

Reduced epibenthic predation on intertidal bivalves after a severe winter in the European Wadden Sea

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ABSTRACT: One hypothesis to explain the phenomenon of high bivalve recruitment after severe winters in coastal North Sea sediments is reduced epibenthic predation. Using predator exclusion experiments, I tested the hypothesis that epibenthic predation on the juvenile bivalves *Cerastoderma edule*, *Macoma balthica* and *Mya arenaria* was lower after a severe winter (1995 to 1996) than after a moderate (1996 to 1997) and a mild (1997 to 1998) winter. In *C. edule* and *M. arenaria* there was 2-fold evidence for reduced epibenthic predation after the severe winter: (1) significant predation effects occurred only in exclusion experiments after the 2 milder winters but not after the severe winter; and (2) recruits attained larger sizes in August and October after the severe winter suggesting continuous growth rather than truncation of the size spectrum by predators. In *M. balthica*, predation effects were also significant only after the milder winters but there was no effect on size. In all 3 bivalve species, recruitment at the experimental sites in the fall was higher after the severe winter than after the 2 milder ones. These results suggest that high bivalve recruitment after severe winters is primarily caused by the post-settlement factor of reduced epibenthic predation on the tidal flats. The strategy to conduct several predator exclusion experiments in both sand and mud in 3 consecutive years with differential winter conditions, and while considering migration activity and size development in juvenile bivalves, proved useful to distinguish between cage artefacts and predation effects.

KEY WORDS: Winter effects · Recruitment · Intertidal · Predator-exclusion experiments · *Cerastoderma edule* · *Macoma balthica* · *Mya arenaria*

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INTRODUCTION

The importance of the post-settlement factor of epibenthic predation on the population dynamics of bivalves has frequently been documented in the laboratory as well as in the field (e.g. Reise 1985, Möller 1986, Seed 1993, Gosselin & Qian 1997, Hunt & Scheibling 1997). The most important predators on juvenile bivalves in the European Wadden Sea are the shore crab *Carcinus maenas* (Scherer & Reise 1981, Jensen & Jensen 1985, van der Veer et al. 1998), the shrimp *Crangon crangon* (Beukema et al. 1998, van der Veer et al. 1998) as well as the flatfishes plaice

Pleuronectes platessa and flounder *Platichthys flesus* (Smidt 1951, de Vlas 1979). One characteristic of the population dynamics of the common bivalves *Cerastoderma edule*, *Macoma balthica*, *Mya arenaria* and *Mytilus edulis* in the Wadden Sea is high recruitment (sensu Keough & Downes 1982) after severe winters and low recruitment after mild winters (Beukema 1992a, Beukema et al. 2001). One explanation for this phenomenon is reduced epibenthic predation by *Carcinus maenas* and *Crangon crangon*, which return later and in smaller numbers to the tidal flats after severe winters compared to milder ones (Reise 1985, Beukema 1991, 1992b), resulting in a temporal mismatch between these predators and the juvenile bivalve prey (Strasser & Günther 2001). However, experimental evidence for the positive effect of re-

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duced epibenthic predation after severe winters on bivalve recruitment in the European Wadden Sea is as yet lacking. In this study, I took advantage of a series of 3 winters that happened to turn out as severe (1995 to 1996, 83 d with frost), moderate (1996 to 1997, 36 d with frost) and mild (12 d with frost) to test the hypothesis that epibenthic predation is lower after severe winters than after milder ones. A more detailed characterization of the 3 winters is given in Strasser (2000).

The effects of epibenthic predation are commonly tested by predator exclusion experiments using cages (e.g. Virnstein 1978, Reise 1985, McArthur 1998). In the Wadden Sea, such experiments were conducted after mild winters and resulted in much higher bivalve recruitment in cages compared to plots with access to predators (Reise 1985). However, the interpretation of predator exclusion experiments is generally impeded by cage artefacts because cages do not just manipulate the factor predation but may also alter other factors such as hydrodynamic conditions or the deposition of organic material (Virnstein 1978, Peterson 1979). Another artefact for juvenile bivalves is that their active byssus drift (Armonies 1992, 1994) is prevented by closed cages. Even with partial cages, it is not possible to exclude the possibility of artefacts and as a consequence doubts remain as to whether the results of cage experiments can be attributed to the factor predation alone or whether cage artefacts taint the conclusions (Ólafsson et al. 1994). Therefore, this study was specially designed to avoid the pitfalls of cage artefacts when interpreting predator exclusion experiments: (1) control for hydrodynamic artefacts, experiments with exclusion cages, partial cages and uncaged plots were conducted in sandy as well as muddy sediment. If changes in the hydrodynamic regime or the deposition of organic material are an important artefact, then the results should differ between the 2 sediments because in mud the flow velocity is lower and organic sedimentation is higher than in sand. (2) To avoid artefacts caused by migration of bivalves, the drifting activity was minimized by adjusting the duration of the experiments to the lunar drift-rhythm of one of the bivalve species. (3) Since cage artefacts can never be completely ruled out, the experimental reasoning in this study was not based on single experiments but on a series of several experiments that were conducted identically in the same months after the severe and the 2 milder winters. Thereby, cage artefacts were standardized as much as possible and conclusions were only drawn from differences in the results between years. If reduced epibenthic predation is the cause for high bivalve recruitment after severe winters, the predation effects after the severe winter of 1995 to 1996 must have been lower than after the moderate (1996 to 1997) and the mild (1997 to 1998) winters.

Reduced epibenthic predation may not just result in increased recruitment but may also affect the size distribution of the juveniles. I hypothesize that low predation leads to a more or less continuous growth of the juveniles in the course of the year. In contrast, high predation should prevent juvenile bivalves from living long enough to reach larger sizes which will result in a truncated size spectrum. Therefore, if epibenthic predation was lower after the severe winter, the proportion of large juveniles at the end of the year should be higher than after the moderate and mild winters.

