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## Differential recruitment of bivalve species in the northern Wadden Sea after the severe winter of 1995/96 and of subsequent milder winters

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**Abstract** High recruitment of the bivalves *Cerastoderma edule*, *Mytilus edulis*, *Macoma balthica* and *Mya arenaria* in summer after severe winters is an often reported phenomenon in the Wadden Sea. After the severe winter of 1995/96 however, only *Cerastoderma* and *Mytilus* followed this pattern in the Sylt-Rømø Bight. Repeated sampling of *Cerastoderma*, *Macoma* and *Mya* following a severe (1995/96), a moderate (1996/97), and a mild winter (1997/98) revealed that early recruitment was highest after the mild winter. In *Cerastoderma* the eventual high recruitment at the end of summer 1996 was caused by reduced benthic mortality. Low recruitment of *Macoma* and *Mya* after the severe winter may have been caused by a higher susceptibility to epibenthic predation and/or a higher susceptibility to passive re-suspension than in *Cerastoderma* and *Mytilus*. In all cases, post-settlement processes were decisive for reproductive success.

**Keywords** Bivalvia · Recruitment · Winter effects · Population dynamics · Wadden Sea

### Introduction

In the intertidal Wadden Sea, bivalves show huge annual variations in recruitment success (Beukema 1982, 1992a; Beukema et al. 2001). At least part of this variation appears to be closely related to winter temperature. The four most common bivalves in the Wadden Sea, *Cerastoderma edule*, *Macoma balthica*, *Mya arenaria*, and *My-*

*tilus edulis*, all showed generally higher recruitment after severe than after mild winters (Beukema 1992a; Beukema et al. 2001). While recruitment may be close to zero in some years, exceptionally high abundances in the order of  $10^4$ – $10^5$  individuals (ind)  $m^{-2}$  appear to be common on the tidal flats of the Wadden Sea after severe winters. Examples of such high recruitment for *Cerastoderma*, *Macoma*, and *Mya* were the winters of 1941/42 (Smidt 1951), of 1946/47 (Smidt 1951; Kühl 1955), and of 1978/79 (Reichert and Dörjes 1980; Reise 1987; Obert and Michaelis 1991). After the winter of 1946/47, spat of *Mytilus edulis* was also “tremendously abundant” (Bahr 1950), but no quantitative data were given.

Two hypotheses have often been put forward to explain the high reproductive success of bivalves after severe winters. (1) Enhanced egg production after severe winters will lead to high recruitment. This hypothesis rests on the fact that with decreasing winter temperature, intertidal bivalves produce more eggs in the following spring (Honkoop and Van der Meer 1997, 1998; Beukema et al. 1998). Provided planktonic mortality does not differ between years, this will result in increased spatfall. (2) Benthic predation is reduced after severe winters. This hypothesis is supported by studies showing that after severe winters epibenthic predators such as *Carcinus maenas* and *Crangon crangon* return later and in smaller numbers to the tidal flats (Reise 1985; Beukema 1991, 1992b), hence bivalve recruits are partly released from predation pressure.

A series of four winters that turned out to be exceptionally severe (1995/96), moderate (1996/97), and very mild (1994/95 and 1997/98) offered the opportunity to investigate the recruitment pattern of the four major intertidal bivalves in relation to winter temperature in the Sylt-Rømø Bight. In terms of duration of ice coverage on the German North Sea coast, the winter of 1995/96 was among the ten most severe winters of the last century (Strübing 1996). Near Sylt average water temperatures were 4–5°C lower than during the previous five winters (Martens 2001). Therefore, we expected high bivalve recruitment in 1996 and lower recruitment in the other three years.

Communicated by H.-D. Franke

We dedicate this paper to our colleague, Alexandra Rasel, who died in 1998 after heart surgery at the age of 26.

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Abundances of juvenile bivalves are generally highest shortly after peak settlement and then decline in the course of the season (see Van der Veer et al. 1998). In a previous study in the Sylt-Rømø Bight most bivalve spatfall occurred during a single period of about 2 weeks (Armonies 1996). Our study was specifically designed to test two hypotheses: (1) High bivalve recruitment after severe winters is due to high abundance of juvenile bivalves at the beginning of the season. This would support the importance of pre-settlement factors such as enhanced egg production after severe winters. (2) High bivalve recruitment at the end of the year is the outcome of reduced mortality in the course of the season. This would stress the importance of post-settlement factors such as epibenthic predation.

