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Predation by crustaceans on native and non-native Baltic clams

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ABSTRACT: We studied the effect of crustacean predators on native/non-native *Macoma balthica* bivalves in aquarium experiments. North Sea *M. balthica* (NS *Macoma*) were recently observed in the southern Baltic Sea. They differ genetically and in terms of morphology, behaviour and evolutionary history from Baltic Sea *M. balthica* (BS *Macoma*), and this may affect predation pressure and community structure. We hypothesised that predators consume more of the prey they co-exist with. NS *Macoma* and BS *Macoma* were exposed to crustacean predators common in the North Sea (*Carcinus maenas* and *Crangon crangon*) and in the Baltic Sea (*C. crangon* and *Saduria entomon*). Contrary to our hypotheses, the North Sea predators ate more BS *Macoma*, and *S. entomon* ate more NS *Macoma*. The crush-limited *C. maenas* preyed more on globular BS *Macoma*, whereas *S. entomon*, which do not crush but pry open the bivalve shell, ate more NS *Macoma*, which have a lighter (thus probably thinner) shell than BS *Macoma*. When NS and BS *Macoma* were offered together, BS *Crangon* ate more NS *Macoma*. We also studied BS *Crangon* consumption of *M. balthica* to assess whether sizes offered fall within the size spectrum that *C. crangon* can eat. Small (20 to 40 mm long), medium (40 to 50 mm) and large (50 to 60 mm) *C. crangon* especially ate small *M. balthica*. Differences in shape, size and meat/shell weight ratio between the BS and NS *Macoma* partly explained the differences in the susceptibility to predation by native and non-native predators.

KEY WORDS: Native · Non-native · Predator · Prey · Baltic Sea · North Sea · *Macoma balthica*

INTRODUCTION

The co-existence of predator and prey depends on the outcome of their interactions that have developed throughout history. Ultimately many species have the means to recognise prey and predators, and to find and avoid them (Busdosh et al. 1982, Ejdung 1998). Today animals disperse more rapidly to new areas through artificial waterways (Olenin & Leppäkoski 1999), are introduced by humans, or shift their distribution due to global climate change. These introduced predators and prey may be able to adapt to the prevailing conditions and establish viable populations. Yet they have different evolutionary histories and may lack the ability to detect predators or prey never encountered before. Their effect on the community structure and predator–prey interactions is difficult to predict. Therefore, questions arise on whether the newcomers will be eaten, out-competed or able to co-exist with organisms already present in the area, and how predator–prey interactions will be affected.

Macoma balthica (L.) has a distribution from arctic to temperate areas (Bachelet 1980, Beukema & Meehan 1985, Meehan et al. 1989, Kuparinen et al. 1996, Hummel et al. 1997, Cederwall 1999). Populations from various locations around the world show genetic differentiation (Meehan et al. 1989, Väinölä & Varvio 1989, Hummel et al. 2000, Luttikhuizen et al. 2003a, Väinölä 2003, Nikula et al. 2007) and differences in shell characteristics (Beukema & Meehan 1985). This may affect their survival, behaviour, function in the ecosystem, interaction with predators and the benthic community structure. *M. balthica* that occur in the Baltic Sea (BS *Macoma*) and in the North Sea (NS *Macoma*) have

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different genetic composition (Väinölä & Varvio 1989, Hummel et al. 2000, Luttikhuizen et al. 2003b, Väinölä 2003). NS *Macoma* settle earlier in the year and grow faster than BS *Macoma* and thus their natural size distributions are different (Ankar 1980, Bouma et al. 2001, Ejdung & Elmgren 2001). We refer to *M. balthica* specimens with different genetic identities as different groups. In 1995, NS *Macoma* individuals were found in the Baltic for the first time in the deeper parts of the Gdansk area, and 2 yr later also in shallower areas (Hummel et al. 2000). BS and NS *Macoma* are important as prey in their respective habitats; thus it is of interest to study whether and how predator–prey interactions in the Baltic are altered with the intrusion of NS *Macoma*.

In the Dutch part of the North Sea, *Macoma balthica* is confined to the Wadden Sea, the Delta estuaries and a narrow zone along the coast, from the upper part of the intertidal to the shallow subtidal zone (Holtman et al. 1996). *M. balthica* is one of the dominant species (in terms of abundance and biomass) over large areas in the Baltic Sea (Ankar & Elmgren 1976, Cederwall et al. 1998, Falandysz et al. 2000), and occurs in shallow and deeper areas (80 m; E. Flach unpubl., Cederwall 1999), from the south to the northern low-saline Bothnian Bay (Väinölä & Varvio 1989).

