

Matthias Strasser · Torsten Reinwald · Karsten Reise

Differential effects of the severe winter of 1995/96 on the intertidal bivalves *Mytilus edulis*, *Cerastoderma edule* and *Mya arenaria* in the Northern Wadden Sea

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Abstract Intertidal mussel beds were severely damaged by scouring ice floes during the winter of 1995/96. Aerial surveys before and after the winter showed that more clusters of mussel beds vanished in a region with a higher areal share of tidal flats and a lower salinity, suggesting that the amount of ice present determined the magnitude of the disturbance on beds of *Mytilus edulis*. Nehls and Thiel [(1993) Neth J Sea Res 31:181–187] observed a strikingly similar spatial pattern of disturbances caused by severe storms in the Wadden Sea. Areas on mussel beds mechanically undisturbed by ice showed no reduced abundance and biomass of mussels, indicating that temperature alone was of little importance as a lethal factor. Conversely, *Cerastoderma edule* was strongly affected by low temperature. On average 80% died during the winter with extinctions up to 100% in the high tidal zone. At the lowest tidal level, surviving cockles were larger than those killed by the frost. A reinvestigation of sampled sites in autumn revealed that substantial further mortality had occurred during spring and summer which may constitute a time-lag effect of the preceding winter. There was no increased mortality in juvenile and adult *Mya arenaria* during the winter of 1995/96, confirming that this clam is a hard-winter species like *Macoma balthica*.

Keywords *Mytilus edulis* · *Cerastoderma edule* · *Mya arenaria* · Winter effects · Wadden Sea

Introduction

Any comprehensive assessment of winter ice effects in the Wadden Sea would be incomplete without a survey

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M. Strasser (✉) · T. Reinwald · K. Reise
Foundation Alfred Wegener Institute for Polar and
Marine Research, Wadden Sea Station Sylt, 25992 List, Germany
e-mail: mstrasser@awi-bremerhaven.de
Tel.: +49-4651-956136, Fax: +49-4651-956200

on bivalve mortality. Bivalves play a dominant role in the Wadden Sea ecosystem. In terms of biomass they are by far the most important component of the intertidal zone. The three species, *Cerastoderma edule* (cockle), *Mya arenaria* (soft-shell clam), and *Mytilus edulis* (mussel) make up about 50% of the macrobenthic biomass (Reise and Lackschewitz 1998). As major consumers of phytoplankton and as a food source for various species of birds, decapod crustaceans and fish, they greatly influence the benthic-pelagic energy flow. In addition, mussel beds constitute the basement for the only major hard substrate community in the Wadden Sea.

Total biomass in the intertidal Wadden Sea is subject to large fluctuations between years which is primarily caused by biomass fluctuations of *Mya*, *Mytilus* and especially *Cerastoderma* (Beukema 1979). While it is generally agreed that most of this fluctuation is caused by differential recruitment (Reise 1985; Beukema 1982, 1992), mortality during severe winters may also have a great impact on the standing stocks.

Among the three bivalves, *Cerastoderma* is considered to be most sensitive to low winter temperatures (Beukema 1990). Complete or almost complete extinctions of intertidal populations have been reported for the winters of 1928/29 (Blegvad 1929; Smidt 1944), for 1941/42 (Smidt 1944), for 1946/47 (Smidt 1951; Kristensen 1957), and for 1978/79 (Beukema 1979; Dörjes 1980; Figge et al. 1980; Reise 1985). In the Dutch Wadden Sea, cockle stocks sharply declined during the winter of 1978/79 (Beukema 1979), but died out completely only in the high intertidal (Beukema 1985).

For *Mytilus edulis* there is a double danger of getting damaged by severe winters. Firstly, it can be directly harmed by low temperatures, secondly it can be scoured off by drifting ice floes. In the latter case the mussels may survive wherever they are transported to. Freezing temperatures resulted in direct mortality of close to 100% during the winter of 1928/29 in a Danish estuary (Blegvad 1929), and in a mortality rate of 34% during the winter of 1984/85 in the German Wadden Sea (Obert and Michaelis 1991). These mortalities occurred al-

though *Mytilus* is the species with the highest freezing resistance of the three bivalves considered here (Theede 1965; Theede and Lassig 1967; Bourget 1983). In the Dutch Wadden Sea, mortalities after severe winters are relatively low and therefore the mussel is considered a hard-winter species there (Beukema 1990). An example of complete removal of a mussel bed by ice scouring is given in Obert and Michaelis (1991) for the winter of 1984/85. After the winter of 1946/47 – the severest winter on the German coasts of the last century (Strübing 1996) – *Mytilus* beds had almost completely disappeared from the entire East Frisian Wadden Sea (Bahr 1950).