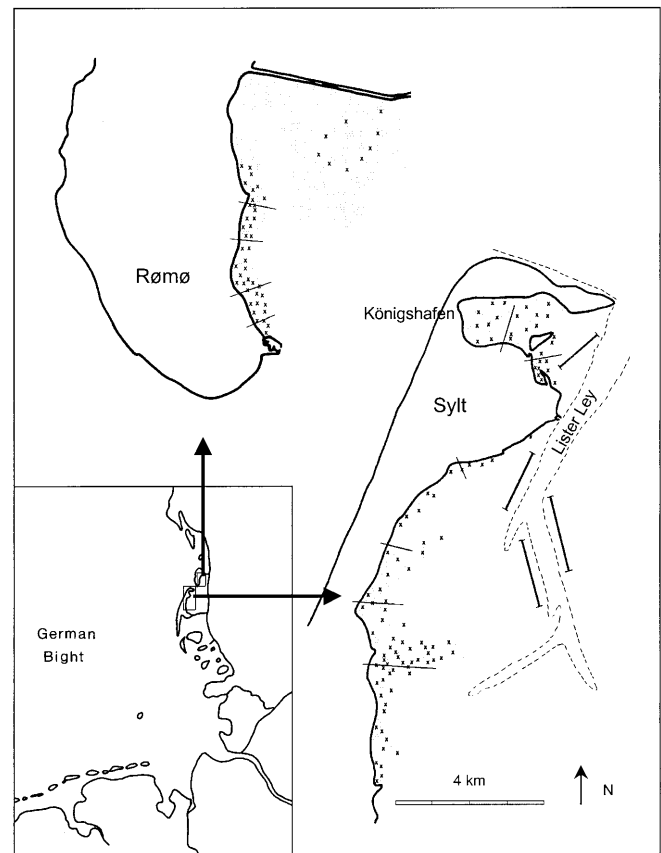
## Materials and methods

The study was conducted in the Sylt-Rømø tidal basin in the northern Wadden Sea (German Bight). The basin encloses 407 km<sup>2</sup> of which one third belongs to the intertidal zone. This zone consists largely of sand flats (72%) and, to a lesser extent, muddy sand (25%) and mud flats (3%). Salinity usually remains between 30 and 32 psu. The tides are semidiurnal with a mean tidal range of 1.8 m. For further information about the area see Gätje and Reise (1998).

### Sampling of juvenile *Cerastoderma*, *Macoma* and *Mya*

Intertidal abundances of *Cerastoderma*, *Macoma*, and *Mya* were determined along the east coasts of the islands Sylt and Rømø on a 20 km scale. A total of 146 stations were randomly selected (Fig. 1) including different tidal levels and different sediment types (see Strasser et al. 1999). Twenty-two stations were located in the high intertidal (>0.0 = mean tidal level), 46 stations in the mid-intertidal (-0.5 to 0.0 MTL), 36 stations in the upper low intertidal (-0.7 to -0.5 MTL), and 42 stations in the lower low intertidal (below -0.7 MTL). The unequal numbers of sites at different tidal levels roughly reflects the areal proportions in the study area. All stations were sampled once in each of the years 1995 to 1998. A global positioning system (Garmin GPS 50) was used to relocate the stations. Depending on weather conditions, completion of the sampling program took 5–8 weeks. For better comparability, the sampling program was not started until most juvenile bivalves had reached a size of at least 0.8 mm. Accordingly, the respective main sampling periods were July/August 1995, September/October 1996, July/August 1997, and August 1998. At each station five or six sediment cores of 20 cm<sup>2</sup> (1995) or 10 cm<sup>2</sup> (1996–1998) of 3 cm depth were collected randomly within a 9 m<sup>2</sup> area using a Perspex tube. All samples were fixed in 5% formalin-sea water solution buffered with 10% hexamethylentetramine. Bivalves were separated from the sediment using a shaking-decantation procedure (Armonies and Hellwig 1986) and sieved through a 0.5 mm screen. Sorting, identification and counting of the bivalves was done under a dissecting microscope. The maximum shell length of the bivalves was measured with an ocular micrometer.

For a more detailed analysis of the temporal course of recruitment, ten additional "transects" were established in the same study area (straight lines in Fig. 1) and sampled four or five times in the years 1996–1998. Sampling of the ten transects was usually completed within 1 week. Each transect consisted of three sampling stations (upper, mid-, and low intertidal) and four subsamples were taken per station. In May 1996 only 24 of the 30 stations were sampled. The decline of juvenile abundance in the course of a season required an increase in the sampling area. In 1996 we sampled 5 cm<sup>2</sup> × 1 cm depth in May and June, and 10 cm<sup>2</sup> × 3 cm



