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

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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 the dark were lower than in the 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; it takes time and requires 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, the juveniles' use of nursery areas 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, can be 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 two migrations. In May the postlarvae (300 µm, 1–3 months in age) migrate to the low tidal flats, where they settle initially, to the nurseries (spring migration) on high, silty tidal flats (Armonies and Hellwig-Armonies 1992). During 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 and North Seas (winter migration) (Beukema and De Vlas 1989).

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Migration occurs via byssus drifting, whereby increased drag on byssus threads decreases the sinking rates of juvenile molluscs (Sigurdsson et al. 1976; Sörlin 1988). Sinking rates for small bivalves with a byssus thread can be up to five times slower than those without a thread, depending on shell size and thread length (Sörlin 1988; Beukema and 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 1993; Hiddink et al., 2002, in press), but the costs of migration to and from the nursery have been considered in only one paper (Hiddink and Wolff, in press); 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 1993). 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* under both daylight and dark conditions.

Materials and methods

In the present study, we considered both the spring and winter migrations 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 (Fig. 1). For 0-group *M. balthica*, the top layer of the sediment was collected and sieved through 500 and 1,000 μm mesh in the laboratory. *M. balthica* that passed through 1,000 μm 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 experi-

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

Byssus drifting of 0-group *M. balthica*

We investigated the byssus drifting of the 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 bivalves were collected with a pipette and put in a petri dish with Alcian blue solution, thereby staining mucopolysaccharides in the byssus threads blue. Subsequently, individuals were examined for the presence of a byssus thread under a binocular microscope at $\times 25$ magnification.

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

Potential fish predators of migrating *M. balthica* were collected with different fishing gears at six locations in the Oosterschelde estuary and Wadden Sea, at locations where we expected migrating *M. balthica* (Fig. 1A), on eight 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 the 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 during the day than at night (McIntosh and Townsend 1995; De Robertis et al. 2000; Forward and Rittschof 2000). Therefore, we predicted that the number of migrating bivalves would be higher at night than during the day, either due to adaptation of the bivalves or to high predation on migrating bivalves in the daytime or both processes. From January to March 2001 five samples were collected with four 2-mm-mesh plankton nets on the tidal flats of the Groninger Wad, in the eastern Dutch Wadden Sea (Fig. 1B; Table 2). The nets (diameter 19 cm) were placed 5 cm above the sediment surface and could rotate freely on a pole (see Fig. 1E in Armonies 1994). The nets fished passively on the current during immersion. Sampling dates were chosen so that low water (LW) and sunset and sunrise approximately coincided (Table 2; Fig. 2). Day-length in January was < 8 h, while the time between two low tides is approximately 12.4 h. The locations of the nets were submerged for approximately 6 h between two low tides. Therefore, with a deviation of < 3 h between LW and sunrise or sunset, there was a good separation of day and night catches (Fig. 2).

Log-transformed catch numbers were analysed in a three-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 two circular tanks or carousels (Fig. 3). Carousel A (Fig. 3A) was already in use for migration studies in 1973 (Venema and Creutzberg 1973; Creutzberg et al. 1978); carousel B (Fig. 3B) (De Jonge and Van den Bergs 1987)

Fig. 1A,B. 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 set

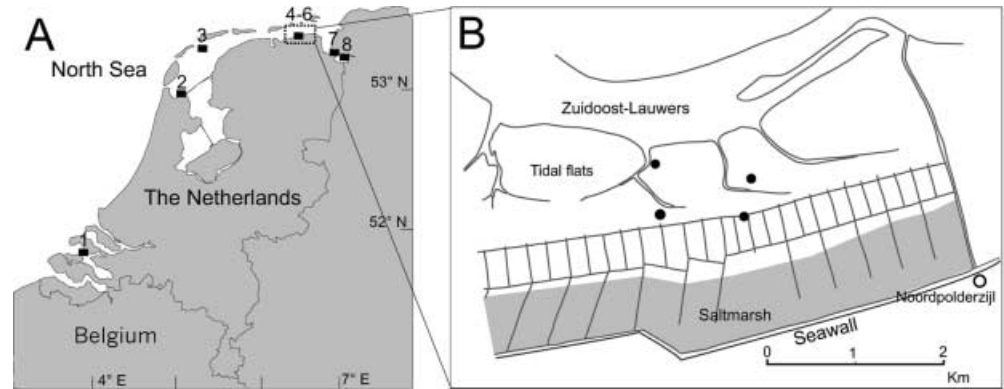


Table 1. Locations, sampling dates and gear used for sampling pelagic fishes in estuarine areas in winter (for locations see Fig. 1A)