Mya arenaria is less resistant to freezing than *Mytilus* (Theede 1965; Theede and Lassig 1967; Bourget 1983), but it is also considered a hard-winter species by Beukema (1990). At least the older specimens are generally protected from low temperatures by their burrowing depth of about 20 cm. After the severe winter of 1962/63, *Mya* was the only surviving species at one site in the Danish Isefjord (Rasmussen 1973). Nevertheless, in Danish estuaries, mortality was up to 80% after the winter of 1928/29 (Blegvad 1929) and one population perished completely during the winter of 1962/63 (Muus 1967). In the Wadden Sea, *Mya* was nearly extinct after the winter of 1941/42 (Smidt 1944). According to Kühl (1951), ice scouring during the winter of 1946/47 had killed the *Mya* spat that lives in the upper part of the sediment, while deeper living adults remained largely unaffected.

Considering the duration of ice coverage on the German North Sea coast, the winter of 1995/96 ranks 9th harshest of the last century (Strübing 1996). A characterization of the biological oceanography of this winter in the Sylt-Rømø tidal basin is given in Martens (2001). In this study we investigated for the severe winter of 1995/96, (1) the decline of mussel beds on a large scale using aerial observations and on a small scale by detailed examination of two beds, (2) the mortality effects on cockles with special reference to tidal level, and (3) the differential effects on juvenile and adult *Mya arenaria* at sites where they occurred abundantly before the winter.

The fourth important intertidal bivalve in the Wadden Sea, *Macoma balthica*, has not been included in this investigation because it does not seem to suffer from cold temperatures. After the severe winters of 1941/42 and 1962/63 its abundance remained high (Smidt 1944; Ziegelmeier 1964).

Materials and methods

Mytilus edulis

Intertidal mussel beds in the North Frisian Wadden Sea (Figs. 1, 2) were mapped from an airplane flying at a height of approximately 300 m during low tide periods, three times between July and September in 1995 and in 1996. The fractal structure of mussel beds made it unfeasible to estimate the area covered. However, mussel beds tended to occur in clusters, often elongated in parallel with tidal divides or alongside tidal channels. These clusters were drawn on maps of 1:100,000 scale by three observers during