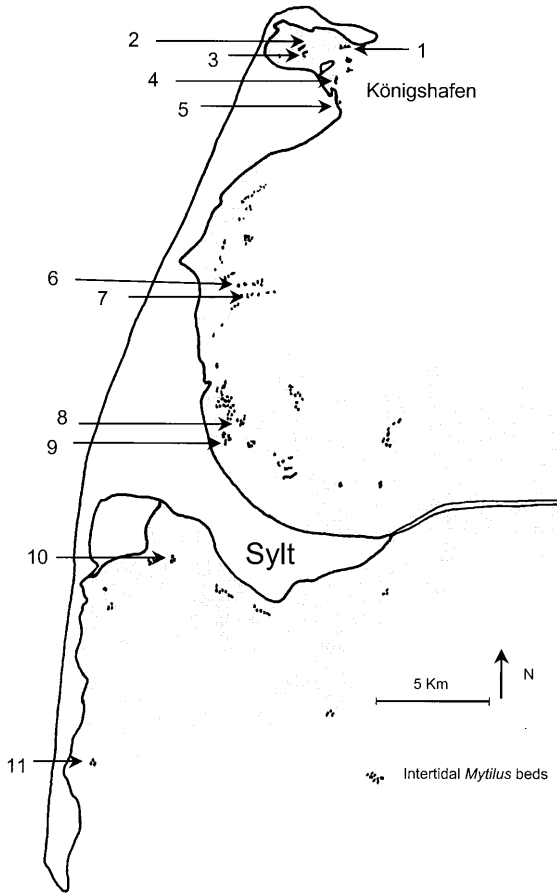
**Fig. 1** Location of the intertidal sampling stations ( $x$ ,  $n=146$ ), intertidal transects (*thin straight lines*,  $n=10$ ), and subtidal transects (*thick straight lines*,  $n=4$ ) along the east coasts of the islands Rømø and Sylt in the northern Wadden Sea. *Shaded areas* depict intertidal zone, *dashed line* represents the 5 m isobath below mean low tidal level

depth in August. In 1997 and 1998 we sampled 10 cm<sup>2</sup> × 1 cm depth in April (1997), May (1997 and 1998), and June (1997), and 20 cm<sup>2</sup> × 3 cm depth in July (1998) and August (1997 and 1998). Sorting and extraction was as above but a 0.125 mm screen was used. In September (1997) and October (1996 and 1998) an area of 284 cm<sup>2</sup> × 10 cm depth was sampled. By this time most juvenile bivalves exceeded 1.5 mm and the samples were sieved in the field through a 1.0 mm mesh. The coefficient of variation ( $CV = \text{standard deviation} \times \text{mean}^{-1}$ ) was used as a measure of deviation from the sample mean. In all three bivalve species there was no significant correlation (Spearman's  $R$ ,  $P > 0.05$ ) between average  $CV$  of each sampling date and the respective sampling areas. We therefore assume that different sample sizes did not significantly bias our results.

In the subtidal near Sylt, four transects were sampled in August/September of 1996–1998 alongside the main tidal channel called Lister Leg (Fig. 1). Two transects consisted of five sampling stations and two of ten sampling stations. At each station one box-core of 0.02 m<sup>2</sup> was taken and the sediment sieved through a 1.0 mm screen. Water depth ranged between 2 and 6 m, substrates ranged from muddy to coarse sand. Bivalves were fixed in 5% formalin-sea water solution buffered with hexamethylentetramine and counted in the laboratory. Abundances between years were compared using analysis of variance (ANOVA). In some cases heteroscedasticity (tested by Bartlett's Chi<sup>2</sup>-test) could not be completely removed but was decreased by logarithmic transformation. The Newman-Keuls test was used for post hoc comparisons.

Sampling of *Mytilus edulis*

No significant numbers of mussel spat were encountered outside the established mussel beds. Therefore, *Mytilus edulis* was sampled on 11 intertidal mussel beds along the east coast of Sylt (Fig. 2) in August 1996. These mussel beds were resampled in July 1997 except for bed No 8, which had disappeared. To consid-



**Fig. 2** Location of intertidal *Mytilus edulis* beds (aerial survey 1996) with sampled beds numbered 1 to 11

er the structural complexity of the mussel beds, seven types of microhabitats were defined: center of the bed with (I) or without (II) *Fucus*; peripheral 1 m zone of the bed, seaward, with (III) or without (IV) *Fucus*; peripheral 1 m zone, landward, with (V) or without (VI) *Fucus*, as well as tide pools inside the bed (VII). For each mussel bed the areal proportions (%) of each microhabitat were visually estimated to the nearest 5% (Table 1). On each mussel bed one sample was taken from each microhabitat. Numbers of types of microhabitats (= numbers of subsamples per mussel bed) present on individual beds ranged from 2 to 5 (mean 3.8). In each subsample all mussels were removed below 500 cm<sup>2</sup>. Mussels were disentangled from the coherent clumps in the laboratory, and all mussels that did not pass a 1.0 mm mesh were counted and categorized into 10 mm size intervals. For each size class, abundances in the subsamples (microhabitats) were weighted by the respective proportions of the microhabitat on each mussel bed and the mean of these 2–5 values gave the final mean mussel abundance of the mussel bed. Abundances of the size classes in 1996 and 1997 were compared using the *t*-test, after homoscedasticity of the data was confirmed by Bartlett's Chi<sup>2</sup>-test.