Macoma balthica is an important food source for epibenthic predators (Bonsdorff et al. 1995a, Norkko 1998). In shallow North Sea areas, the main invertebrate predators on *M. balthica* are the brown shrimp *Crangon crangon* (L.) and the crab *Carcinus maenas* (L.) (Boddeke 1996, Hostens 2000). NS *Crangon* mainly feed on intertidal bottoms, since subtidal areas have less food due to tidal flows (Henderson et al. 2006); BS *Crangon* feed subtidally down to ~10 m (Bonsdorff et al. 1995b). The northern distribution limit of *C. maenas* is just north of the island of Bornholm (55° 19′ N, 15° 11′ E; Bonsdorff 2006), thus it does not occur in the Baltic proper. The predatory isopod *Saduria entomon*, absent in the North Sea, occurs throughout the Baltic. These predators are omnivores (Green 1957, Mattila et al. 1990, Cohen et al. 1995 and references therein, Ejdung & Elmgren 2001) and include *M. balthica* in their diet (Mattila et al. 1990, Ejdung & Bonsdorff 1992, van der Veer et al. 1998). *C. maenas* and *S. entomon* can feed on all prey sizes (1 to 6 mm) offered in our experiments (Ejdung & Bonsdorff 1992, Hiddink et al. 2002). *C. crangon* (15 to 25 mm long) eat *M. balthica* up to 1.5 mm long (Hiddink et al. 2002) but information on the *M. balthica* size span that medium (40 to 50 mm long) and large (50 to 60 mm) *C. crangon* can eat is to our knowledge lacking.

The main aim of the present study was to assess the effect of predators on the natural size distribution of native and non-native bivalve prey. This was done by studying the effect of the predatory *Crangon crangon*, *Carcinus maenas* and *Saduria entomon* on the survival of BS and NS *Macoma*, i.e. we investigated the interaction between predators and the natural size distribution of native and non-native prey. The underlying hypothesis was: predators eat more of the familiar prey, i.e. NS predators eat more NS *Macoma* and BS predators more BS *Macoma*, as predators recognise familiar prey more quickly. We also studied *C. crangon*'s consumption of *M. balthica* prey size to assess whether sizes offered fell within the size spectrum that *C. crangon* can eat.

MATERIALS AND METHODS

Sample collection and treatment. ***Predator–prey size range experiment:*** *Macoma balthica*, *Crangon crangon* and sediment from the BS were used in the predator–prey size range experiment. BS *Macoma* were collected using a benthic sled at 20 m depth, and specimens retained on 1 and 0.5 mm (summer) and 0.3 mm (autumn) sieves were used in the experiments. *C. crangon* were collected at a sandy beach close to the Askö laboratory (Sweden, 58° 49′ N, 17° 38′ E; annual temperature variation 2 to 14°C, salinity variation 6 to 8 PSU, no tidal cycle) by dragging a 2 mm mesh net over the bottom in summer and with an epibenthic sled at 10 m depth in autumn. Sediment was collected at the same time as *C. crangon*. All animals were kept in a temperature-regulated room with salinity, temperature and light conditions similar to those in the field. BS *Macoma* length (maximum distance along the anterior–posterior shell axis) was measured under a dissecting microscope (10×) to the nearest 0.05 mm. *C. crangon* length was estimated with a measuring slate for fish, from the tip of the rostrum to the end of the telson in stretched-out specimens.

Single and mixed prey experiments: Animals were collected in the Netherlands and Sweden, where the experiments were conducted. NS *Macoma* were collected during low tide, with a pitchfork in a Westerschelde tidal flat, southwestern Netherlands (Kruiningen, 51° 25′ N, 04° 21′ E), where the annual temperature variation is 3 to 25°C, salinity variation is 6 to 27 PSU (H. Hummel unpubl.), and mean tidal range is ~5 m (Herman et al. 2001). BS *Macoma* were collected with a benthic sled subtidally (10 to 20 m depth) in the Baltic proper (Askö Laboratory). Specimens retained on 0.5 mm sieves were brought to the laboratory and kept in a temperature-regulated room. BS *Macoma* were transported to the Netherlands by air and NS *Macoma* were transported to Sweden by car (single prey experiment) and by air (mixed prey experiment). During transportation (24 to 48 h) the bivalves were kept in humid sandy sediment, wrapped up in wet paper, placed in plastic jars and kept at 7 to 8°C. Immediately on arrival, they were transferred to jars filled with a few cm of sediment and aerated water. No difference in behaviour was seen between recently caught and transported *M. balthica.* A gradual acclimation (4 d) to experimental salinities started 1 d after arrival under light and temperature conditions similar to those used in the experiments.

NS predators *Carcinus maenas* were collected in the Westerschelde intertidal zone by hand at low tide, and *Crangon crangon* with a push-net along the edge of the water, at low water (0.5 to 1 m depth). BS predators *Saduria entomon* were collected close to the Askö Laboratory with a benthic sled at ~25 m depth, and *C. crangon* with an epibenthic sled at 5 m depth. In the laboratory, the crustaceans were gradually adapted to conditions used in the respective experiments. The predators were starved 2 d prior to the experiment. Damaged specimens or specimens with a soft carapace were not used.