MATERIALS AND METHODS

Study site and experimental design. This study was conducted in Königshafen Bay, a sheltered area in the north of the German island of Sylt in the European Wadden Sea (Fig. 1). The intertidal zone of the bay covers an area of about 4 km² and tides are semi-diurnal with a mean tidal range of 2 m. Salinity is usually between 30 and 32 psu. About 90% of the bay consists of sandy sediments and 10% of muddy or mixed sedi-

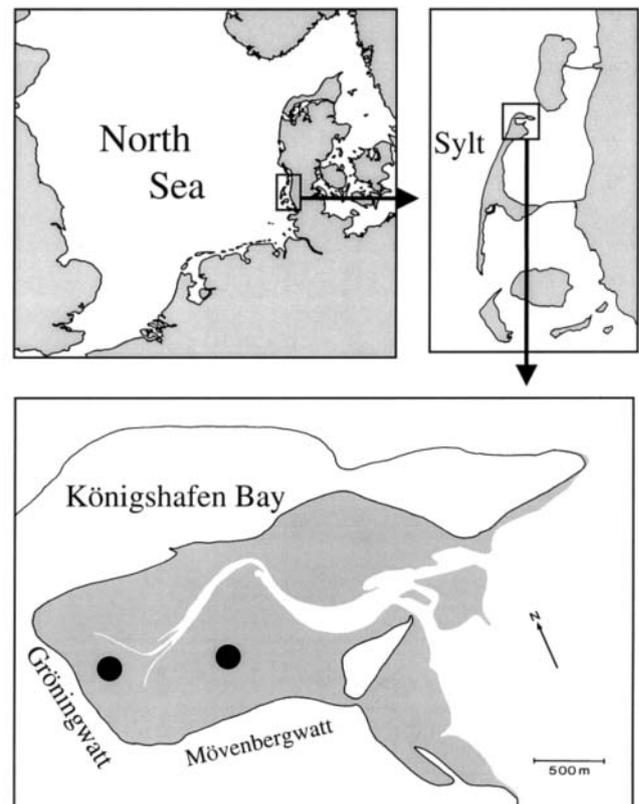


Fig. 1. The 2 experimental sites (●) in Gröningwatt (mud) and Mövenbergwatt (sand) in Königshafen Bay in the north of the German island of Sylt, North Sea

ments. Detailed information on the ecology and hydrography of the bay is given in Reise (1985) and Gätje & Reise (1998). In the study area, the 3 bivalve species *Cerastoderma edule*, *Macoma balthica* and *Mya arenaria* typically show a peak settlement period in spring or early summer (Armonies 1996, Strasser et al. 2001). Although *C. edule* and *M. arenaria* larvae may be found in the water column until October (Strasser & Günther 2001), settlement is usually quantitatively unimportant after July (Armonies 1996, Strasser et al. 2001). *C. edule*, *M. balthica* and *M. arenaria* larvae settle at sizes of about 250 to 300 μm (Thorson 1946) and in their first year, the juveniles may reach sizes of up to 15, 10 and 20 mm, respectively (Beukema et al. 1993).

Predator exclusion experiments were conducted in a sandy area (Mövenbergwatt) and a muddy area (Gröningwatt) in the mid intertidal of Königshafen Bay (Fig. 1). Each experiment consisted of 3 treatments: (1) Epibenthic predators were excluded by cylindrical cages covered on top and on the sides with 1 mm mesh nylon netting. The cages were built of 2 PVC rings (thickness 3 cm, diameter 19 cm, total area 284 cm²) that were connected by 3 PVC crosspieces of 3 cm width. Cages were pushed about 10 cm into the sediment and secured with three 50 cm long iron stakes (see Strasser 2000). (2) For partial cages the same construction was used but $\frac{1}{3}$ of the side remained free of netting allowing access of predators to the experimental plots. (3) Uncaged areas served as control plots for cage artefacts.

In the Wadden Sea, juvenile *Cerastoderma edule* show a pronounced drifting activity at spring tides (Armonies 1992). To avoid cage artefacts caused by the prevention of natural migration of *C. edule*, all cage experiments were run for 10 to 12 d in the period between full moon and new moon. To find out at which time of the year predation effects occur, cage experiments were conducted in June/July, August and October of the years 1996, 1997 and 1998. For each period, experiments were conducted simultaneously in sand and mud except for June 1996 (sand only). In each experiment, the experimental plots were randomly chosen in an area of about 100 m². Each treatment was replicated 8 times. The openings of the partial cages were pointed in different directions to avoid biases due to a preferred drifting direction of the bivalves. Every 1 or 2 d, the cages were freed from entangled algae and holes in the netting caused by pecking birds were repaired. At the end of each experiment, the sediment on the experimental plots was excavated down to 3 cm and washed through 500 μm (mud) or 1000 μm (sand) sieves in the laboratory. The sampled area was 284 cm² except for July 1996 (6 cm²) and August 1996 (142 cm²). The sieve residues were transferred to petri

dishes, and juvenile bivalves, shrimp and shore crabs were sorted and measured to the nearest 1 mm under 10-fold magnification. At the end of each experiment exclusion cages and partial cages were removed from the experimental plots. Subsequent experiments were conducted in adjacent areas to avoid resampling of the same plots.

Statistical analysis. To compare the predation impact after the severe winter with the predation impact after the 2 milder winters, I used 2-way analysis of variance (ANOVA) with treatment (exclusion cage, partial cage, control) and year (1996, 1997, 1998) as fixed factors. Separate ANOVAs were calculated for each species in the same months (June/July, August, October) of 1996, 1997 and 1998. Heteroscedasticity of the datasets (tested with Cochran's *C*-test) was removed by log transformation. Tukey's honest significant difference (HSD) test for unequal n (Spjøtvoll/Stoline test) was used for post-hoc comparisons because the loss of 1 or 2 replicates in some experiments resulted in unbalanced data sets (StatSoft 1997). Significant recruitment differences between partial cages and uncaged controls indicated a cage artefact. Since cage artefacts occurred in some experiments, only those results were regarded as a predation effect in which bivalve abundances inside the exclusion cages were significantly higher than abundances both inside the partial cages and in uncaged controls.