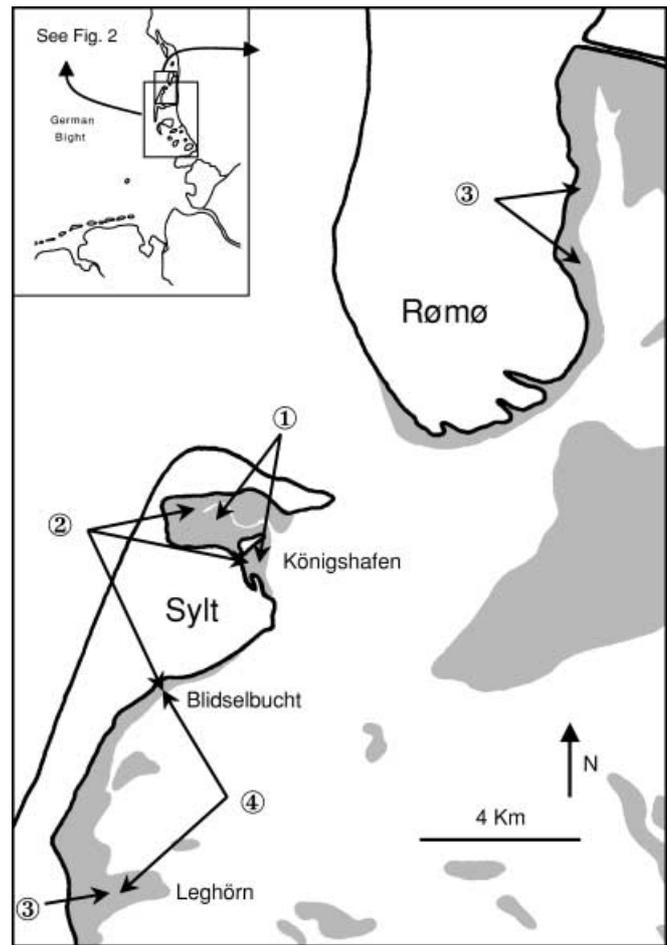


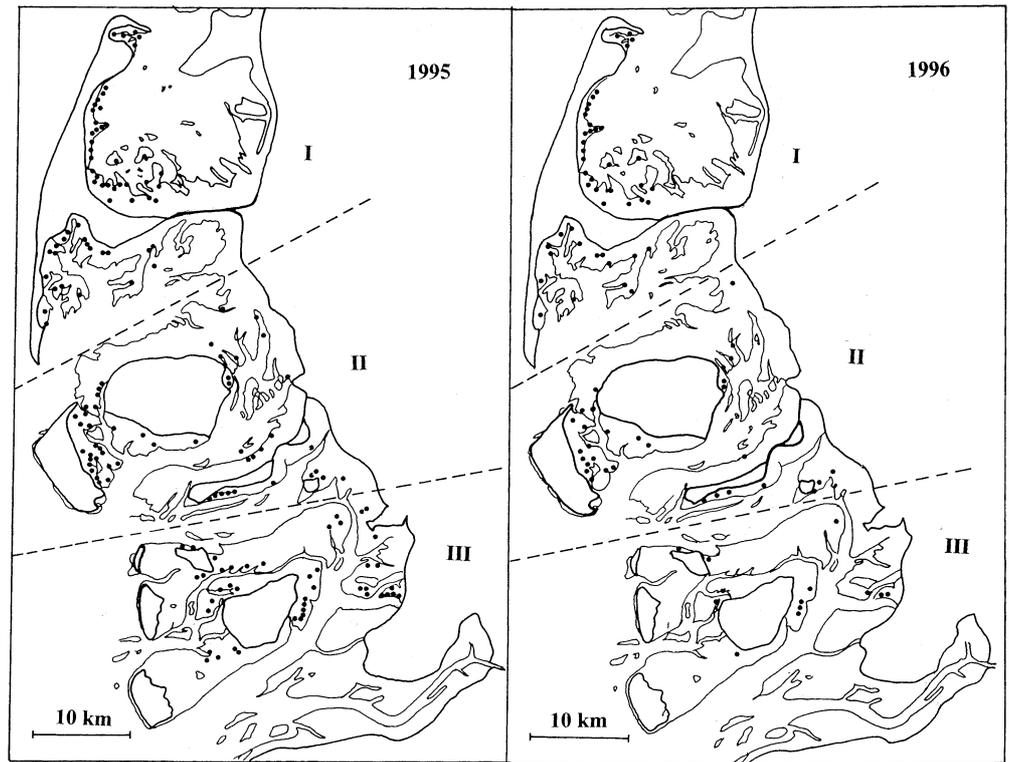
Fig. 1 Map of study area and sampling sites of *Mytilus edulis* beds (1), adult *Cerastoderma edule* (2), adult (3) and juvenile (4) *Mya arenaria* in the Sylt-Rømø Bight. Shaded areas depict the intertidal zone

flights. Time of low tide varied up to 74 min between mussel beds near the tidal inlets (i.e., Amrum harbor) and near the mainland coast (i.e., Dagebüll harbor). It was not possible to be above each site exactly at mean low water. Thus, some clusters were missed during individual surveys. Maps therefore present the added sightings from the three surveys each year.

The condition of two mussel beds was evaluated in Königshafen (Oddewatt to the east and Mövenbergwatt to the west, Fig. 1) in March 1996. The damage-rate of the beds was assessed along 15 transects on the larger bed in Oddewatt and along 6 transects in Mövenbergwatt. On each transect of 20 m in length, *Mytilus* was counted by hand in 80 subsamples of 0.25 m² in the field. Subsamples with >75 mussels 0.25 m⁻² – corresponding to >300 individuals (ind) m⁻² – were classified as unaffected by ice scouring. More than 95% of the subsamples that fell in this category consisted of >1,000 ind m⁻². Subsamples with <75 ind 0.25 m⁻² were classified as damaged by ice scouring if the clay-like sediment which is typical for the basement of *Mytilus* beds appeared on the surface with empty mussel shells embedded. If this sediment type was absent, the subsample was also considered as unaffected (7% of subsamples in Oddewatt, 1% in Mövenbergwatt) but were not included in the calculation of the damage rate.

Abundance and biomass were determined by collecting mussels from 10 unaffected areas of 200 cm² in Oddewatt and five unaffected areas in Mövenbergwatt. Mussels were dried for 3 days at 70°C and burned in a furnace for 12 h at 550°C. Ash-free dry weight (AFDW) was calculated as the weight loss of the mussels.