Sediment was collected with a pitchfork (Westerschelde) and a benthic sled (Askö) from the same sites as the bivalves. Sediment passing through a 0.5 mm metal net was used in the Netherlands experiment. The BS sediment, which is more fine-grained than that in the Westerschelde, was sieved through a 0.3 mm metal net and used in experiments conducted in Sweden. Potential differences that may occur in meiofaunal abundances in the sieved sediment are of minor importance, since the predators do not actively feed on meiofauna (Pihl & Rosenberg 1984, Pihl 1985, Ejdung & Bonsdorff 1992, Feller 2006). The sampling area in the Westerschelde estuary has a mean natural salinity of ~15 PSU; therefore the 30 PSU Oosterschelde water available at the Dutch experimental site was diluted with fresh water to ~15 PSU. In the Askö experiments, salinity was increased to ~10 PSU by adding salt (hw-Marinemix+Bioelements, Wiegant) to the natural brackish water.

Bivalve length was measured initially and at the end of the experiments. *Macoma balthica* and *Crangon crangon* were measured as described in the preceding section. The carapace width was measured to the nearest mm for *Carcinus maenas*, and the length of *Saduria entomon* from the anterior cephalon to the tip of the telson.

Experiments. *Predator–prey size range:* An experiment estimating *Macoma balthica* sizes eaten by small, medium and large *Crangon crangon* was conducted. Prey size selection by small (20 to 40 mm), medium (40 to 50 mm) and large (50 to 60 mm) BS *Crangon* was studied in experiments conducted at the Askö laboratory. The experiments were run in duplicate and conducted in summer (May and June) and in autumn (August and September). *C. crangon* 20 to 60 mm long were each offered a total of 67 BS *Macoma* of sizes between 1 and 11 mm (summer) and 94 BS *Macoma* 0.4 to 10 mm long (autumn) (Table 1). *C. crangon* were not added to the control treatment. BS *Macoma* were added to each of 8 aquaria and after ~24 h, 1 *C. crangon* was added to 6 aquaria, and the remaining 2 aquaria were controls. The plastic aquaria (area 289 cm^2, 17 × 17 × 10 cm) filled with ~4 cm sieved sediment (summer 0.5 mm, autumn 0.3 mm mesh sieve) were placed in a temperature-regulated room (daily light cycle 12 h light:12 h dark) and connected to the seawater system. A layer of ~4 cm seawater (summer, 12.5 ± 2.5°C, 5.8 ± 0.1 PSU; autumn, 17.5 ± 1.5°C, 5.6 ± 0.2 PSU) was maintained over the sediment throughout the experiment. A net placed on top of the aquaria prevented *C. crangon* from escaping. After 14 d the experiment was ended, and BS *Macoma* retrieved on a 0.3 mm mesh sieve were measured and counted.

Single prey: Aquarium experiments designed to study the effect of predatory crustaceans on single or mixed *Macoma balthica* prey groups were set up using a similar experimental design in the Netherlands and in Sweden. Each predator species was offered either NS or BS *Macoma* (single prey experiments), or a mixture of NS and BS *Macoma* (mixed prey experiments). Prior to the start of the experiment, the collected *M. balthica* were divided into size classes (Table 2), then clams from each size-class were picked in batches giving a natural size span of 40 specimens. These batches were randomly selected and 1 batch was added to each aquarium. Further, we compared shape, colour, size and weight between NS and BS *Macoma*.

In the single and mixed prey experiments, square plastic aquaria (17.5 × 17.5 × 11 cm, area 306 cm^2) were used, each filled with ~3 cm sieved sediment. The

Table 1. Predator–prey (*Crangon crangon* and *Macoma balthica*) size range experiment; 2 size distributions of *M. balthica* were used, since small specimens were not available for the summer experiment. Data are no. of *M. balthica* of each size range added initially to each aquarium

Size (mm)	Summer	Autumn
0.4–1	0	20
1–1.9	10	20
2–2.9	20	20
3–3.9	20	20
4–4.9	7	7
5–5.9	2	2
6–6.9	2	2
7–7.9	1	1
8–8.9	1	1
9–9.9	1	1
10–10.9	3	0

overlying water was aerated by air-stones throughout the experiment, and the aquaria were kept in a temperature-regulated room. The light:dark cycle was set to 12:12 h and strip-lights simulated daylight.

Single prey – NS predators: The predation of *Carcinus maenas* (length ~11 mm) and *Crangon crangon* (~41 mm) on BS and NS *Macoma* was studied during 7 d in March and April at the Netherlands Institute of Ecology (NIOO), Yerseke. Six treatments, replicated 6 times, were set up: (1) NS *Macoma* and *Carcinus*, (2) BS *Macoma* and NS *Carcinus*, (3) NS *Macoma* and *Crangon*, (4) BS *Macoma* and NS *Crangon*, (5) NS *Macoma* control, and (6) BS *Macoma* control. Initially 40 *M. balthica* (corresponding to natural abundances in both areas; Bouma et al. 2001, Hiddink et al. 2002, M. Blomqvist pers. comm.) were added to each aquarium, and when no clams were seen on the sediment surface (after ~4 h, sediment depth 2.8 to 3.1 cm—*M. balthica* can burrow >3 cm within this time; Tallqvist 2001), 1 predator was added per aquarium to the 'predator treatments'; 3 replicates only were included in the NS *Macoma* and *Crangon* treatment, since some *C. crangon* moulted during the experiment. The size range of *M. balthica* was 1 to 6 mm (Table 2). Temperature and salinity during the experiment were 10.9 ± 0.1°C and 15.8 ± 0.1 PSU (mean ± SE), respectively.