No.	Location	Date	Gear and mesh
1	Oosterschelde	7 Feb 2000	Beamtrawl, 4 mm
2	Den Oever	29 Feb 2000	Plankton net (1 m ²), 1 mm
3	Terschelling	3 Mar 2000	Plankton net (1 m ²), 1 mm
4	Noordpolderzijk	9 Dec 1999	Plankton net (0.019 m ²), 2 mm
5	Noordpolderzijk	27 Jan 2000	Plankton net (0.019 m ²), 2 mm
6	Noordpolderzijk	16 Mar 2001	Plankton net (0.019 m ²), 2 mm
7	Ems	26 Mar 2001	Anchor seine, 1 cm
8	Dollard	26 Mar 2001	Large fykes, 1 cm

was an improvement of carousel A. In the carousels, water current was generated by paddles in the inner cylinder (A) or by two 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 (grain size <0.5 mm). Experiments were carried out during the period that migration occurred 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 for 0-group or 150 for 1-group *M. balthica*) were released into a carousel and allowed to bury for 30 min. We checked whether they had buried for the 1-group; for the 0-group 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, which 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.

Table 2. Dates on which the number of 1-group *Macoma balthica* migrating during the day and night in winter were estimated. The time of low water (LW-1 morning 1st day; LW-2 evening 1st day; LW-3 morning 2nd day), sunrise (1 morning 1st day; 3 morning 2nd day), sunset (2 evening 1st day) and the moon phases are given

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

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 mm (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) was determined. In the analysis, we used the number of *M. balthica* that had disappeared or been eaten. 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 light-experiments were done during daylight hours, but we also examined the interaction of darkness and current on the number of eaten *M. balthica*, for both the 0- and the 1-group. Experiments in darkness were carried out during daytime under a black sheet in a dark laboratory, with plaice and flounder as predators. In this way, we separated the effect of the diurnal rhythm of the predators from the lighting conditions, which allowed more precise conclusions on the effect of light.

In addition to the carousel experiments (Table 3), we carried out predation experiments with 1-group *M. balthica* and several 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 two-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* (Fig. 4). In a petri dish, the entire

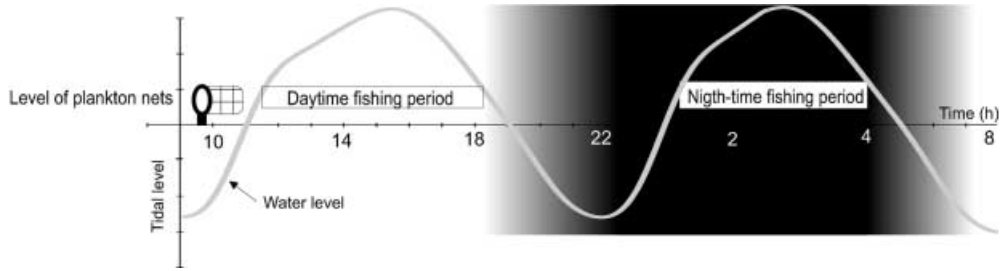


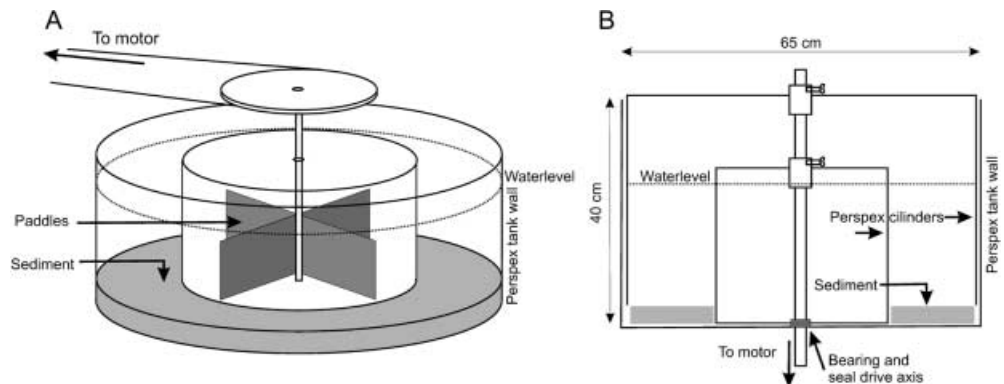
Fig. 2. Set-up of the day/night migration sampling of *Macoma balthica* in the field; an example of a 24 h period with a 14 h night. Water level, day and night, and level of the plankton net together determine the day and night fishing periods. In this example, low water and sunset/rise are not perfectly synchronised, as is the case for all data in Table 2; however, there is still good separation of fishing into light and dark periods

byssus thread was approximately 2 cm in length, whereas, in the vertical tube, it 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.