Fig. 2 Clusters of intertidal mussel beds in the North Frisian Wadden Sea (Sylt to Eiderstedt Peninsula) from three aerial surveys before (1995) and after (1996) a severe winter with ice cover in the intertidal zone. Losses of mussel beds increase from north to south



Cerastoderma edule

Mortality of *Cerastoderma* during the winter of 1995/96 was determined in March 1996 along six transects in Königshafen (Westfeuerwatt and Oddewatt, two transects each in the high (above mean tidal level), mid- (0.0 to -0.5 m) and low intertidal (below -0.5 m) and two transects (mid- and low intertidal) in Blidselbucht, south of List harbor (Fig. 1). Five transects (one in Westfeuerwatt, two in Oddewatt, two in Blidselbucht) were resampled in October 1996. Each transect consisted of 10 or 11 subsamples taken along about 250 m. For each subsample, an area of 1 m² was raked down to 5 cm depth. In March 1996 all open and closed double shells, which were still connected by the ligament, were collected and immediately examined after arrival in the laboratory. Cockles were classified as (1) alive, (2) having died during the winter of 1995/96, and (3) having died before the winter. Living cockles were actively pumping water through their siphons after being placed in sea water of room temperature. Shells of these specimens could not be opened by hand. Cockles were considered as having died during the winter of 1995/96 if (a) intact or decaying flesh was visible inside open shells or if (b) the periostracum on the ventral margin and on the pallial sinus was still attached and intact. Cockles were regarded as having died some time before the winter if no periostracum was visible and/or the inner sides of the shells were fouled by microorganisms, algae, or byssus threads. Assignment of cockles to one of the categories was in almost all cases unequivocal. If doubts occurred concerning the time of death, cockles were considered as having died before the winter. Abundance of live cockles before the beginning of winter was calculated as abundance of live cockles in March 1996 + abundance of cockles that were classified as having died during the winter. In October 1996 only live cockles were collected. Maximum shell length was measured to the nearest 0.1 mm using callipers.

Mya arenaria

Juvenile abundance was determined at two sites near Sylt in October 1995 and in April 1996 (Fig. 1). At each site 6–10 sediment

cores of 20 cm²×5 cm depth were randomly collected in an area of about 9 m² using a perspex tube. The sediment was sieved through a 0.5 mm screen and clams were sorted under a dissecting microscope.

Adults were sampled at three high density sites (see Strasser et al. 1999) near Rømø and Sylt (Fig. 1). At each site four or five subsamples of 0.1 m² were taken by excavating the sediment down to 35 cm with a fork. Live clams were separated from the sediment by hand and counted in the laboratory.

Results

Winter effects on *Mytilus edulis*

Clusters of mussel beds, as discernable from the air, declined in number from summer 1995 to 1996 by 42% (Fig. 2). This decrease was hardly noticeable in the northern third of the area but was conspicuous further south (Table 1).

Two clusters of mussel beds in Königshafen at the northern end of the island of Sylt were investigated at the ground. On the larger mussel bed (Oddewatt) 60% of

Table 1 Number of discernable clusters of mussel beds in the North Frisian Wadden Sea from aerial surveys before (1995) and after (1996) a severe winter with ice cover in the tidal zone. For location of subareas see Fig. 2

Year	1995	1996	Decline in %
Total region	153	89	42
Subarea I (north)	57	45	21
Subarea II (middle)	52	31	40
Subarea III (south)	44	13	70

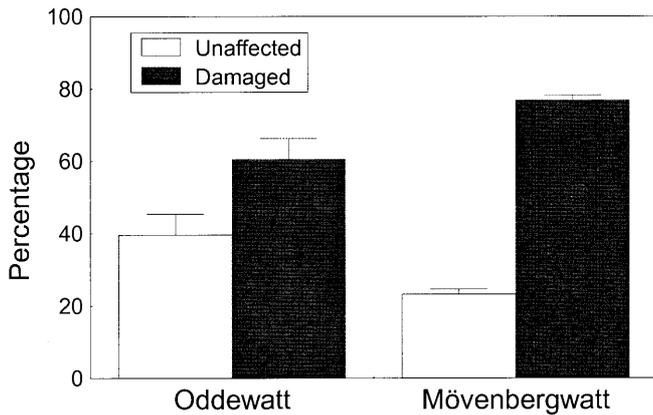


Fig. 3 Ice scouring effects on two *Mytilus* beds in Königshafen in March 1996 measured along 15 (Oddewatt) and 6 (Mövenbergwatt) transects as percentage + SE of unaffected (□) and damaged (■) subsamples. Unaffected samples consisted of >75 mussels 0.25 m^{-2} ; damaged samples of <75 mussels 0.25 m^{-2} , embedded in the clay-like sediment typical for mussel beds