## Results

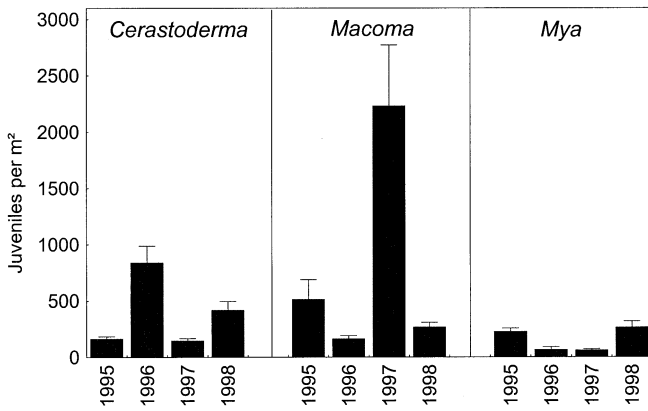
### Recruitment until late summer

In each of the bivalves *Cerastoderma*, *Macoma* and *Mya* abundance of recruits differed significantly between the years 1995–1998 (ANOVA;  $F_{Cer}=8.7$ ,  $F_{Mac}=10.4$ ,  $F_{Mya}=33.3$ ;  $df=3, 580$ ;  $P<0.001$ ). Only in *Cerastoderma* was recruitment higher after the severe winter of 1995/96 (838 ind m<sup>-2</sup>) than after the milder winters (<420 ind m<sup>-2</sup>). This difference was significant between 1996 and 1997 (Newman-Keuls test,  $P<0.001$ ). *Macoma* showed highest recruitment after the moderate winter of 1996/97 and recruitment of *Mya* was highest after the two mild winters of 1994/95 and 1997/98 (Fig. 3).

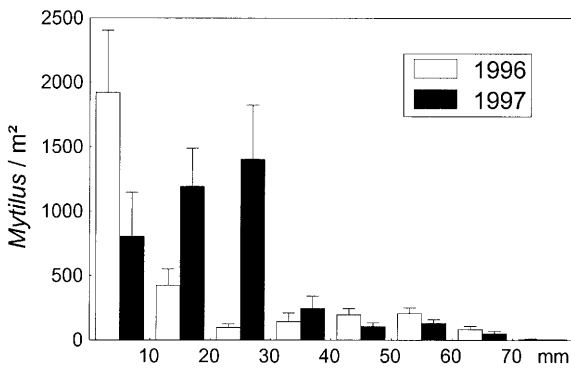
Recruitment of *Mytilus* – defined as abundance of the size class 1–10 mm – was 2.3 times higher after the severe winter of 1995/96 (1,919 ind m<sup>-2</sup>) than after the moderate winter of 1996/97 (805 ind m<sup>-2</sup>; *t*-test,  $P=0.08$ ). Abundance of the 1-year group – defined as the size class 10–30 mm – dominated the length–frequency

**Table 1** Spatial percentages of microhabitats found on *Mytilus edulis* beds in August 1996 and July 1997

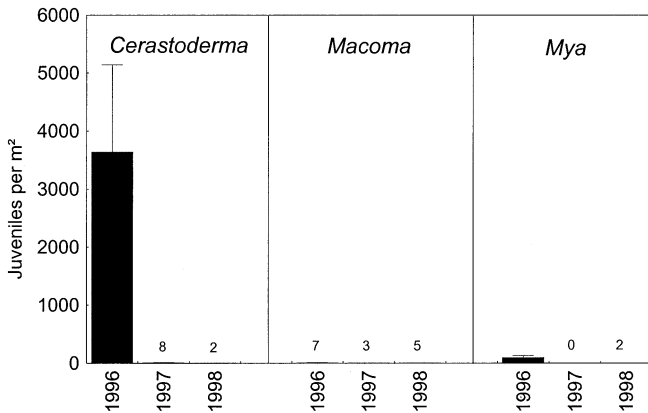
Year Bed no..	Microhabitats													
	Centre <i>Fucus</i>		Centre No <i>Fucus</i>		Seaward <i>Fucus</i>		Seaward No <i>Fucus</i>		Landward <i>Fucus</i>		Landward No <i>Fucus</i>		Tide pool No <i>Fucus</i>	
	1996	1997	1996	1997	1996	1997	1996	1997	1996	1997	1996	1997	1996	1997
1	10	5	40	45	20	20			20	20			10	10
2			55	55			20	20			20	20	5	5
3	55	60	5		20	20			20	20				
4	35	35	25	25	20	20			20	20				
5			65	70			15	15			15	15	5	
6			40	40			40	40			20	20		
7			50	55	35	35			10	10			5	
8			60		20				20					
9							40	40			60	60		
10			60	60			20	20			20	20		
11	10	10	40	40			30	30			10	10	10	10