Pelagic fish in estuarine areas in winter

Because different fishing methods were used at every location (see Fig. 1), no quantitative data on pelagic fish abundance are given. Herring (*Clupea harengus*; locations 1 and 7, $n=20$ stomachs), sprat (*Sprattus sprattus*; locations 1–5 and 7, $n=58$ stomachs), three-spined stickleback (*Gasterosteus aculeatus*; locations 2, 4 and 8, $n=20$ stomachs) and smelt (*Osmerus eperlanus*; locations 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 at only one 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 four small *Mytilus edulis* (< 1 mm) and various polychaetes in the stomachs of *S. sprattus* (mussel and Phyllodoceidae) and *O. eperlanus* (*Nereis*).

Fig. 3A,B. Carousels used in laboratory migration experiments. **A** Carousel A was redrawn and modified from Creutzberg (1961); **B** carousel B was redrawn and modified from De Jonge and Van den Bergs (1987)



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

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

The number of migrating lugworms (*Arenicola marina*) in winter was higher at night (0.65 net^{-1}) than in the 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 (Fig. 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, Fig. 6; Table 5). The predator (presence and species) × 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 *P. platessa* in daylight with current than in darkness with or without current (Fig. 7; Table 6). *P. platessa* was inactive during darkness, as the number of *M. balthica*

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

Predator species and number	Length (cm)	Carousel	Duration (min)	<i>M. balthica</i> age	Initial no. of <i>M. balthica</i>	Replication			
						Light, current	Light, no current	Dark, current	Dark, no current
None		A	120	0	500	6	6	0	0
<i>Pomatoschistus microps</i> (10)	4	B	120	0	500	6	6	0	0
<i>Pleuronectes platessa</i> (10)	3	B	120	0	500	6	5	4	4
None		B	150	1	150	4	3	0	0
<i>Carcinus maenas</i> (2)	4	A	80	1	150	7	7	0	0
<i>Merlangius merlangus</i> (2)	15	B	150	1	150	3	3	0	0
<i>Pleuronectes platessa</i> (2)	10	B	150	1	150	4	4	0	0
<i>Platichthys flesus</i> (4)	10	A	150	1	150	4	5	0	0
<i>Platichthys flesus</i> (2)	10	B	150	1	150	6	8	5	5

consumed in darkness was less than the number disappearing without predators (compare with Fig. 6). It should be noted that “light” data in Fig. 7 are equal to the *P. platessa*-data in Fig. 6.

Control experiments with 1-group *M. balthica* and without predators experienced a loss of ca. three *M. balthica* due to handling, irrespective of the presence of current (Fig. 8). 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 (Fig. 8). The two-factor ANOVA data in Table 7 show 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 showed that the effect of migration on the predation risks also depended on light conditions for 1-group *M. balthica* (Fig. 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 *Macoma 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

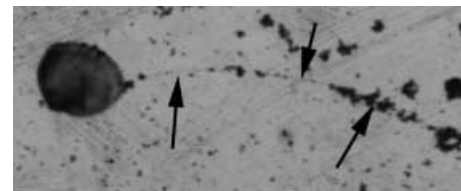


Fig. 4. *Macoma balthica*. Photograph of a 0-group *M. balthica* (approximately 1 mm length) in a petri dish, shortly after byssus drifting in a water current, showing a byssus thread. The byssus (arrows) was stained with Alcian blue. Particles in the picture are due to excess Alcian blue

