren deze aantallen laag. De rest van de verdwenen dieren is waarschijnlijk opgegeten door predatoren tijdens de migratie of op ongeschikte plekken terechtgekomen en doodgegaan.

Ik heb onderzocht of deze hoge sterfte gedurende de migratieperioden is te verklaren door predatie (het vangen en opeten van prooi) door vis en krabben op migrerende *Macoma*. In een rond aquarium met stroming kwamen de nonnetjes uit het zand en gingen migreren, zonder stroming bleven de nonnetjes ingegraven in het zand. Deze

opstelling werd gebruikt om predatie-experimenten te doen met en zonder stroming, in licht en donker. In licht aten vissen en strandkrabben meer migrerende dan ingegraven nonnetjes, in donker was er geen verschil. Vanwege dit verschil tussen licht en donker, viel te verwachten dat er 's nachts meer nonnetjes migreren dan overdag, omdat overdag de vissen veel nonnetjes eten of omdat de nonnetjes de vissen ontwijken door 's nachts te migreren. Op het wad bleken nonnetjes inderdaad vooral 's nachts en bij lage temperaturen te migreren. Bovendien werden er geen nonnetjes gevonden in de magen van vrijzwemmende vissen die overdag gevangen werden. Samenvattend kan een hogere predatiedruk van vissen en krabben op migrerende dan op ingegraven nonnetjes het mechanisme zijn dat het grote aantal verdwijnende nonnetjes gedurende migratieperioden verklaard.

De volgende alinea's gaan over de mogelijke voordelen van migratie. Ik heb hierbij gekeken naar verschillen in predatiedruk in de kinderkamers en op de verblijfplaatsen van de volwassen dieren, in tegenstelling tot het voorgaande stuk dat ging over predatie tijdens migraties. De tijd die predatoren (roofdieren) op het wad kunnen besteden aan voedsel zoeken wordt beperkt door het tij. Vogels kunnen alleen voedsel zoeken op drooggevallen platen, daarom is de predatiedruk van vogels op het lang droogvallende hoge wad waarschijnlijk hoger dan op het lage wad. Uit de literatuur is bekend dat vogels bij voorkeur grote nonnetjes eten. Krabben en garnalen zijn alleen actief zijn op het wad bij hoogwater. Garnalen (*Crangon crangon*) bleken groter en talrijker te zijn op het lage dan op het hoge wad. Krabben (*Carcinus maenas*) waren talrijker op het hoge wad, maar gemiddeld groter op het lage wad. Uit selectie-experimenten in het laboratorium en maaginhoudanalyses bleek dat krabben, garnalen en kleine vis (samen het zogenaamde epibenthos, dieren die op de bodem leven) alleen kleine nonnetjes (<5 mm) eten. Op grond van deze waarnemingen verwachtte ik dat de predatiedruk op kleine nonnetjes hoger is op het lage wad, terwijl de predatiedruk op de grote nonnetjes hoger zou zijn op het hoge wad. Hierdoor zou een migratie naar en van het hoge wad voordelig kunnen zijn voor de nonnetjes. Deze hypothese werd getest in een experiment waar selectief twee groepen predatoren (vogels enerzijds en krabben, garnalen en vissen anderzijds) buitengesloten werden met kooien, hoog en laag op het wad. De dichtheden van nonnetjes in deze kooien werd na enkele maanden vergeleken met niet-gemanipuleerde controlegebieden, waar de predatoren normaal toegang hadden. Predatie door vogels bleek zowel laag als hoog op wad geen significant effect te hebben op de dichtheden van jonge en volwassen nonnetjes. De dichtheden van jonge nonnetjes in kooien waar krabben, garnalen en vissen waren buitengesloten, waren hoger dan in de controlegebieden waar deze dieren vrije toegang hadden. Dit verschil was, zoals verwacht, veel groter op het lage dan op het hoge wad. Jonge nonnetjes worden dus op het lage wad veel meer gegeten dan op het hoge wad. Jonge nonnetjes kunnen daarom predatie door epibenthos ontwijken door op het hoge wad leven.