the bed were classified as damaged and 40% as unaffected (Fig. 3). The rate of damage on the bed in Mövenbergwatt was 77%. Here, ice cover was more continuous and lasted longer than in Oddewatt. Average mussel (>5 mm length) abundance in unaffected areas was $2,060 \pm 398$ (SD) ind m^{-2} in Oddewatt and $2,150 \pm 565$ (SD) ind m^{-2} in Mövenbergwatt. Biomass values amounted to $1,986 \pm 455$ (SD) g m^{-2} AFDW in Oddewatt and $2,060 \pm 606$ (SD) g m^{-2} AFDW in Mövenbergwatt.

Winter effects on *Cerastoderma*

When gaps in the ice cover occurred for a short time in mid February 1996, plenty of decaying cockles were found on the sediment surface. Immediately after the ice shield had melted in March, we determined highest mortality in the high intertidal with rates of 93 and 100% (Fig. 4). Mortality rates decreased towards the low tidal level (29–65%). Highest mortality rates were found in Westfeuerwatt. During strong easterly winds in March at this site the high and mid-intertidal was not covered by water at high tide and the sediment was still frozen down to 5 cm. At the same time, the sediment was not frozen and covered with water at all tidal levels in Oddewatt and Blidselbucht, where the flats are characterized by a steeper slope.

On average, abundances of live cockles decreased from about 15 ind m^{-2} before the winter of 1995/96 (calculated as live + dead specimens in March 1996) to about 3 ind m^{-2} in March 1996 (Fig. 5). This equals a mortality rate of 80%. By October 1996, abundances of adult cockles had declined even further to only 0.3 ind m^{-2} (max. of 0.6 ind m^{-2}), corresponding to a mortality rate of 98% between late 1995 and October 1996. Average abundances of live cockles before winter increased from the low (7.6 ind m^{-2}) to the high tidal level (19.5 ind m^{-2}). After the winter this pattern was reversed (0.5 ind m^{-2} in the high and 3.8 ind m^{-2} in the low intertidal).

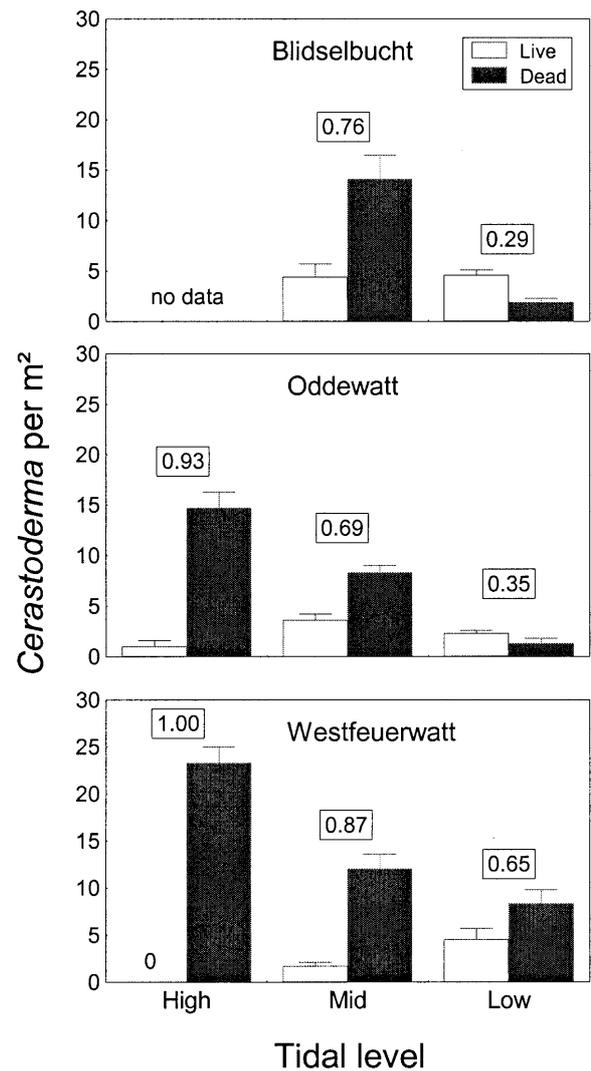


Fig. 4 Mean abundance + SE of live (□) and dead (■) *Cerastoderma* along eight transects at different tidal levels at three sites near Sylt in March 1996. Numbers above the bars show the mortality rate at the respective tidal level