Single prey – BS predators: The predation of *Saduria entomon* (length ~23 mm) and *Crangon crangon* (38 mm) on BS and NS *Macoma* was studied during 12 d in October at the Askö Laboratory. Six treatments with 6 replicates each were set up: (1) NS *Macoma* and BS *Saduria*, (2) BS *Macoma* and *Saduria*, (3) NS *Macoma* and BS *Crangon*, (4) BS *Macoma* and *Crangon*, (5) NS *Macoma* control and (6) BS *Macoma* control. Initially 40 *M. balthica* were added to each aquarium and ~4 h later, 1 predator was added per aquarium to the 'predator treatments'. Initial sizes of *M. balthica* ranged from 1 to 6 mm (Table 2). Sediment depth, temperature and salinity were 2.4 to 2.9 cm, 12.3 ± 0.1°C and 10.0 ± 0.1 PSU, respectively.

Table 2. Number of *Macoma balthica* of various size ranges added initially to each aquarium in the single prey and mixed prey experiments. NS: North Sea; BS: Baltic Sea; NL: Netherlands; Swe: Sweden

Expt		Size (mm)	NS *Macoma*	BS *Macoma*
Single prey	NL	1–1.9	1	12
		2–2.9	9	18
		3–3.9	18	7
		4–4.9	11	2
		5–5.9	1	1
	Swe	1–1.9	1	11
		2–2.9	10	16
		3–3.9	22	6
		4–4.9	6	6
		5–5.9	1	1
Mixed prey	Swe	1–1.9	2	2
		2–2.9	6	6
		3–3.9	9	9
		4–4.9	3	3

Mixed prey – BS predators: The predation of *Saduria entomon* (~30 mm) and *Crangon crangon* (~42 mm) on a mixture of BS and NS *Macoma* was studied during 7 d in June at the Askö Laboratory. The treatments replicated 8 times each were: (1) NS + BS *Macoma* and BS *Saduria*, (2) NS + BS *Macoma* and BS *Crangon*, (3) NS + BS *Macoma* control. A total of 20 NS and 20 BS *Macoma* were randomly assigned to the aquaria, and after ~4 h, 1 predator was added per aquarium to the 'predator treatment'; 6 replicates only were included in the analyses of the *S. entomon* treatment, since 2 *S. entomon* molted during the experiment. Clam sizes initially added ranged from 1 to 5 mm (Table 2). Sediment depth, temperature and salinity were 2.3 to 3.0 cm, 8.8 ± 0.1°C and 9.4 ± 0.1 PSU, respectively, during the experiment. A similar mixed prey experiment was attempted for the North Sea but no data are presented, due to high clam mortality.

***Morphology of BS and NS Macoma*:** In March and April we assessed whether BS and NS *Macoma* differ in shape, size and shell and meat weight, which may affect predation; 20 specimens each of BS and NS *Macoma* of the 1–6 mm size classes and 5 specimens of the 7–10 mm size classes were measured to the nearest 0.05 mm under a dissecting microscope (10×) with an ocular scale. Clams were divided into length classes of 1.0–1.95 mm to 10–10.95 mm. Shell length (greatest length), height (distance of umbo to outer margin at an axis perpendicular to the length axis) and width (greatest distance between the convex outsides of the closed valves) were measured on all specimens according to Beukema & Meehan (1985). Individuals of similar length (4 to 5 per interval with <0.1 mm difference, in total 80 specimens) were selected with a length interval of 0.5 mm for dry weight per length estimates for 1.6 to 11 mm long *M. balthica*. After a few seconds in boiling water the shells opened and the meat was removed. Meat and shell were dried separately (60°C for 24 h) and weighed to 0.1 mg accuracy.

Statistical analyses. The number of *Macoma balthica* eaten in the single and mixed prey experiments was analysed with a 2-factor ANOVA with predator and *M. balthica* as factors and the number eaten as the dependent variable. Contingency tables were used to test whether predators ate more or less compared to what would be expected based on the number of prey offered. Size, meat weight, shell weight and ratio (meat:shell weight) between NS and BS *Macoma* populations were analysed with analysis of covariance

(ANCOVA; log-transformed data) with length as covariate and group as factor. Dependent variables were height, width, meat weight, shell weight or meat:shell weight ratio. The total consumption of *M. balthica* by *Crangon crangon* in the predator–prey size range experiment was analysed using a 1-factor ANOVA. The number of different clam sizes eaten by *C. crangon* was analysed using contingency tables. Variance homogeneity was tested with Cochran's test and significant results were further analysed with the LSD test. We used Statistica 7.1 for all analyses.