One-way ANOVA with year (1996, 1997, 1998) as the fixed factor was used to test whether: (1) the recruitment of each bivalve species on the control plots was higher in October after the severe than after the milder winters; and (2) the average size of each bivalve species inside the exclusion cages was higher after the severe than after the milder winters. Results were termed a 'size effect' when the average bivalve size was significantly higher after the severe than after the moderate and after the mild winter. I used only the bivalves inside the exclusion cages for the comparison of sizes between years because some subsamples of the treatments 'partial cage' and 'control' contained no bivalves (especially in August and October), resulting in heterogeneity of the dataset which made a statistical analysis impossible. Whenever a statistical analysis was possible, there were no significant size differences between bivalve species inside exclusion cages, partial cages and control plots (calculated for each of the 3 species in each single experiment, 1-way ANOVA, $p > 0.05$). One-way ANOVA was also used to compare the abundances of the predators *Carcinus maenas* and *Crangon crangon* at low tide between the treatments 'exclusion cage', 'partial cage' and 'control'. Removal of heteroscedasticity and post-hoc comparisons were made as above. For all statistical calculations the program Statistica (StatSoft 1997) was used.

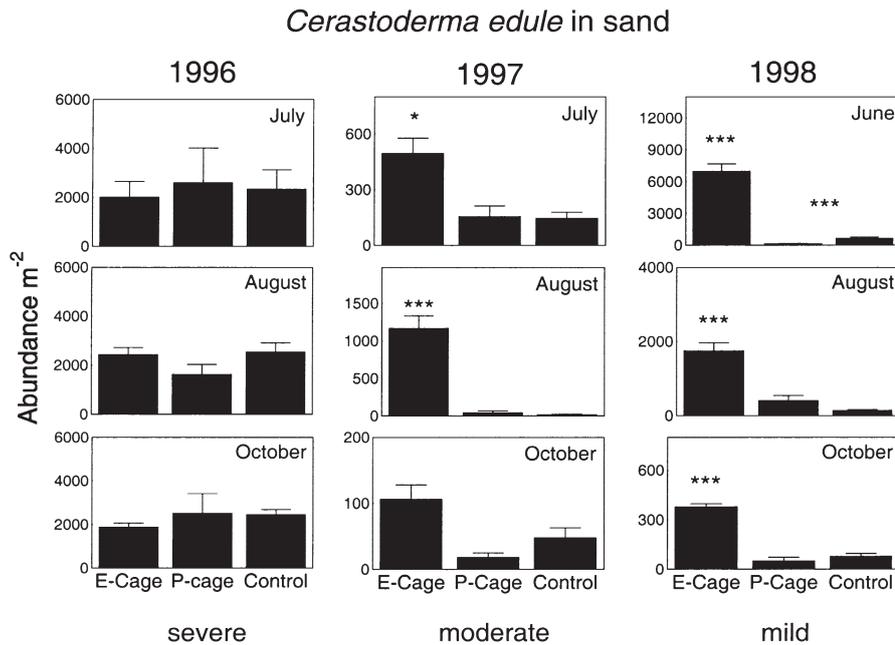


Fig. 2. *Cerastoderma edule*. Average recruitment + SE in exclusion cages (E-cage), partial cages (P-cage) and uncaged controls in sandy sediment in different months of 1996, 1997 and 1998. Note different scaling of the y-axis. Indicated are significant differences (***) = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$) between exclusion cages compared to partial cages and controls (asterisks above column E-cage) and significant differences between partial cages and controls (asterisks between P-cage and control). Preceding winter conditions are indicated below

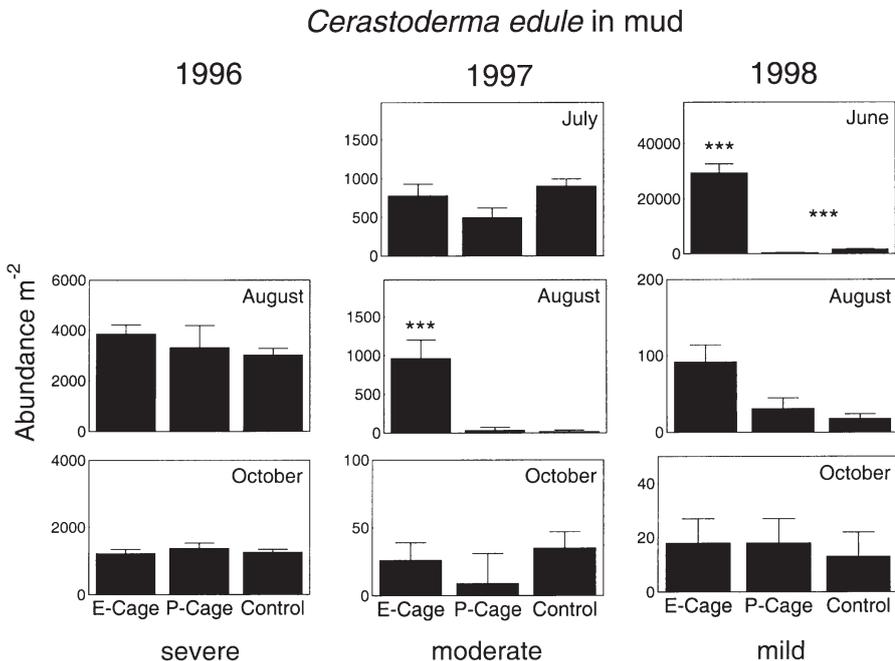


Fig. 3. *Cerastoderma edule*. Average recruitment + SE in exclusion cages (E-cage), partial cages (P-cage) and controls in muddy sediment in different months of 1996, 1997 and 1998. For further information see the Fig. 2 legend

RESULTS

Predation effects and temporal course of recruitment

In *Cerastoderma edule* both in sand (Fig. 2) and mud (Fig. 3) significant predation effects were observed after the moderate (1996 to 1997) and the mild (1997 to 1998) winters but not after the severe winter (1995 to 1996). In 1996, recruitment in sand constantly remained around 2500 ind m^{-2} on the control plots between July and October. In mud, in 1996, recruitment was about halved from 3000 ind m^{-2} in August to 1300 ind m^{-2} in October. After the moderate winter, there were significant predation effects in July (sand and mud) and August (sand). Recruitment on the control plots declined from about 150 to 30 ind m^{-2} in sand and from about 800 to 50 ind m^{-2} in mud. After the mild winter, there were significant predation effects in all months (June/July: sand and mud; August and October: sand only). On the control plots recruitment declined from about 1000 to below 80 ind m^{-2} in both sediment types.