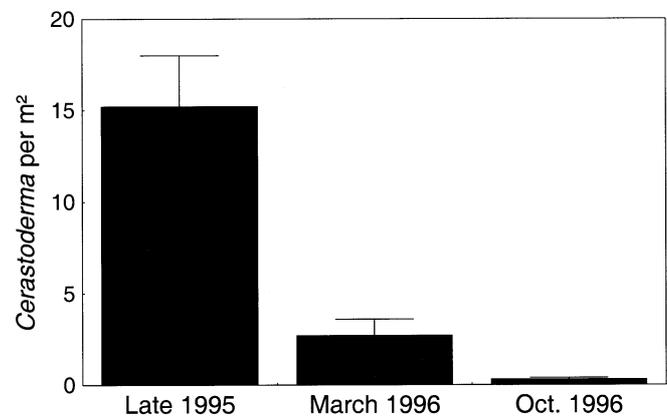


Fig. 5 Mean abundance + SE of live *Cerastoderma* sampled along five transects in March and October 1996. Abundance of live cockles in late 1995 was calculated as abundance of live cockles in March 1996 + abundance of cockles classified as having died during winter

Table 2 Mean size \pm standard deviation (SD) of live and dead *Cerastoderma* at the sampling sites in March 1996. *n* number of cockles

Area	Tidal level	Live			Dead		
		<i>n</i>	Size (mm)	SD	<i>n</i>	Size (mm)	SD
Blidselbucht	Mid	44	32.7	± 2.0	141	32.5	± 2.7
	Low	51	39.1	± 0.6	20	39.1	± 3.0
Oddewatt	High	10	30.9	± 4.1	147	30.4	± 3.7
	Mid	40	36.2	± 5.0	92	35.8	± 5.7
	Low	26	42.5 ^a	± 3.8	14	38.5	± 6.2
Westfeuerwatt	High	0	–	–	257	24.5	± 2.5
	Mid	19	30.8	± 3.3	131	30.3	± 3.2
	Low	50	32.9 ^a	± 2.0	90	31.2	± 3.8

^a Significant (*t*-test, $P < 0.05$) size differences between live and dead cockles

Table 3 Mean abundances \pm standard deviation (SD) and difference of juvenile and adult *Mya* before and after the winter of 1995/96 at five sites near Rømø and Sylt

Juveniles		October 1995		April 1996		Difference 1995/96
Site	Tidal level	Mean/m ²	SD	Mean/m ²	SD	
Sylt 1	Low	400	± 316	100	± 211	-75%
Sylt 2	Low	1,778	$\pm 1,063$	583	± 585	-67%
Adults		June/July 1995		September 1996		Difference 1995/96
Site	Tidal level	Mean/m ²	SD	Mean/m ²	SD	
Rømø 1	Mid	438	± 165	466	± 178	+6%
Rømø 2	Low	74	± 21	86	± 50	+16%
Sylt 3	Low	112	± 70	78	± 32	-30%

Cockle size decreased from the low to the high tidal level, that is with decreasing submersion time (Table 2). Average size ranged from 24 mm in the high intertidal (Westfeuerwatt) to 41 mm in the low intertidal (Oddewatt). Live cockles were significantly larger than dead cockles in the low intertidal of Westfeuerwatt and Oddewatt (*t*-test, $P < 0.05$), but not in Blidselbucht and at other tidal levels.

Age determination was difficult because many shells did not exhibit clear winter rings. The majority of cockles were estimated to be 3 or 4 years old. Older cockles of up to 8–9 years were found close to the low-tide line.

Winter effects on *Mya arenaria*

Changes in abundance before and after the winter of 1995/96 differed between juveniles and adults (Table 3). At two sites with 400 juveniles (juv) m⁻² and 1,778 juv m⁻² (<5 mm) abundances decreased significantly by 75% and 67%, respectively (*t*-test after log transformation, $P < 0.05$). In contrast, there was no significant difference in abundance of adults before and after the winter (*t*-test after log transformation, $P > 0.05$). Size of adults ranged from 30 to 50 mm near Rømø and from 50 to 70 mm near Sylt.

Discussion

In the severe winter of 1995/96, ice floes of about 1–2 m in thickness (observed maximum 2.7 m) developed in the intertidal zone of the northern Wadden Sea. Floes usually consisted of frozen seawater onto which snow soaked in seawater became deposited. The high thickness of floes was achieved by piling up one floe onto another during tidal drift processes: a floe coming to rest by friction on the sediment surface is overtopped by another in the course of the rising tide. This process may repeat itself during subsequent tides. It may also occur that one floe slides underneath another. As a result, floes resembling little icebergs are drifting forth and back, driven by tidal currents and the wind.