RESULTS

Predator–prey size range

In the summer experiment, large and medium *Crangon crangon* consumed an average of 41 and 35 *Macoma balthica*, respectively, which is significantly more than the 12 specimens consumed by small *Crangon* ($F_{3,14}$ = 14.96, p < 0.001; LSD test, p < 0.05). In the autumn, no differences were found (small *Crangon* consumed 44 *M. balthica*, medium 48, and large 60) ($F_{3,14}$ = 15.79, p < 0.001; LSD test, p > 0.05). Of all clam sizes offered in summer, small *Crangon* consumed more of the 1 to 3 mm clams, medium *Crangon* consumed more of the 1 to 4 mm clams and large *Crangon* consumed more of the 2 to 4 mm clams (χ^2, p < 0.05). In autumn small and medium *Crangon* consumed more of the 0.4 to 3 mm clams, and large *Crangon* consumed more of the 1 to 4 mm clams (Table 3; χ^2, p < 0.05). Small and medium *Crangon* consumed mainly clams <3 mm, and large *Crangon* consumed mainly 1 to 4 mm sized clams. The largest clams eaten by large *Crangon* were 5 to 6 mm in summer, and 4 to 5 mm in autumn (Fig. 1).

Single prey experiments

BS or NS *Macoma* and NS predators

Survival was 100% in the BS *Macoma* control and 72% in the NS *Macoma* control. We assumed that prey mortality in the control took place early in the experiment, and estimated the number of clams eaten by subtracting the mean control mortality from the number of clams missing. Thus the analysis is conservative, and may underestimate the number of clams eaten by the predators. *Carcinus maenas* consumed significantly more clams than did *Crangon crangon* (Fig. 2a, Table 4; p < 0.05). Both predators consumed significantly more of the BS *Macoma* than of the NS *Macoma* (Fig. 2a, Table 4; p < 0.05). Bivalve length ranged from 1 to 6 mm at the start of the experiment (Table 2). Of the sizes offered, *C. maenas* consumed more 2 to 4 mm BS *Macoma* (Table 3; χ^2, p < 0.05), and more 1 to 3 mm sized BS *Macoma* were eaten in the *C. crangon* treatment (Table 3; χ^2, p < 0.05).

Table 3. Sizes of *Macoma balthica* eaten by *Carcinus maenas*, *Saduria entomon* and *Crangon crangon* in laboratory experiments. *C. crangon* sizes (length): S = 20 to 40 mm; M = 40 to 50 mm; L = 50 to 60 mm. (–) Not determined

	Crangon size	North Sea *Macoma* Eaten (mm)	North Sea *Macoma* Preferred (mm)	Baltic Sea *Macoma* Eaten (mm)	Baltic Sea *Macoma* Preferred (mm)
Predator–prey size					
Summer					
C. crangon	L	–	–	1–4	2–4
	M	–	–	1–4	1–4
	S	–	–	1–4	1–3
Autumn					
C. crangon	L	–	–	0.4–5	1–4
	M	–	–	0.4–4	0.4–3
	S	–	–	0.4–4	0.4–3
Single-prey					
Netherlands					
C. maenas		1–5	–	1–6	2–4
C. crangon	S to M	1–4	–	1–5	1–3
Sweden					
S. entomon		2–6	3–5	1–6	1–4
C. crangon	S to M	2–5	3–4	1–5	2–3
Mixed prey					
Sweden					
S. entomon		1–5	3–4	1–5	–
C. crangon	S to M	1–5	3–4	1–4	–

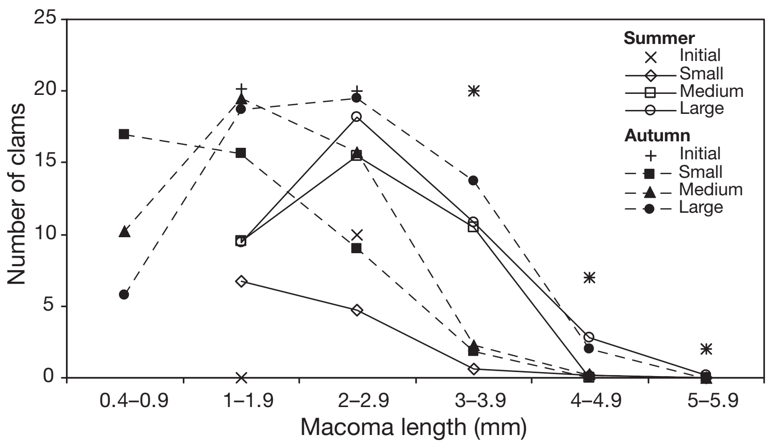

Fig. 1. Baltic Sea *Macoma balthica* eaten by small, medium and large *Crangon crangon* (see Table 3 for definition of sizes)