Behalve predatie door vogels, krabben, garnalen en vissen, zou predatie door wormen ook belangrijk kunnen zijn voor het kinderkamergebruik van het nonnetje. Deze alinea

gaat over het effect van de predatie door de wadpier en de zeeduizendpoot op nonnetjes. Wormen kunnen zeer hoge dichtheden bereiken op het wad en zouden daarom, zelfs als één worm maar zeer weinig nonnetjes consumeert, de dichtheden van nonnetjes negatief kunnen beïnvloeden. In de magen van de zeeduizendpoot *Nereis diversicolor* en de wadpier *Arenicola marina* werden nonnetjes (<1,5 mm) gevonden, een direct bewijs dat de nonnetjes door de wormen gegeten worden. Ook laboratoriumexperimenten lieten zien dat deze wormen zeer kleine nonnetjes kunnen eten. Om te zien of wadpier en zeeduizendpoot de dichtheden van jonge nonnetjes beïnvloeden, werden de dichtheden van de wadpier (in gebieden van 0,25 tot 1m$^{2)}$ en zeeduizendpoot (in 0.03 m^2 kooien) experimenteel verhoogd. Na enkele weken werd het effect op de dichtheden van *Macoma* bekeken. Beide wormensoorten bleken een significant negatief effect te hebben op de dichtheden van zeer kleine nonnetjes. Op grond van de analyse van de maaginhouden en veldexperimenten kon berekend worden dat, gedurende een korte periode in het voorjaar, wadpieren tussen 45 en 102 *Macoma* per m^2 per dag en zeeduizendpoten tussen 5 en 116 *Macoma* per m^2 per dag consumeren. Deze aantallen zijn meer als tienmaal zo hoog dan de consumptie door garnalen en krabben. Desondanks kan de jaarlijkse variatie in aantallen nonnetjes op het Groninger wad niet verklaard worden door verschillen in talrijkheid van deze wormen tussen jaren. Omdat beide wormen relatief homogeen over het wad verspreid zijn, vormen de wormen namelijk geen reden voor het nonnetje om op het hoge of lage wad te leven.

Naast predatie zouden ook verschillen in groeisnelheid tussen het lage en hoge wad een reden kunnen zijn voor de migratie van *Macoma*. Op het Groninger wad waren er slechts kleine verschillen in schelplengte en lichaamsgewicht tussen het lage en hoge wad. Ook in kooien, waar predatoren die delen van de sifon (voedselopname-orgaan) van nonnetjes afbijten en het voedselzoeken remmen afwezig waren, waren de verschillen in groeisnelheid tussen laag en hoog op het wad klein. Daarom zijn verschillen in groeisnelheid waarschijnlijk geen reden voor het kinderkamergebruik van het nonnetje.

Om vast te stellen in hoeverre de onderzochte factoren de sterfte van het nonnetje kunnen verklaren, werd in een model het aandeel van consumptie door de bekende predatoren in de sterfte van het nonnetje berekend. Een groot deel van de sterfte van het nonnetje op het Groninger wad kan verklaard worden aan de hand van de uit de empirische onderzoeken bekende predatie door garnalen, krabben, wormen en scholeksters.

Alle voor- en nadelen van migraties en kinderkamergebruik voor het nonnetje werden in hetzelfde model tegen elkaar afgewogen om te bepalen wat het effect van migraties op de fitness van het nonnetje is. In dit model werd het aantal overlevende en zich voortplantende nonnetjes over een periode van vijf jaar werd berekend als een functie van predatie door garnalen, kleine en grote krabben, zeeduizendpoten en wadpieren hoog en laag op het wad en extra sterfte tijdens migraties. Bovendien werden, op