In *Macoma balthica*, significant predation effects were—as in *Cerastoderma edule*—only observed after the 2 milder winters (Figs. 4 & 5). Recruitment was generally higher in mud than in sand. In 1996, recruitment on the control plots declined from 3600 to 650 ind m^{-2} between August and October in mud, and from 1500 to 350 ind m^{-2} between July and October in sand. In 1997, predation effects occurred in August in both sand and mud. In mud, recruitment on the control plots declined from about 2600 to 100 ind m^{-2} between July and August. In sand, recruitment was low throughout the year (about 50 ind m^{-2}). In 1998, a predation effect occurred in June both in sand and mud. Between June and October recruitment declined from about

2500 to 400 ind m⁻² in mud and 800 to 100 ind m⁻² in sand.

In *Mya arenaria*, considerable recruitment only took place in mud. As in *Cerastoderma edule* and *Macoma balthica* significant predation effects occurred only after the 2 milder winters but not after the severe winter (Fig. 6). In 1996, recruitment declined from about 700 ind m⁻² in August to 50 ind m⁻² in October. In 1997, a predation effect occurred in August and by October, there were no individuals left on the control plots. In 1998, a predation effect occurred in June. Recruitment declined from about 500 to 20 ind m⁻² between June and October.

In summary, significant predation effects were only found after the moderate and the mild winter but not after the severe winter (Table 1). Regarding the control plots, recruitment of each bivalve species in October was significantly higher after the severe than after the 2 milder winters (Fig. 7).

Cage artefacts

Significant cage artefacts (indicated by significant differences between partial cages and uncaged controls) occurred in *Cerastoderma edule* and *Mya arenaria* in June 1998 (sand and mud; Figs. 2, 3 & 6). In *Macoma balthica*, cage artefacts occurred in August 1996 (sand and mud), October 1997 (mud), June 1998 (sand and mud) and August 1998 (mud) (Figs. 4 & 5). In all these cases, the recruitment inside the partial cages was lower than recruitment on the control plots.

In August 1996, recruitment of *M. balthica* on the control plots was not only higher than inside the partial cages but also higher than inside the exclusion cages. The lower recruitment inside the partial cages coincided with generally higher abundances of the predators *Carcinus maenas* (5 to 30 mm) and *Crangon crangon* (10 to 25 mm) at the end of the experiments (Table 2). Presumably these predators took shelter inside the partial cages from their own predators. The higher abundances inside the partial cages compared to the exclusion cages and control plots were statistically significant in 1996 (*C. maenas* and *C. crangon*) and in 1998 (*C. crangon*) (Tukey HSD-test, $p < 0.05$). It is important to note that the predator abundances inside the partial cages and on control plots presented in Table 2 (sampled only at the end of the experiments and at low tide) are an underestimation of the abundances of the predators on accessible plots (partial cages and controls) in the course of the experiment. Juvenile shore crabs and shrimp perform tidal migrations and feed primarily when the tide is in (Reise 1985). In the study area, at high tide, both species may attain densities of 150 ind m⁻² in the summer months (P. Polte unpubl. data). Occasionally *C. maenas* larvae settled in the exclusion cages so that up to 65 *C. maenas* of 2 to 5 mm were observed inside the cages at the end of an experiment. However, these small crabs do not seem to prey on juvenile bivalves since there was no significant correlation (Spearman R , $p > 0.05$) between the bivalve recruitment and the number of *C. maenas* <5 mm inside the exclusion cages.

Table 1. *Cerastoderma edule*, *Macoma balthica* and *Mya arenaria*. Statistical results of the predator exclusion experiments. F -values and significance levels (p) of the factor treatment and of the interaction of the factors treatment and year in 2-way ANOVAs. Predation effect (yes or no) indicates whether recruitment in exclusion cages was significantly higher than recruitment in both partial cages and controls

Species	Month	Sediment	Factor treatment		Interaction treatment/year		Predation effect		
			F	p	F	p	1996	1997	1998
<i>C. edule</i>	Jun/Jul	Sand	49.33	<0.001	34.63	<0.001	No	Yes	Yes
	Jun/Jul	Mud	86.47	<0.001	59.12	<0.001	–	No	Yes
	Aug	Sand	89.38	<0.001	15.89	<0.001	No	Yes	Yes
	Aug	Mud	51.52	<0.001	18.08	<0.001	No	Yes	No
	Oct	Sand	19.12	<0.001	3.46	<0.05	No	No	Yes
	Oct	Mud	0.31	0.737	1.07	0.379	No	No	No
<i>M. balthica</i>	Jun/Jul	Sand	29.50	<0.001	17.87	<0.001	No	No	Yes
	Jun/Jul	Mud	71.69	<0.001	62.65	<0.001	–	No	Yes
	Aug	Sand	20.85	<0.001	8.31	<0.001	No	Yes	No
	Aug	Mud	23.42	<0.001	3.60	<0.05	No	Yes	No
	Oct	Sand	2.23	0.116	0.75	0.562	No	No	No
	Oct	Mud	9.14	<0.001	2.17	0.082	No	No	No
<i>M. arenaria</i>	Jun/Jul	Mud	36.05	<0.001	15.01	<0.001	–	No	Yes
	Aug	Mud	14.17	<0.001	4.45	<0.05	No	Yes	No
	Oct	Mud	5.78	<0.005	4.99	<0.05	No	No	No