These 'icebergs' scour the sediment surface (Fig. 6). Depressions down to 25 cm into the sediment have been measured. The elevated, reef-like mussel beds present obstacles in the way of the scouring floes. Their tracks are very conspicuous on mussel beds, leaving an aisle of bare mud without mussels, closely resembling the effects of dredging by the commercial mussel fishery. Removal of mussels may also occur when ice floes become stranded onto mussel beds with the falling tide. Bladder wrack (*Fucus vesiculosus*) attached to mussels by byssus threads (see Albrecht 1998) may adhere to the floes from underneath. When the subsequent rising tide is lifting the floes, clumps of wrack with mussels may be carried away, leaving a gap where a continuous cover of mussels had been.

Fig. 6 Ice floes of up to 2 m height and scouring tracks generated by drifting floes during the winter of 1995/96 in Königshafen



The above are all personal observations made during the winter 1995/96 and earlier ones with conspicuous ice cover. Effects of ice-rafting have been described also on the ribbed mussel *Geukensia demissa* and furoid algae from New England salt marshes (Hardwick-Witman 1985). Our present results indicate that in the winter 1995/96 these mechanical effects of ice floes were the primary cause for the decline of mussels in the tidal zone. On those parts of the mussel beds where the surface structure was without any visible traces of ice floes, abundance and biomass were in the same ranges as reported earlier from these beds (Asmus 1987; Reise et al. 1994; Hertzler 1995). Thus it seems that mortality by lethal temperatures was low until March, immediately after the ice had gone. However, we cannot exclude the possibility of a time-lag in mortality caused by sublethal effects of the winter. A strong recruitment on most mussel beds in the subsequent summer masked any direct effects of the preceding winter.

In contrast to lethal temperatures, mechanical effects of the winter were obvious. More than half of the area of the two mussel beds investigated was severely damaged, with aisles and patches lacking mussels in an otherwise continuous carpet of byssus-connected mussels. In addition, the aerial surveys revealed that entire clusters of mussel beds had vanished from the tidal zone, particularly in the southern part of the North Frisian Wadden Sea. This southern part has a higher areal share of tidal flats (Spiegel 1998) and a lower salinity than the north (Becker 1998). It is therefore conceivable that a stronger ice de-

velopment caused more detrimental scouring effects in the south than in the north, whereas temperature differences causing differential mortality in mussels are unlikely to occur within this homoclimatic region of 80 km in length (see Riecke 1998).

Nehls and Thiel (1993) reported negative effects of heavy storms on the persistence of intertidal mussel beds in the North Frisian Wadden Sea. They mapped mussel beds from aerial surveys in 1989 and subsequent to the storms which occurred in spring 1990. The pattern of decline with respect to the presence/absence of clusters of mussel beds is strikingly similar to the one we described for the summers of 1995 and 1996 with the intervening severe winter (see Nehls and Thiel 1993; Fig. 2). In the northern part of the region, islands provide a better shelter against storm disturbances than in the southern part. Apparently, two different, independent causes generated an almost identical spatial pattern in the clusters of mussel beds.

With respect to the low persistence of mussel beds in the southern part of the North Frisian Wadden Sea, the effects of storms and ice are additive. Furthermore, it seems possible that the lower frequency of disturbances in the northern part of the area allows for a more structurally robust development of mussel bed clusters. This would make these beds less susceptible to the effects of storms and may be also to ice floes, constituting an example for a positive feedback mechanism. This may explain why clusters of mussel beds tend to be more extensive in the north than in the south of the North Frisian Wadden Sea. By extrapolation we further suggest that

this may explain why intertidal mussel beds are scarce in the central, more estuarine region of the Wadden Sea lacking chains of barrier islands.

The picture of direct winter effects on intertidal cockle populations of the Wadden Sea is very different from the one for mussels described above. The winter of 1995/96 caused a mass mortality among *Cerastoderma edule* of at least 80% of the intertidal population. This rate was determined immediately after melting of the ice in March 1996 and it might be an underestimate since the mortality rate had increased to 98% by October 1996. Kristensen (1957) and Jepsen (1965) similarly noted a time-lag effect in the mortality of cockles subsequent to severe winters. They both suggest that a sudden rise of temperature following cold winters caused more mortality than the frost before. We do not know whether the mortality between March and October can be attributed to sublethal winter effects or whether it was mainly caused by other factors such as predation or parasitism. In any case, these results stress the need to take sublethal effects into consideration when the effects of severe winters are to be assessed. With a population decline of 80–98% in the intertidal zone, the reduction of cockles after the winter of 1995/96 is similar to other severe winters of the last century. Complete or nearly complete extinctions of cockles in the Wadden Sea were also reported after the winters of 1927/28, 1941/42, 1946/47, and 1978/79 (Smidt 1944, 1951; Kristensen 1957; Beukema 1979; Dörjes 1980; Reise 1985).