grond van literatuurgegevens, de predatie door de scholekster en infectie door de parasitaire trematode *Parvatrema affinis* berekend. *Parvatrema* infecteert alleen grote nonnetjes op het hoge wad. Een infectie leidt bij de gastheer tot parasitaire castratie, waardoor de gastheer een fitness krijgt van nul. In het model werd ook de fitness van nonnetjes die op verschillende momenten migreerden, en dus gedurende andere perioden hoog en laag op het wad leefden, vergeleken. Het bleek dat de fitness het hoogst was voor nonnetjes die zich na het larvale stadium direct vestigen op het hoge wad, hier blijven tot hun eerste winter en dan naar het lage wad migreren. Voor dieren die zich in tegenstelling tot deze beste strategie op het lage wad vestigen, zoals in de Waddenzee gebeurt door de invloed van de stroming, is een snelle migratie naar het hoge wad de beste strategie. De kosten van deze migratie worden hierbij ruim gecompenseerd door het verschil in predatiedruk door garnalen tussen het lage en hoge wad. De wintermigratie terug naar het lage wad is voordelig omdat *Macoma* hierdoor de nadelige infectie door *Parvatrema* ontwijkt. Sommige andere predatoren, zoals de zeeduizendpoot en de scholekster, hadden wel effect op de fitness van *Macoma*, maar lijken geen invloed te hebben op de migratiestrategie die de hoogste fitness voor *Macoma* oplevert, omdat de ruimtelijke verschillen in predatiedruk klein en de migratiekosten hoog zijn.

Uit het bovenstaande kan de conclusie getrokken worden dat de migratie naar en van kinderkamers op het hoge wad de fitness van *Macoma balthica* verhoogt. Dit komt doordat zowel de garnaal *Crangon crangon* als de parasiet *Parvatrema affinis* een groot verschil in talrijkheid tussen het lage en hoge wad laten zien en bovendien sterk selecteren op de grootte van de nonnetjes die ze eten of infecteren.
Door de snelle lengtegroei van *Macoma* gedurende zijn eerste levensjaar verandert hij binnen 9 maanden van een prooi voor garnalen, die ontweken kunnen worden op het hoge wad, in een gastheer voor *Parvatrema*, die ontweken kan worden op het lage wad. Hoewel de kosten van de migratie voor het nonnetje hoog zijn, is het netto-effect van migraties en kinderkamergebruik op de fitness positief, omdat het verschil in predatiedruk tussen het hoge en lage wad groot is.