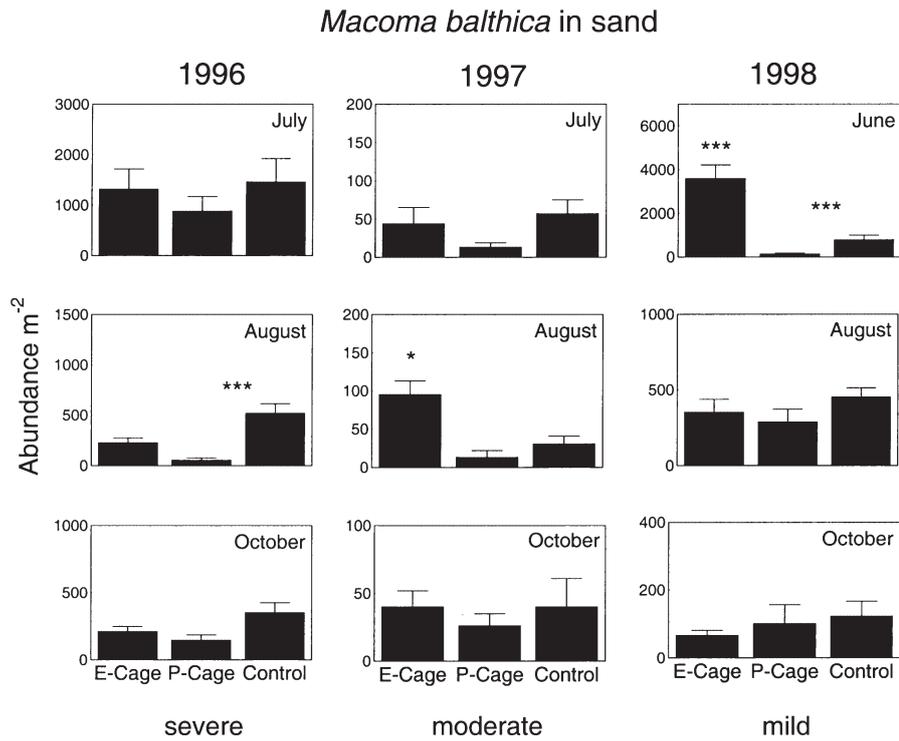


Fig. 4. *Macoma balthica*. Average recruitment + SE in exclusion cages (E-cage), partial cages (P-cage) and controls in sandy sediment in different months of 1996, 1997 and 1998. For further information see the Fig. 2 legend

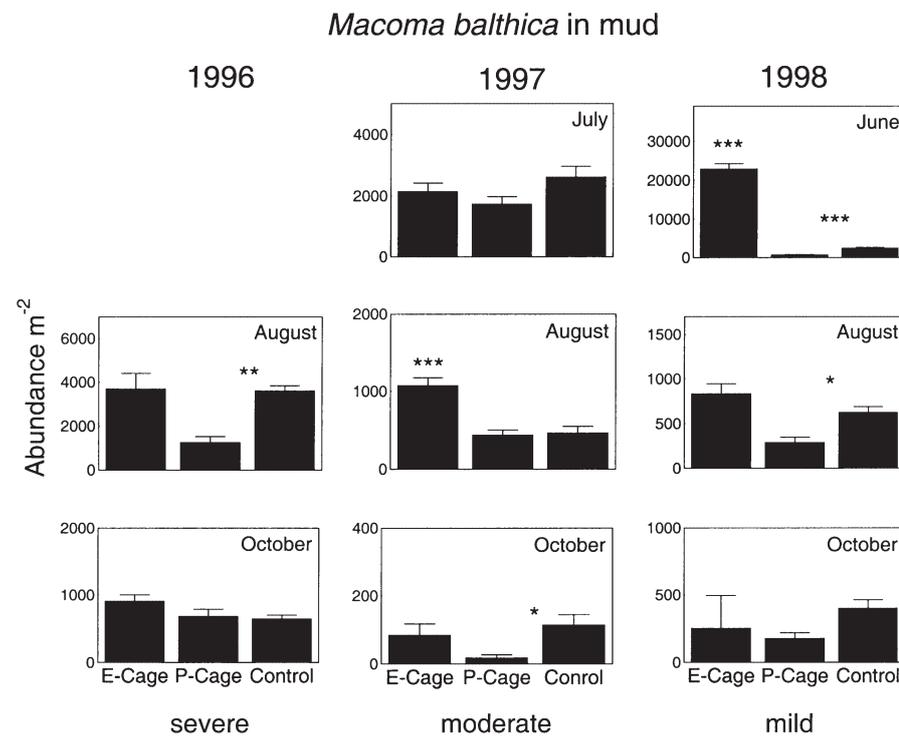


Fig. 5. *Macoma balthica*. Average recruitment + SE in exclusion cages (E-cage), partial cages (P-cage) and controls in muddy sediment in different months of 1996, 1997 and 1998. For further information see the Fig. 2 legend

Size effects

The average size of *Cerastoderma edule* and *Mya arenaria* in August and October was significantly larger after the severe than after the moderate and the mild winters (Table 3). While these species attained average sizes of about 4 mm in August 1996 and 7 mm in October 1996, they remained below 3.2 mm throughout 1997 and 1998. In contrast, no significant size effect was observed in *Macoma balthica*, for which the average size did not exceed 3.9 mm in all years examined.

DISCUSSION

Predation effects or cage artefacts?

In all 3 bivalve species, recruitment was significantly higher in exclusion cages than in partial cages and uncaged controls after the moderate and the mild winters, but not after the severe winter. Does this mean that epibenthic predation was lower after the severe winter or can the results also be explained by cage artefacts? Major possible artefacts will be discussed separately.

Artefacts caused by changes of the hydrodynamic regime and attraction of larvae

Cages do not only manipulate the density of predators but may also affect the hydrodynamic conditions and the settlement of larvae (Peterson 1979, Reise 1985, Ólafsson et al. 1994 and references therein). Reduction in current velocities by the cages may reduce disturbance of the sediment and enhance the amount of food available, thereby reducing bivalve mortality. In addition, bi-

Table 2. *Carcinus maenas* (>5 mm carapace width) and *Crangon crangon* (10 to 25 mm length). Average abundance ± SD per treatment at the end of cage experiments. N = number of experiments per year