**Fig. 3** Average abundances  $m^{-2} \pm SE$  of *Cerastoderma*, *Macoma*, and *Mya* recruits  $>0.5$  mm in late summer, 1995–1998



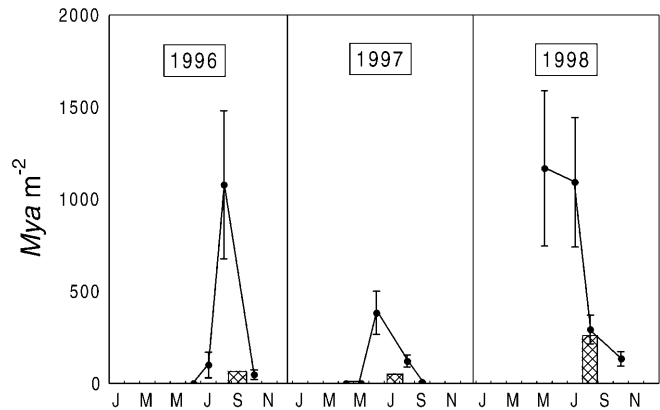
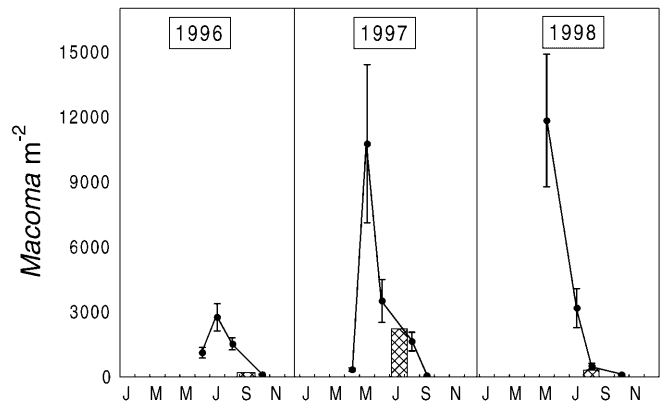
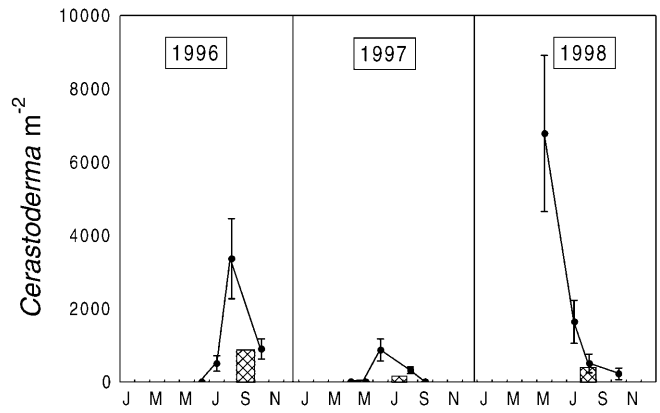
**Fig. 4** Length-frequency distribution (error bars=SE) of *Mytilus edulis* in July 1996 (□) and August 1997 (■) in mussel beds near Sylt



**Fig. 5** Average abundances  $m^{-2} \pm SE$  of *Cerastoderma*, *Macoma*, and *Mya* in four subtidal transects sampled in August/September 1996–1998

distribution in 1997 (Fig. 4) and was significantly higher than in 1996 ( $t$ -test,  $P < 0.05$ ), indicating a high survival of the 1996 cohort.

In the subtidal, recruitment of *Cerastoderma*, *Macoma* and *Mya* was always below  $100 \text{ ind } m^{-2}$  except for 1996 when *Cerastoderma* reached a mean of  $3,800 \text{ ind } m^{-2}$  (Fig. 5). Both *Cerastoderma* and *Mya* showed significantly higher recruitment after the severe winter than after the milder winters (Newman-Keuls test,  $P < 0.001$ ).



**Fig. 6** Seasonal mean abundance  $\pm SE$  of *Cerastoderma edule*, *Macoma balthica*, and *Mya arenaria* from 30 stations in the Sylt-Rømø Bight in 1996–1998. Columns represent mean abundance and sampling period of the late summer sampling program with 146 sampling stations (cf. Fig. 3)

$m^{-2}$  (Fig. 5). Both *Cerastoderma* and *Mya* showed significantly higher recruitment after the severe winter than after the milder winters (Newman-Keuls test,  $P < 0.001$ ).

Juvenile dynamics between spring and fall

With increasing winter temperature, the recruitment season of *Macoma*, *Cerastoderma*, and *Mya* started earlier.

After the moderate and mild winters (1997 and 1998) *Macoma* recruitment was highest in May, while it was highest in June after the severe winter of 1995/96 (Fig. 6). *Cerastoderma* and *Mya* recruitment was highest in May after the mild winter, in June after the moderate winter, and in August after the severe winter (1996). Mean abundance of all bivalve recruits declined sharply between spring and fall in all years. However, both the degree of the decline and the level of abundance at the beginning of the season varied between species and years. In no species was the peak recruitment at the beginning of the season highest after the severe winter of 1995/96. Recruitment at the end of the season was generally not related to peak recruitment at the beginning of the season.