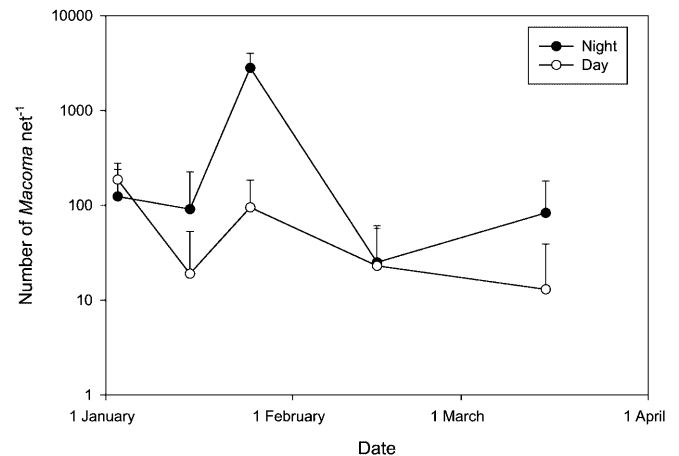


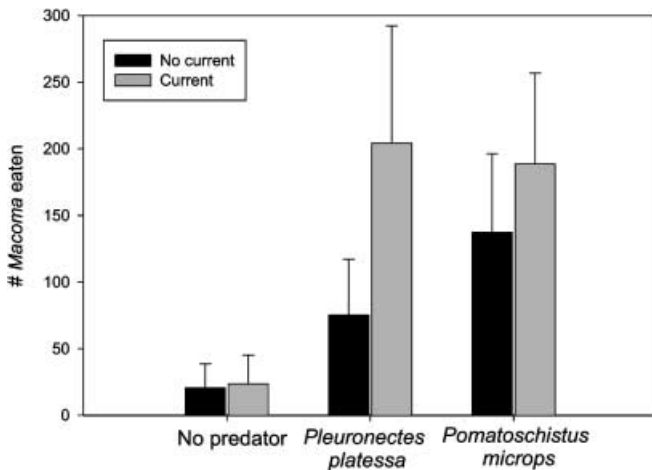
Fig. 5. *Macoma balthica*. Number of migrating *M. balthica* (+SD) on the tidal flats of the Groninger Wad in winter 2001, during day and night

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 stomachs of the pelagic fish that we caught in the daytime in the field. Unfortunately, therefore, the mechanism cannot be validated. Nevertheless, literature reports suggest fish predation on migrating infauna. The

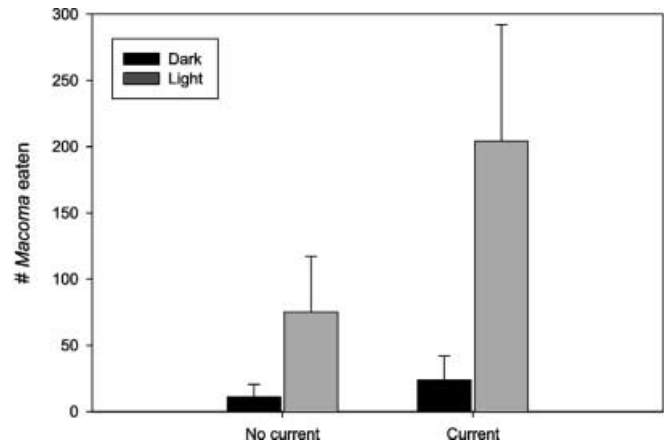
Table 4. Three-factor ANOVA (type I error) of the log-transformed number of *Macoma balthica* net⁻¹ during the day and night in winter

Source	df	MS	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×Day/Night	4	5.5	6.03	0.0013
Residual	27	0.9		

**Fig. 6.** *Macoma balthica*. Number of 0-group *M. balthica* eaten (+SD) in carousel experiments in light, with and without current, with three predator groups**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	MS	F-ratio	P-value
Predator	2	67,393	22.76	0.0000
Current	1	31,510	10.64	0.0029
Predator × Current	2	10,902	3.68	0.0381
Residual	28	2,961		
Total	33			

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 the migrating polychaete *Nereis virens*. Hostens and Mees (1999) observed a proportion of 1% benthic polychaetes in stomachs of the 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 when they are buried in the sediment, but were probably eaten during the pelagic long-distance migrations (several kilometres) they undertake (Essink et al. 1989), even though these migrations are largely nocturnal (Lawrie and Raffaelli 1998). These records of infaunal organisms in the

**Fig. 7.** *Macoma balthica*. Number of 0-group *M. balthica* eaten (+SD) by juvenile *Pleuronectes platessa* in carousel experiments in light and dark, with and without current**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	MS	F-ratio	P-value
Light	1	66,368	23.65	0.0003
Current	1	22,404	7.98	0.0135
Light × Current	1	14,951	5.33	0.0368
Residual	14	2,806		
Total	17			

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

Migration in the presence of pelagic and epibenthic predators is dangerous in the light, for both 0-group and 1-group *M. balthica*, but in the dark no difference exists in the 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 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.