Year	N	<i>Carcinus maenas</i>			<i>Crangon crangon</i>		
		Exclusion cage	Partial cage	Control	Exclusion cage	Partial cage	Control
1996	5	0.23 ± 0.26	1.00 ± 0.70	0.10 ± 0.17	0.28 ± 0.31	0.90 ± 0.93	0.05 ± 0.11
1997	6	0.38 ± 0.32	0.90 ± 0.93	0.13 ± 0.16	0.36 ± 0.39	3.69 ± 2.10	0.79 ± 0.61
1998	6	0.30 ± 0.41	1.42 ± 2.25	0.25 ± 0.19	0.34 ± 0.64	2.92 ± 1.99	0.29 ± 0.42

valve settlement may be increased by reduced currents or by larvae that are attracted by the cage netting. However, these artefacts cannot explain the different results after the severe compared to the 2 milder winters for 2 reasons: (1) partial cages and uncaged plots were used to control for these artefacts. Misinterpretation of the experiments was avoided by regarding only those results as predation effects in which recruitment in exclusion cages was significantly higher than in partial cages as well as in uncaged plots; and (2) the artefactual influence caused by reduced currents should be less pronounced in mud because there the currents are naturally lower and the organic deposition higher than in sand. Since predation effects were generally found simultaneously in sand and mud (Table 1), there was no indication for hydrodynamic cage artefacts.

Multiple compensatory artifacts

Predation effects might have been confounded with 'multiple compensatory artefacts' (Summerson & Peterson 1984). This means that in a first step, bivalve recruitment was artificially elevated by the positive effects of reduced currents inside exclusion and partial cages. In a second step, recruitment inside partial cages was reduced to the level of uncaged plots by cage-attracted predation. There is evidence that this type of artefact affected my experiments since the predators *Carcinus maenas* and *Crangon crangon* were found in larger numbers inside the partial cages compared to the control plots (Table 2). Therefore, multiple compensatory artifacts are an alternative interpretation for each single experiment. However, this artifact cannot explain why significantly higher recruitment inside the exclusion cages was only observed after the moderate and the mild winter but not after the severe winter.

Migratory artefacts

Recruitment inside exclusion cages could be higher than inside partial cages and control plots if the natural migration activity of the juvenile bivalves present on the experimental plots was prevented by the exclusion cages. Such an artefact was unlikely for *Mya arenaria*: it is primarily transported passively by erosion of the sediment (Emerson & Grant 1991, Armonies 1996) and in the sheltered study area erosive energy is usually low. In contrast, *Cerastoderma edule* and *Macoma balthica* show a pronounced active migration behaviour (Günther 1991, Armonies 1992, 1996, 1998) that does not depend on wind-induced erosion. In the study area, *C. edule*

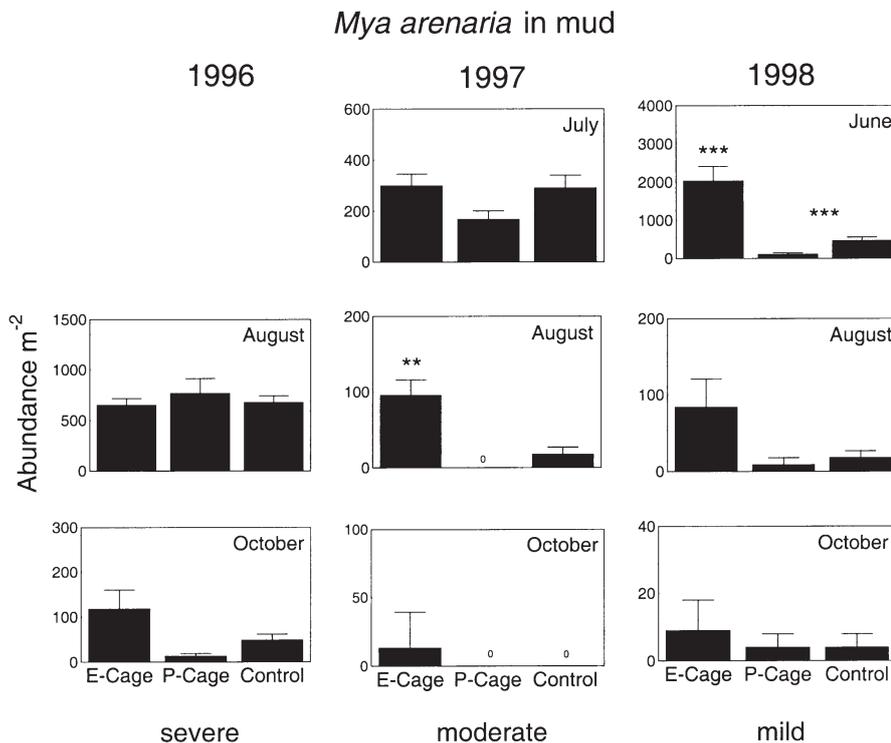


Fig. 6. *Mya arenaria*. Average recruitment + SE in exclusion cages (E-cage), partial cages (P-cage) and controls in muddy sediment in different months of 1996, 1997 and 1998. For further information see the Fig. 2 legend

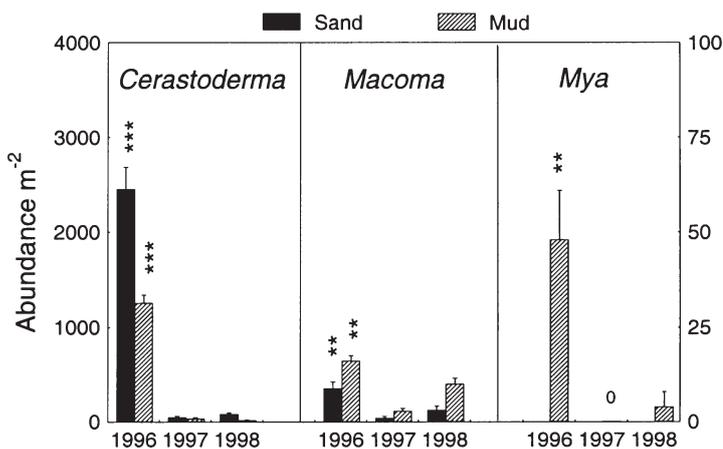


Fig. 7. *Cerastoderma edule*, *Macoma balthica* (left y-axis) and *Mya arenaria* (right y-axis). Average recruitment + SE on control plots in sandy and muddy sediment in 1996, 1997 and 1998. Asterisks denote significant differences (** = $p < 0.01$, *** = $p < 0.001$) in recruitment after the severe winter (1996) compared to the moderate (1997) and the mild (1998) winters

has a semilunar drift periodicity, while *M. balthica* has a 10 d drift rhythm that is not linked to the lunar phases (Armonies 1992). The drifting activity of *C. edule* was minimized and standardized by conducting all experiments exclusively in periods between new and full moon. For *M. balthica*, however, it was beyond the scope of this study to adjust the duration of the experiments to its 10 d drifting periodicity. The relatively high number of experiments in which the recruitment of *M. balthica* in exclusion cages differed significantly from uncaged controls may indicate that migratory artefacts were not properly prevented. Therefore, for