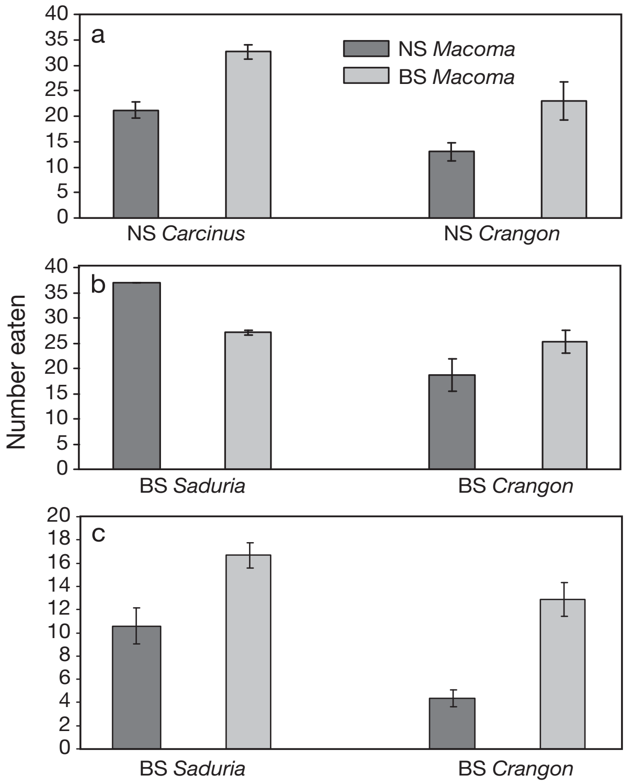

Fig. 2. Number of *Macoma balthica* (mean ± SE) eaten by predators (*Carcinus maenas*, *Crangon crangon* and *Saduria entomon*) from (a) the North Sea (NS) and (b) the Baltic Sea (BS) with only BS or NS *Macoma* present; and from (c) the BS with NS and BS *Macoma* present

BS or NS *Macoma* and BS predators

Survival in controls was 95% for BS *Macoma* and 82% for NS *Macoma*, and control mortality was compensated for as described in the previous paragraph. *Saduria entomon* consumed more clams than did *Crangon*, and more of the NS *Macoma* (Fig. 2b, Table 4; $p < 0.05$). BS *Crangon* consumed more BS than NS *Macoma* (Fig. 2b, Table 4; $p < 0.05$). Bivalve length ranged from 1 to 6 mm when the experiment started (Table 2). Of the clam sizes offered, *Saduria* consumed more of the 3 to 5 mm NS *Macoma* and the 1 to 4 mm BS *Macoma*, and BS *Crangon* consumed more of the 3 to 4 mm NS *Macoma* and the 2 to 3 mm BS *Macoma* (Table 3; χ^2, $p < 0.05$).

Table 4. Two-factor ANOVA on the number of *Macoma balthica* eaten by predators in the single and mixed prey experiments

Source	df	MS	*F*	p
Single prey				
Predator	3	379.67	13.40	<0.0001
M. balthica group	1	219.21	7.73	<0.01
Predator × *M. balthica* group	3	279.45	9.86	<0.0001
Error	37			
Mixed prey				
Predator	1	171.43	16.14	<0.0001
M. balthica group	1	364.58	34.32	<0.0001
Predator × *M. balthica* group	1	10.01	0.94	0.3413
Error	24			

Mixed prey experiment—BS and NS *Macoma* and BS predators

Survival was >94% for BS and NS *Macoma* in the control. *Saduria entomon* consumed more clams than did BS *Crangon*. Both *Saduria* and BS *Crangon* consumed more NS than BS *Macoma* (Fig. 2c, Table 4; $p < 0.05$). Initial bivalve sizes ranged from 1 to 5 mm (Table 2). Of the clam sizes offered, *Saduria* and *Crangon* ate more 3 to 4 mm long NS *Macoma* (Table 3; χ^2, $p < 0.05$).

Morphology of *Macoma balthica*

The 2 *Macoma balthica* groups were different in shape and colour, even at the smallest sizes (Fig. 3). BS *Macoma* were mainly white and NS *Macoma* were yellow, orange, red, bluish and white, but juvenile specimens were transparent. BS *Macoma* were slightly higher (Fig. 4a) and considerably wider (Fig. 4b) than NS *Macoma* (Table 5). The dry weight of the meat at similar length was not different. Shell dry weight, however, was higher in BS *Macoma* than in NS *Macoma* (Fig. 4c), resulting in a higher meat:shell ratio in NS *Macoma* (Table 5). Thus, BS *Macoma* were more globular and had a heavier shell than the flatter NS *Macoma*.