For *Cerastoderma*, highest peak recruitment at the beginning of the season was about twice as high after the mild winter (6,780 ind m<sup>-2</sup> in 1998) than after the severe winter (3,360 ind m<sup>-2</sup> in 1996). However, at the end of the season, highest recruitment was found after the severe winter of 1995/96 (900 ind m<sup>-2</sup>), indicating that benthic mortality in 1996 was reduced (Fig. 6). Abundances at the beginning and at the end of the season were lowest after the moderate winter (in 1997).

In contrast, peak abundances of *Macoma* recruits were about equally high at the beginning of the season after the moderate (11,000 ind m<sup>-2</sup>) and mild winter (12,000 ind m<sup>-2</sup>) which was about four times higher than after the severe winter (3,000 ind m<sup>-2</sup>). In all years, abundances decreased to 100 or fewer individuals m<sup>-2</sup> by September/October.

Peak abundances of *Mya* recruits were higher at the beginning of the season after the severe (1,100 ind m<sup>-2</sup>) and after the mild winter (1,200 ind m<sup>-2</sup>) than after the moderate winter (400 ind m<sup>-2</sup>). In September/October, recruitment was generally low (48, 6, and 133 ind m<sup>-2</sup> in 1996, 1997, and 1998, respectively).

## Discussion

### Differential recruitment success after the severe winter

Recruitment success after the severe winter of 1995/96 was species-dependent. Exceptionally high recruitment on intertidal flats in late summer was observed in *Cerastoderma* but not in *Macoma* and *Mya*. This pattern was even more pronounced in the subtidal where recruitment generally failed except for *Cerastoderma* in 1996. We assume that our results accurately describe the recruitment pattern in the Sylt-Rømø Bight for three reasons: (1) sampling on a large (20 km) spatial scale avoids upscaling artefacts from a rather localized study. Thus our results are unlikely to be affected by current-induced differences in local larval supply; (2) the high number of sites visited is likely to sufficiently account for the inherent patchiness in the distribution of juvenile bivalves, and (3) our sampling design in which stations were sampled randomly in the first year and revisited in

subsequent years is a particularly powerful tool for detecting year-to-year differences in marine benthic species (Van der Meer 1997).

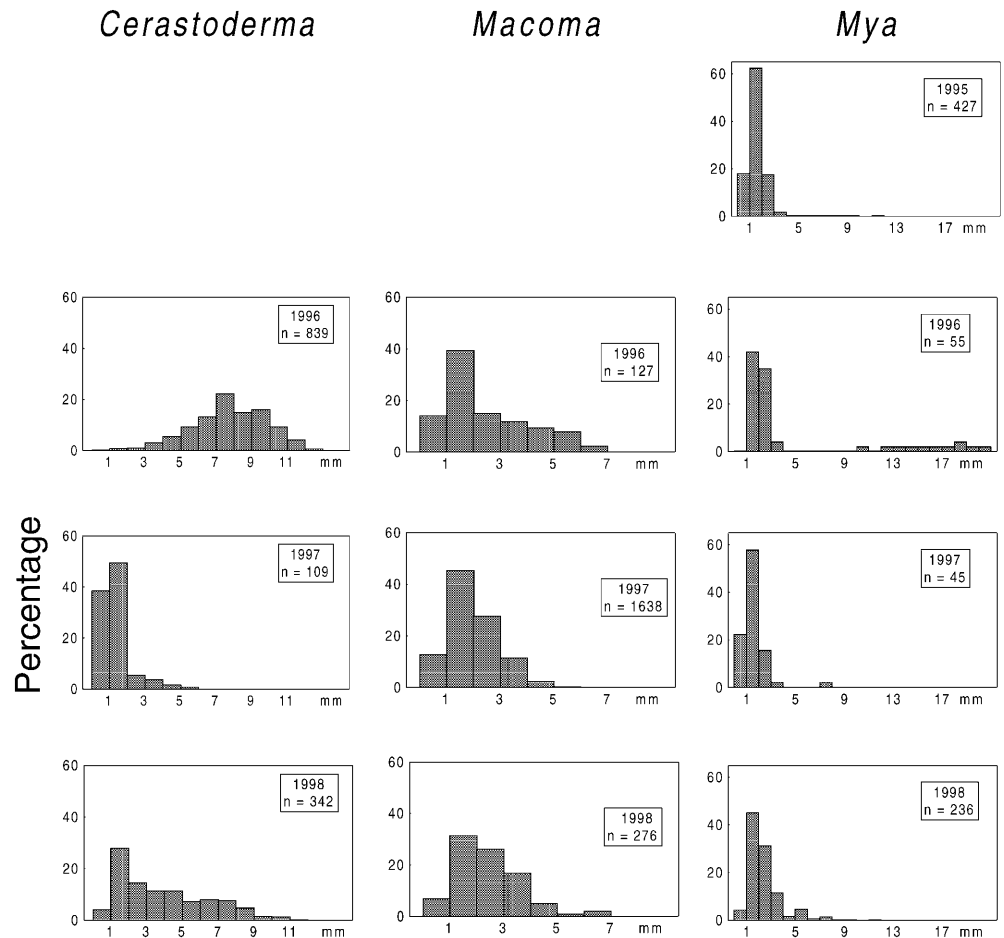
It is conceivable that the accuracy of the results has suffered from the relatively long time (5 to 8 weeks) needed to complete the summer sampling program. However, the seasonal sampling program with four or five sampling dates – which served as a control – confirmed the correctness of the obtained recruitment pattern. In the seasonal program, 30 stations were distributed along ten transects over the same study area and sampling was usually completed within 1 week. In all species and in all years the abundances from the late summer program fitted into the seasonal trend of the ten transects (Fig. 6).