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Dit proefschrift is het resultaat van vier jaar werk, dat ik gelukkig niet alleen heb hoeven doen. In dit dankwoord wil ik graag iedereen bedanken die heeft bijgedragen aan de totstandkoming van dit proefschrift. In de dankwoorden ('Acknowlegdements') van de afzonderlijke hoofdstukken worden de mensen bedankt die belangrijk waren voor het tot stand komen van deze specifieke hoofdstukken genoemd.
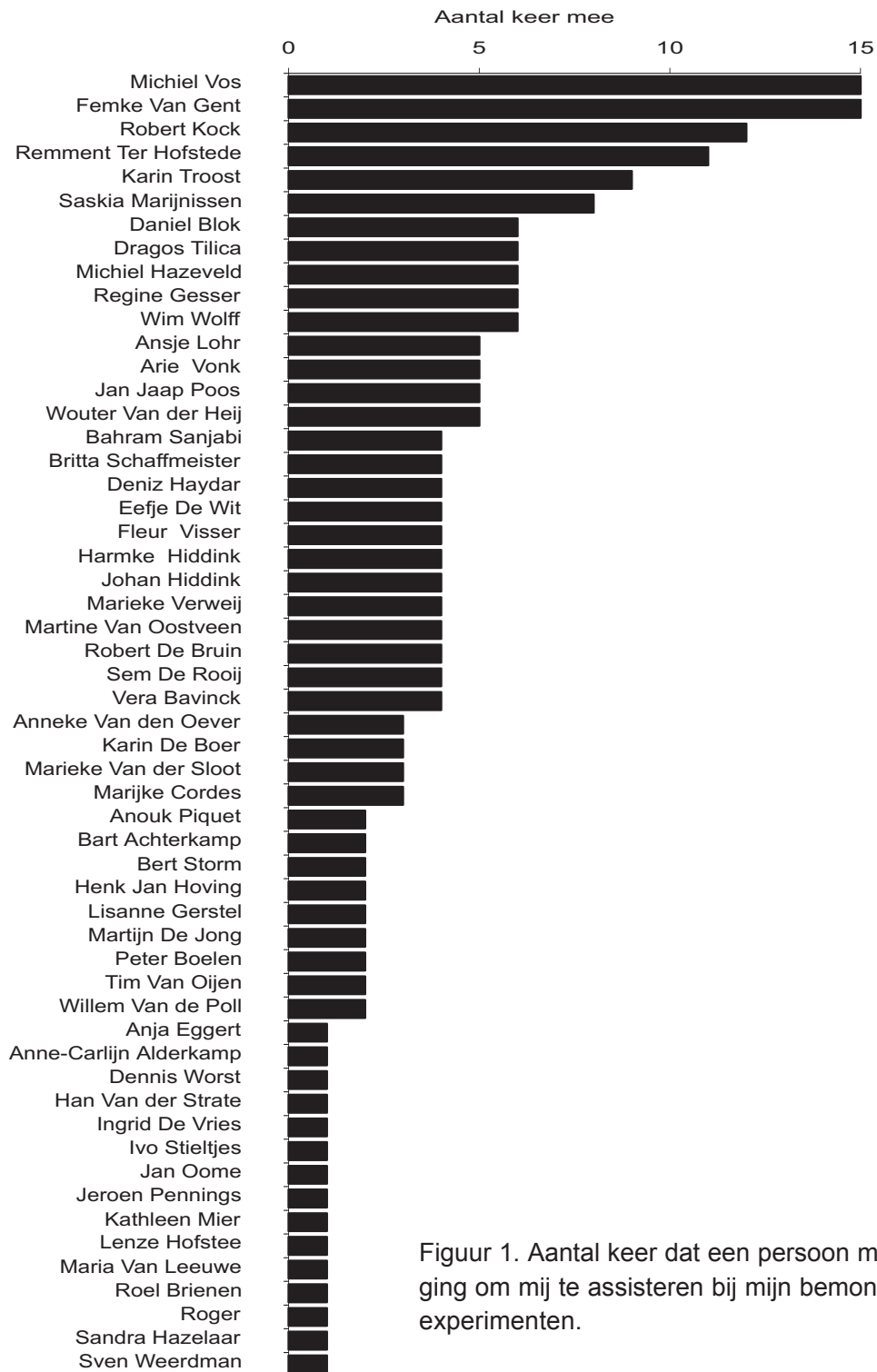
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Aantal keer mee

| | 0 | 5 | 10 | 15 |

Michiel Vos
Femke Van Gent
Robert Kock
Remment Ter Hofstede
Karin Troost
Saskia Marijnissen
Daniel Blok
Dragos Tilica
Michiel Hazeveld
Regine Gesser
Wim Wolff
Ansje Lohr
Arie Vonk
Jan Jaap Poos
Wouter Van der Heij
Bahram Sanjabi
Britta Schaffmeister
Deniz Haydar
Eefje De Wit
Fleur Visser
Harmke Hiddink
Johan Hiddink
Marieke Verweij
Martine Van Oostveen
Robert De Bruin
Sem De Rooij
Vera Bavinck
Anneke Van den Oever
Karin De Boer
Marieke Van der Sloot
Marijke Cordes
Anouk Piquet
Bart Achterkamp
Bert Storm
Henk Jan Hoving
Lisanne Gerstel
Martijn De Jong
Peter Boelen
Tim Van Oijen
Willem Van de Poll
Anja Eggert
Anne-Carlijn Alderkamp
Dennis Worst
Han Van der Strate
Ingrid De Vries
Ivo Stieltjes
Jan Oome
Jeroen Pennings
Kathleen Mier
Lenze Hofstee
Maria Van Leeuwe
Roel Brienen
Roger
Sandra Hazelaar
Sven Weerdman

Figuur 1. Aantal keer dat een persoon mee naar het wad ging om mij te assisteren bij mijn bemonsteringen en experimenten.

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Jan Geert Hiddink