Fig. 3. *Macoma balthica*. Juveniles (ca. 1–3 mm long) from the Baltic Sea (left) and North Sea (right)

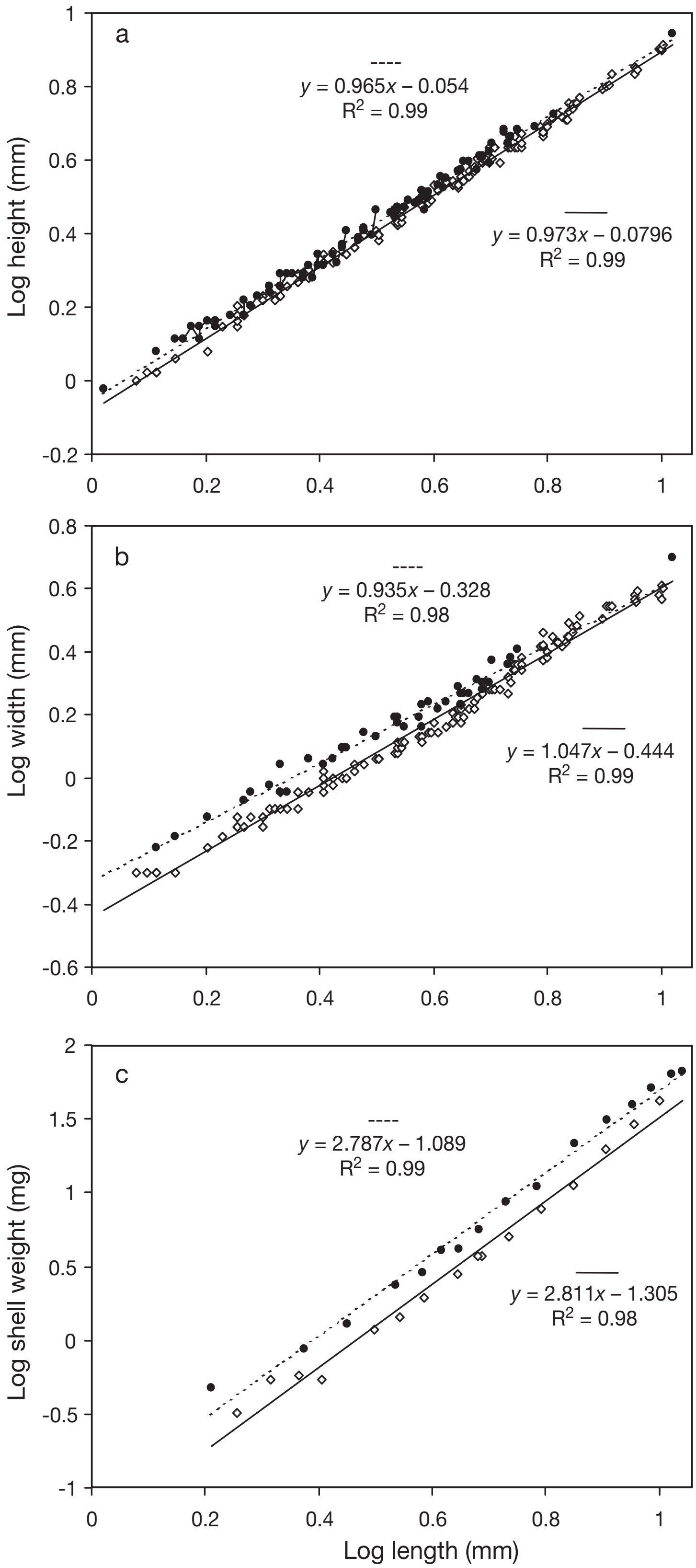

Fig. 4. (a) Height and length, (b) width and length, and (c) shell dry weight and length for North Sea *Macoma balthica* (◇) and Baltic Sea *M. balthica* (●)

DISCUSSION

Influence of prey type and prey size

Carcinus maenas, *Saduria entomon*, and *Crangon crangon* consumed more specimens of non-sympatric *Macoma balthica*, which is contrary to our hypothesis. It was only in the BS single prey experiment that BS *Crangon* ate more of the native BS *Macoma*. We suggest that the reason for the choice for non-native prey is connected to differences in morphology, behaviour or smell, whereby the non-native prey is detected earlier by the predator, that its morphology makes it easier to prey upon or that the prey is unable to detect the foreign predator. Predators and prey that live together often have developed morphological and behavioural defences or skills to successfully attack prey or escape predators. An arms race between predator and prey may occur when they live together and undergo reciprocal adaptations to enhance survival or foraging success (Vermeij 1982, Kopp & Tollrian 2003). NS and BS *Macoma* in our experiment probably had not been exposed to the 'foreign' predator earlier, at least not since the last ice age (NS *Macoma* to *S. entomon*, BS *Macoma* to *C. maenas*), thus it is not likely that morphological or behavioural defences developed.