Assessment of *Mytilus* recruitment required a separate sampling method since juvenile *Mytilus* predominantly accumulate within established mussel beds. This procedure could only be conducted in two of the years and therefore the results lack the rigor of a long-term study. Nevertheless it is safe to say that *Mytilus* – like *Cerastoderma* – showed relatively high recruitment success after the severe winter. At least until 1999, the year-class of 1996 still dominated the intertidal *Mytilus* population in the northern Wadden Sea (Nehls 1999), indicating that recruitment after the severe winter was indeed unusually high.

### Hypotheses explaining high recruitment success after severe winters

*Cerastoderma* and *Macoma* produce more eggs after severe winters than after mild winters (Honkoop and Van der Meer 1997, 1998; Beukema et al. 1998). If this pre-settlement factor was the driving force for high reproductive success after severe winters, then the higher number of eggs would lead to higher larval supply, higher settlement and higher early recruitment. However, our results show no indication of enhanced early recruitment after the severe winter, because highest abundances of *Cerastoderma*, *Macoma*, and *Mya* were found in spring after the mild winter. For *Cerastoderma* – the only one of the three species with high reproductive success in 1996 – early recruitment after the severe winter was about 50% lower than after the mild winter. Since juvenile bivalves are subject to high instantaneous mortality after settlement (Van der Veer et al. 1998 and references therein), early recruitment data should only be compared if the time between peak settlement and benthic sampling date is about the same. In a previous study in the Sylt-Rømø Bight, *Cerastoderma*, *Macoma* and *Mya* all showed a single peak settlement over a period of about 2 weeks, while later settlement was quantitatively unimportant (Armonies 1996). Such a peak settlement period most likely also occurred in 1996 and 1998 because in these two years the temporal course of cockle larval abundances was characterized by major peaks at the beginning of the seasons (Strasser and Günther 2001). In 1996 and 1998 these major larval peaks were recorded

**Fig. 7** Length–frequency distributions of *Cerastoderma*, *Macoma*, and *Mya* in late summer of the years 1995–1998



about 5 and 3 weeks prior to benthic sampling, respectively. Did this time difference of about 2 weeks significantly bias our early recruitment numbers? Assuming that natural mortality of juvenile bivalves follows an exponential curve, the instantaneous rate of decrease ( $k$ , week<sup>-1</sup>) of juvenile *Cerastoderma* in summer 1996 can be estimated using the equation  $N_t = N_0 \times e^{-kt}$  where  $N_t$  is the recruitment in October,  $N_0$  the recruitment in August and  $t$  the number of weeks between August and October (here: 10). Accordingly, the instantaneous rate of decrease of juvenile cockles was 0.132 week<sup>-1</sup> in the summer of 1996. With this rate, the early recruitment peak in 1996 would have amounted to 4,380 ind m<sup>-2</sup> (instead of 3,360 ind m<sup>-2</sup>) if recruitment had been determined 2 weeks earlier. Since this value is still about 35% lower than the early recruitment peak in 1998 (6,780 ind m<sup>-2</sup>), it is reasonable to assume that our early recruitment data were not significantly biased and early cockle recruitment was indeed lower after the severe than after the mild winter. We consequently conclude that the high reproductive success of *Cerastoderma* after the severe winter cannot be explained by enhanced egg production. A similar conclusion was reached for *Macoma* in the Dutch Wadden Sea (Honkoop et al. 1998).