M. balthica migration artefacts serve as an alternative explanation for higher recruitment inside exclusion cages if one regards each experiment separately. However—as in multiple compensatory artefacts—migratory artefacts do not explain why recruitment inside exclusion cages was only higher after the moderate and the mild but not after the severe winter.

Higher order artefacts

Peterson & Black (1994) warned that artefacts may be inconsistent across experimental treatments and called these 'higher order artefacts'. The conclusion of reduced epibenthic predation after the severe winter could be confounded with higher order artefacts if migration artefacts or multiple compensatory artefacts differed between the severe winter on the one hand and the moderate and mild winter on the other. However, the conclusion of lower epibenthic predation after the severe winter is supported by the larger size of *Mya arenaria* and *Cerastoderma edule* which cannot be explained by higher order artefacts. For *Macoma balthica* however, there was no size effect and higher order artefacts cannot be ruled out since its drifting periodicity was not considered in the experimental set-up (see above). Nevertheless, it is reasonable to assume that epibenthic predation after the severe winter was also reduced for *M. balthica* since all 3 bivalves are preyed upon by the same set of predators (e.g. Reise 1985, van der Veer et al. 1998).

An alternative explanation for the larger size of juvenile *Mya arenaria* and *Cerastoderma edule* after the severe winter is faster growth due to reduced competi-

Table 3. *Cerastoderma edule*, *Macoma balthica* and *Mya arenaria*. Average size \pm SD in the exclusion cages. *F*-values and significance levels (*p*) of 1-way ANOVAs. Size effect (yes or no) indicates whether or not bivalves were significantly larger in 1996 than bivalves in 1997 and 1998

Species	Month	Sediment	Size (mm \pm SD)			<i>F</i>	<i>p</i>	Size effect
			1996	1997	1998			
<i>Cerastoderma edule</i>	Jun/Jul	Sand	2.33 \pm 0.43	2.71 \pm 0.18	2.01 \pm 0.03	17.86	<0.001	No
	Jun/Jul	Mud	—	2.59 \pm 0.29	1.66 \pm 0.15	—	—	—
	Aug	Sand	3.93 \pm 0.27	3.15 \pm 0.18	2.65 \pm 0.11	87.21	<0.001	Yes
	Aug	Mud	4.30 \pm 0.15	2.71 \pm 0.16	2.83 \pm 0.90	23.86	<0.001	Yes
	Oct	Sand	7.41 \pm 0.46	2.04 \pm 0.11	2.04 \pm 0.30	402.39	<0.001	Yes
	Oct	Mud	6.80 \pm 0.47	1.00 \pm 0.00	1.50 \pm 0.50	256.29	<0.001	Yes
<i>Macoma balthica</i>	Jun/Jul	Sand	1.42 \pm 0.49	2.43 \pm 0.43	2.13 \pm 0.05	11.95	<0.001	No
	Jun/Jul	Mud	—	2.76 \pm 0.37	1.90 \pm 0.11	—	—	—
	Aug	Sand	2.71 \pm 0.30	2.00 \pm 0.00	2.56 \pm 0.22	24.00	<0.001	No
	Aug	Mud	2.71 \pm 0.29	2.59 \pm 0.34	3.61 \pm 0.30	25.18	<0.001	No
	Oct	Sand	3.29 \pm 0.39	2.50 \pm 0.55	2.72 \pm 0.95	2.82	0.088	No
	Oct	Mud	4.01 \pm 0.41	3.92 \pm 0.86	3.20 \pm 0.59	3.99	0.036	No
<i>Mya arenaria</i>	Jun/Jul	Mud	—	2.96 \pm 0.58	1.60 \pm 0.18	—	—	—
	Aug	Mud	4.46 \pm 0.61	2.81 \pm 0.93	3.13 \pm 2.39	83.65	<0.001	Yes
	Oct	Mud	6.77 \pm 1.15	1.00 \pm 0.00	2.5 \pm 0.00	119.33	<0.001	Yes

tion for food or space as a consequence of higher invertebrate mortality during severe winters (Möller & Rosenberg 1983). However, the abundances of the dominating filter feeder (*C. edule*) suggest that competition was not lower after the severe than after the following 2 milder winters. Since the strong year class of *C. edule* in 1996 suffered 95% mortality during the moderate winter of 1996 to 1997, the densities of *C. edule* older than 1 yr were below 50 ind m⁻² in 1997 and 1998 in the study area (Strasser 2000). It can be argued that the intraspecific competition of juvenile *C. edule* (2000 ind m⁻² of 4 mm size) in the summer after the severe winter exceeded the competition exerted by the relatively low numbers of other filter feeders after the milder winters. Therefore, I conclude that the larger size of the juvenile bivalves after the severe compared to the milder winters cannot be explained by reduced competition.

In summary, the strategy of conducting several predator exclusion experiments in sand and mud after a severe, a moderate and a mild winter while considering the migration activity and size development of juvenile bivalves proved useful to reduce interference between predation and cage artefacts to a minimum. I conclude that epibenthic predation of *Cerastoderma edule* and *Mya arenaria* was lower after the severe than after the 2 milder winters since cage artefacts do not serve as an alternative explanation for the different results of the predator exclusion experiments between years. Most likely epibenthic predation after the severe winter was also reduced for *Macoma balthica*, assuming that its drifting activity was not significantly different between years.

Which predators were responsible for the predation pattern observed?