Clear differences were found in shell shape, colour and weight between NS and BS *Macoma*. The more globular BS *Macoma* (Beukema & Meehan 1985, Hummel et al. 2000) have a heavier shell than NS *Macoma*, but both have similar meat weight, thus the meat:shell weight ratio of NS *Macoma* rendered them energetically more profitable. These differences may contribute to the discrepancies observed in predation pressure between the 2 populations. That *Carcinus maenas* ate more of the globular heavy-shelled BS *Macoma* than of the flat light-shelled NS *Macoma* may be a consequence of the geometry of the crab's crusher-claw relative to that of the prey's shell (Behrens Yamada & Boulding 1998). Closed *C. maenas* claws leave a space between the fixed and the movable claw so that small and flat bivalves cannot be crushed. The crush-limited *C. maenas* can break the globular BS *Macoma* more easily than the flatter NS *Macoma* of similar size. *Saduria entomon* pry the shell valves apart (Ejdung 1998), and eat more of the flat and light-shelled NS *Macoma*. *Crangon crangon* swallow small *M. balthica* whole, pry open the shell or make a hole in the shell to extract the meat. Small-sized *M. balthica* were eaten by all predators and feeding on smaller prey minimises risks of injuries.

Table 5. *Macoma balthica*. Comparison of size, height, width, meat dry wt, shell (dry wt), and meat:shell ratio of Baltic and North Sea populations

Dependent variable	Source	df	MS	F	p
Log height	Log length	1	9.16	38742	<0.001
	M. balthica group	1	0.02	90	<0.001
	Error		210	0.00	
Log width	Log length	1	9.99	11949	<0.001
	M. balthica group	1	0.16	192	<0.001
	Error		210	0.00	
Log meat	Log length	1	15.82	1050	<0.001
	M. balthica group	1	0.01	0.10	0.753
	Error		28	0.02	
Log shell	Log length	1	12.98	2283	<0.001
	M. balthica group	1	0.31	53.66	<0.001
	Error		28	0.01	
Ratio log meat:log shell	Log length	1	0.14	9.50	0.004
	M. balthica group	1	0.35	23.62	<0.001
	Error		28	0.02	

They also yield a higher net energy reward since it is easier, and costs less energy to crush (*C. maenas*), pry open (*S. entomon*), swallow, pry open or make a hole (*C. crangon*) in smaller bivalves than in larger ones (Juanes 1992, Ejdung & Elmgren 2001, Hiddink et al. 2002). Thus morphological characteristics are one factor that may affect prey choice.

The natural size distribution of *Macoma balthica* differs between the North and the Baltic Sea investigation areas. In the Baltic Sea, more small (1 to 3 mm) *M. balthica* occur during the whole year, but in the North Sea these size classes only occur in high densities during a short summer period. The number and size of prey specimens available affects predation. Still, we used natural, albeit different, size distributions of BS and NS *Macoma* in our experiments to reflect the natural differences in predation pressure on BS and NS *Macoma*.

Carcinus maenas and *Saduria entomon* ate more of the non-sympatric *Macoma balthica*, although they came from size classes that were initially both more and less abundant (single prey experiments). Of the clam sizes offered, NS *Crangon* ate more of the initially most abundant BS *Macoma* sizes (1 to 3 mm), and BS *Crangon* ate more of the initially most abundant size classes of NS *Macoma* (3 to 4 mm) and of BS *Macoma* (2 to 3 mm). In the mixed prey experiment, where size-class distributions were similar for NS and BS *Macoma* and the predators had a choice between the 2 groups, both *Saduria* and BS *Crangon* ate more of the non-sympatric NS *Macoma*. Further, *S. entomon* and *C. crangon* ate more of the NS *Macoma* size classes that had the highest initial abundance. Neither predator had a clear preference for clams of a particular size,but both had a preference for NS over BS *Macoma*. The predator's choice of prey is affected by a combination of morphological characteristics, availability and actual size.

Ecological implications

As observed earlier (Hummel et al. 2000), *Macoma balthica* from the North Sea can indeed enter the Baltic Sea, irrespective of the fact that the salinity gradient in the Baltic Sea is a natural barrier for the dispersal of many aquatic species. Thus they become a non-native prey, and face a new environment and predatory species not encountered earlier. Many studies have focused on the impact of non-native predators on community structure and function (Shiganova et al. 2001, Dick et al. 2002, Rossong et al. 2006). Here we showed that non-native prey surely can have an impact on the existing predator–prey interactions as more of them are eaten compared with the native prey species.

Predators and prey that live together often have developed morphological and behavioural defences or skills to successfully attack prey or escape predators. In intertidal North Sea areas, a relationship exists between the time of arrival of juvenile predators and the recruitment success of bivalves. There seems to be a selective pressure on NS *Macoma* to grow fast so that refuge size is reached (Beukema et al. 1998, van der Veer et al. 1998, Strasser & Günther 2001). In shallow Baltic Sea areas, predation pressure on small BS *Macoma* is rather low (E. Flach unpubl.), as is growth rate during the first summer (Ankar 1980). This partly explains the differences in size distribution between NS and BS *Macoma.* As NS *Macoma* in our experiment probably had not been exposed to *Saduria entomon* earlier, nor BS *Macoma* to *Carcinus maenas*, it is not likely that morphological or behavioural defences developed. This may be the reason that the morphological differences, and maybe also the differences in energetic yield, mainly determine the outcome of the predator–prey relationships for prey that have a natural size distribution. In summary, if the more globular BS *Macoma* are replaced by the thinner NS *Macoma* in the Baltic Sea, the food web structure can be affected.

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