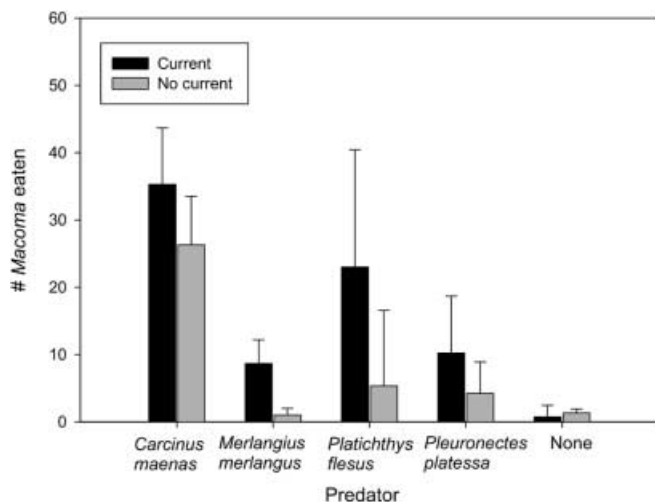


Fig. 8. *Macoma balthica*. Number of 1-group *M. balthica* eaten (+SD) in carousel experiments in light, with and without current, with five predator groups

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 predator groups (none, shore crab, whiting, flounder, plaice)

Source	df	MS	F-ratio	P-value
Predator	4	1.61	17.83	0.0000
Current	1	0.82	9.10	0.0043
Predator × Current	4	0.27	3.05	0.0268
Residual	43	0.09		
Total	52			

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 greater when animals are migrating, and we expect higher migration rates in the dark, while, at the same time, predation is expected to decrease in the dark.

Dark-experiments were conducted during the daytime; therefore, the difference in predation between light and dark really represents the difference in visibility and not in the diurnal rhythms of the predators or of *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 raise 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 and Land 1967; Nilsson 1994). Therefore, it is likely that these *M. balthica* can detect light in some way or another.

We consider light to be a factor affecting the migration risk for *M. balthica*. Turbidity may also be an

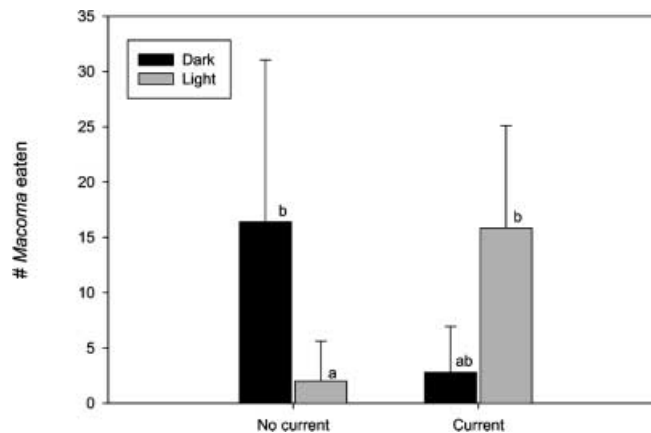


Fig. 9. *Macoma balthica*. Predation of flounder on 1-group *M. balthica* (+SD) during day and night, with and without current. Common letters indicate no significant differences between groups (Student–Newman–Keuls test)

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 centimetres in winter, although visibility on calm days in summer can be up to 1 m. We expect that 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 and Van Der Lingen 1992; Benfield and Minello 1996; Gregory and Levings 1998), while others found that the predation patterns changed, but that the consumption rates stayed the same (Gregory and Levings 1996; Abrahams and Kattenfeld 1997). If turbidity indeed decreases predation rates on migrating *M. balthica*, a smaller risk and a smaller day/night difference of predation on *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 ash-free dry weight 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 of the byssus thread do not seem to be important in comparison to the benefits resulting from migrations.

This study sheds some light on 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 (Hiddink and Wolff, in press). The nightly migrations of *M. balthica* may be an adaptation to avoid predation by diurnal fish. 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* occurs in fast-flowing tidal channels (Hiddink and Wolff, in press), but a low food supply and high sediment mobility may cause quick death at these locations. A single observation of large numbers of dead 1-group *M. balthica* on the saltmarsh vegetation in winter shows that migration to the wrong locations can cause death.

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