The most important predators of juvenile bivalves in the Wadden Sea are decapod crustaceans and flatfish (de Vlas 1979, Reise 1985, van der Veer et al. 1998). However, flatfish generally occur only in low abundances in the study area (Herrmann et al. 1998) and I never observed any at the experimental sites. Therefore, it seems unlikely that flatfish are of major importance for the observed predation pattern. In contrast to flatfish, the common goby *Pomatoschistus microps* was occasionally found inside partial cages. While gobies feed primarily on small crustaceans on the Swedish west coast (Pihl 1985) they also consume *Macoma balthica* in the Baltic Sea (Aarnio & Bonsdorff 1993). In the Wadden Sea, the diet of gobies was mainly comprised of meiofauna, polychaetes and small crustaceans (del Norte-Campos 1995), which may indicate a minor impact on abundances of juvenile bivalves.

The most abundant predators in the experimental area were shore crabs *Carcinus maenas* and shrimp *Crangon crangon*. Since it is known from stomach analyses and direct observations that *C. maenas* and *C. crangon* feed to a large extent on *Cerastoderma edule*, *M. balthica* and *Mya arenaria* (Scherer & Reise 1981, Pihl & Rosenberg 1984, Reise 1985, Jensen & Jensen 1985, Matilla et al. 1990, van der Veer et al. 1998), a large proportion of the bivalve predation in my experiments was most likely caused by these 2 predators. While predation by *C. crangon* is restricted to bivalves <3 mm (Pihl & Rosenberg 1984), *C. maenas* may generally feed on bivalves smaller than 84% of its carapace width (Jensen & Jensen 1985). Both species generally appear later and in smaller numbers on the tidal flats after severe compared to after mild winters (Beukema 1991, 1992b). In the study area, *C. maenas* larvae appeared 6 to 8 wk later in the plankton after the severe winter of 1995 to 1996 than after the moderate (1996 to 1997) and the mild (1997 to 1998) winters, which resulted in a temporal mismatch between *C. maenas* and the bivalves (Strasser & Günther 2001). Therefore, *C. maenas* is probably at least partly responsible for the high bivalve predation after the moderate and the mild winters observed in this study. Considering the important role of *C. crangon* for the bivalve population dynamics in the Dutch Wadden Sea (Beukema 1991, Beukema et al. 1998, van der Veer et al. 1998), a large impact of *C. crangon* can also be assumed for the German Wadden Sea. Especially the high predation in June 1998 can be best explained by predation by *C. crangon* because at that time of the year, *C. maenas* had just settled and was probably too small to feed on the bivalves.

Importance of epibenthic predation for bivalve population dynamics

In *Cerastoderma edule* and *Mya arenaria*, there was 2-fold evidence for reduced epibenthic predation after the severe winter. (1) Significant predation effects were only observed after the moderate and the mild, but not after the severe, winter. Most predation effects were observed in the months June/July and August. As a consequence in October after the 2 milder winters, there was hardly any recruitment left (Fig. 7). (2) In August and October after the severe winter, the average size of the 2 species was significantly larger than after the 2 milder winters (Table 3). While after the 2 milder winters only few individuals reached a size above 3 mm (see Strasser 2000 for length frequency distributions), average size after the severe winter was already about 4 mm in August and 7 mm in October (Table 3). These size differences indicate the

existence of a critical size that must be exceeded to provide the bivalves with a size refuge from predation (Jensen & Jensen 1985, Reise 1985, Möller 1986). In *Macoma balthica*, significant predation effects were also only observed after the 2 milder winters but not after the severe one. However, this lower predation after the severe winter was not expressed in a significantly larger size (Table 3).

It appears that *Cerastoderma edule* benefited most from reduced predation after the severe winter. In sandy sediments, there was no recruitment reduction on the control plots between summer and fall 1996. In muddy sediments, the reduction was also much lower (57%) than after the moderate and the mild winter (>90%). The resulting high recruitment of *C. edule* after the severe winter of 1995 to 1996 was not only observed at the experimental sites in Königshafen Bay but also on a larger scale in the Sylt-Rømø Bight (Strasser et al. 2001) and across the entire Wadden Sea (Strasser et al. 2002). These results suggest that epibenthic predation is the key factor for the regulation of the recruitment dynamics in *C. edule*.

Despite a lack of predation effects in the predator exclusion experiments, the recruitment of *Mya arenaria* and *Macoma balthica* in 1996 was reduced by 77 to 93% between summer and fall, suggesting that substantial predation did not only occur after the moderate (1997) and the mild (1998) winters but also after the severe one. While the recruitment in October after the severe winter was higher than after the 2 milder winters at the experimental sites, recruitment of *M. arenaria* and *M. balthica* was below average on a large scale in the Sylt-Rømø Bight and adjacent areas in the Danish Wadden Sea (Strasser et al. 2001, 2002). The higher mortality in *M. arenaria* and *M. balthica* may be attributed to a food preference of epibenthic predators because *M. arenaria* and *M. balthica* have a thinner shell than *C. edule*. As a consequence, the hypothesized critical size that protects from predation may be lower for *C. edule* than for *M. arenaria* and *M. balthica*. This may explain why: (1) the total number of individuals >3 mm was lower in *M. arenaria* than in *C. edule*; and (2) the average size of *M. balthica* was not significantly larger after the severe than after the milder winters. It may also explain why significant differences between partial cages (with a higher predator density) and control plots occurred most often in *M. balthica*. Epibenthic predation should also be regarded as a major regulatory factor for the recruitment dynamics of *M. arenaria* and *M. balthica* because for both species, the reduced epibenthic predation at the experimental sites resulted in significantly higher recruitment in October after the severe compared to the moderate and the mild winter. In this study, the positive effects of reduced epibenthic predation on

bivalve recruitment were demonstrated only for a single severe winter. However, these results match well with the general observation of high bivalve recruitment of *C. edule*, *M. arenaria* and *M. balthica* (Beukema 1992a, Beukema et al. 2001) and reduced abundances of epibenthic predators after severe winters (Reise 1985, Beukema 1991, 1992b, Strasser & Günter 2001), suggesting that the phenomenon of high bivalve recruitment after severe winters is primarily caused by the post-settlement factor of reduced epibenthic predation.

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