The high abundances of juvenile *Cerastoderma* in October 1996 were brought about by reduced mortality

in the course of the summer (Fig. 6), supporting the view of post-settlement processes being the leading determinant of community structure in soft sediment substrates (Ólafsson et al. 1994). The reduced mortality after the severe winter was most likely caused by reduced epibenthic predation. The major predators of juvenile bivalves in the Wadden Sea are shrimp, *Crangon crangon*, and shore crabs, *Carcinus maenas* (Jensen and Jensen 1985; Reise 1985; Beukema et al. 1998; Van der Veer et al. 1998). After severe winters both species return later to the tidal flats and in smaller numbers than after mild winters (Beukema 1991, 1992b). In 1996, the arrival of *Carcinus maenas* larvae in the Sylt-Rømø Bight was delayed by 6–8 weeks (Strasser and Günther 2001). Alternatively, the low mortality of *Cerastoderma* in 1996 might have been caused by reduced competition for food or space because after severe winters flats are partly cleared from benthic assemblages by ice scouring or freezing (Möller and Rosenberg 1983). Cold-sensitive species such as *Cerastoderma* or *Lanice conchilega* suffered indeed mass mortalities during the severe winter of 1995/96 (Strasser and Pieloth 2001; Strasser et al. 2001). However, a year later abundances of *Lanice* were still low and the strong 1996 year class of *Cerastoderma* suffered high mortality during the following winter (Strasser 2000). Despite low abundances of potential competi-

tors in 1997, bivalve recruitment almost failed completely. We therefore regard reduced competition as an unlikely explanation for the high recruitment of *Cerastoderma* in 1996.

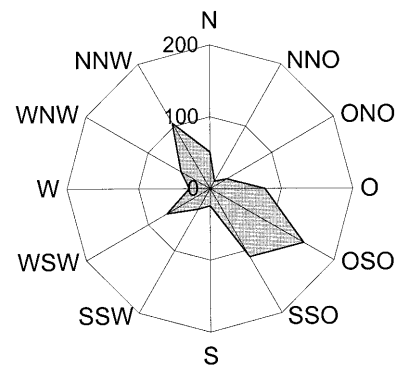
Why was reproductive success after the severe winter high for *Cerastoderma* and *Mytilus* but low for *Macoma* and *Mya*?

The species-specific recruitment success found in this study is in contrast to previous studies from the Wadden Sea where recruitment of different bivalve species had been recorded. In 1942 exceptionally high recruitment was found in *Cerastoderma*, *Macoma*, and *Mya* in the Danish Wadden Sea (Smidt 1951). Similar results were reported after the winter of 1978/79 in the German and Dutch Wadden Sea (Reichert and Dörjes 1980; Beukema 1982; Reise 1987; Obert and Michaelis 1991). Analysis of long-term data from the Dutch Wadden Sea revealed that abundances of *Cerastoderma*, *Macoma*, *Mya*, and *Mytilus* peaked synchronously after severe winters (Beukema 1992a; Beukema et al. 2001).

In this study, maximum abundances of *Cerastoderma*, *Macoma*, and *Mya* were in the same order of magnitude at the beginning of the season after the severe winter (cf. Fig. 6). Nevertheless, only *Cerastoderma* managed to survive in high numbers until October. In their first year *Cerastoderma*, *Macoma* and *Mya* may attain sizes of up to 15 mm, 10 mm and 20 mm, respectively (Beukema et al. 1993). In summer 1996 the length–frequency distribution of *Cerastoderma* was almost normal, with a peak in the 7–8 mm interval (Fig. 7). In all other years and in all other species the length–frequency distribution was skewed to the left and only few individuals exceeded a length of 3 mm.

These results corroborate the hypothesis that survival is enhanced when juveniles manage to grow beyond a critical size for being captured by their main predators (Reise 1985; Möller 1986). It seems possible that juvenile *Cerastoderma* and *Mytilus* reach such a – perhaps species-specific – critical size earlier than *Macoma* and *Mya* due to faster growth, a more robust shell (*Cerastoderma*) and a refuge within tight clumps of adults (*Mytilus*). Further experiments are needed to test the hypothesis that the common predators *Crangon crangon* and/or *Carcinus maenas* preferentially prey on *Macoma* and *Mya*.

An alternative explanation for the observed recruitment pattern is species-specific susceptibility to passive re-suspension of juvenile bivalves into the water column. In the study area westerly winds usually prevail in the summer months. However, in August 1996 easterly winds dominated (Fig. 8) and reached wind speeds  $\geq 4$  Beaufort on 12 days. All intertidal sites sampled in the Sylt-Rømø tidal basin are situated at the eastern side of the islands, and hence are subject to higher wave energy during easterly winds. These waves disturb the sediment surface and may erode small-sized benthos with successive transport of organisms elsewhere. Among the four



**Fig. 8** Prevailing wind directions (h) near the island of Sylt in August 1996

bivalve species, *Macoma* and *Mya* are far more susceptible than *Mytilus* and *Cerastoderma* to passive re-suspension (see Table 3 in Armonies 1996). Therefore, differential susceptibility to passive re-suspension is also a plausible explanation for the observed differential recruitment success.

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