Despite the near extinction of the intertidal population around Sylt by the winter ice, a high recruitment of cockles was observed in summer 1996 (Strasser et al. 2001). Most likely the recolonization of the intertidal flats depended on larval production of subtidal populations which must have survived the winter of 1995/96.

Mortality rate was to some extent dependent on tidal level and size of the cockles. The higher mortality rates at higher tidal levels confirm the results of Beukema (1985) who found 100% cockle mortality only in the high intertidal after the severe winter of 1978/79. This pattern was expected since freezing air temperatures will act both longer and more frequently on the higher tidal flats. At two sites in the low intertidal, survival was better among bigger specimens. Perhaps this may be explained by higher energy reserves of bigger specimens, leading to higher resistance to cold temperatures.

It is quite surprising that we found the highest abundances of cockles in the high intertidal. For instance, Beukema (1985) found high cockle densities only below mean tidal level. This poses the question of whether, in our study, cockles were transported across the tidal levels by drifting ice. However, this is unlikely because, firstly, at the upper sampling sites for cockles no traces of ice drift could be observed and, secondly, the average size of the cockles increased with increasing submersion time which is in line with the general growth pattern on tidal flats (Reise 1985).

Abundance of juvenile *Mya arenaria* was significantly lower after the ice winter of 1995/96 than before the

winter, but spat was not completely eliminated as reported by Kühl (1951) for the winter of 1947/48. In fact, the mortality rates of 67% and 75% correspond well with the average winter mortality rates of *Mya* <2 cm (69% to 99%) observed over a period of 11 years in the Dutch Wadden Sea (Beukema 1979). Abundance of adult *Mya* in the Sylt-Rømø Bight was not affected by the winter of 1995/96 which confirms Kühl (1951) and Beukema (1979). The nearly extinction of *Mya* after the winter of 1941/42 (Smidt 1944) remains the only record from the Wadden Sea where an adult *Mya* population was seriously harmed by a severe winter. In conclusion, both adult and juvenile *Mya* were not unusually affected by the ice winter of 1995/96 and the classification of a hard-winter species in the Dutch Wadden Sea (Beukema 1990) is also justified for the northern Wadden Sea.

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References

- Albrecht AS (1998) Soft bottom versus hard rock: community ecology of macroalgae on intertidal mussel beds in the Wadden Sea. *J Exp Mar Biol Ecol* 229:85–109
- Asmus H (1987) Secondary production of an intertidal mussel bed community related to its storage and turnover compartments. *Mar Ecol Prog Ser* 39:251–266
- Bahr K (1950) Die Ergebnisse der Miesmuscheluntersuchungen an der Ostfriesischen Küste in den Jahren 1947–1950. *Veröff Inst Küst Binnenfisch* 68:1–29
- Becker G (1998) Der Salzgehalt im Wattenmeer. In: Nationalparkamt Schleswig-Holsteinisches Wattenmeer and Umweltbundesamt (eds) *Umweltatlas Wattenmeer*, vol 1. Ulmer, Stuttgart, pp 60–61
- Blegvad H (1929) Mortality among animals of the littoral region in ice winters. *Rep Dan Biol Stn* 35:49–62
- Beukema JJ (1979) Biomass and species richness of the macrobenthic animals living on a tidal flat area in the Dutch Wadden Sea: effects of a severe winter. *Neth J Sea Res* 13:203–223
- Beukema JJ (1982) Annual variation in reproductive success and biomass of the major macrozoobenthic species living in a tidal flat area of the Wadden Sea. *Neth J Sea Res* 16:37–45
- Beukema JJ (1985) Zoobenthos survival during severe winters on high and low tidal flats in the Dutch Wadden Sea. In: Gray JS, Christiansen ME (eds) *Marine biology of polar regions and effects of stress on marine organisms*. Wiley, Chichester, pp 351–361
- Beukema JJ (1990) Expected effects of changes in winter temperatures on benthic animals living in soft sediments in coastal North Sea areas. In: Beukema JJ, Wolff WJ, Brouns JJWM (eds) *Expected effects of climatic change on marine coastal ecosystems*. (Developments in hydrobiology 57) Kluwer Academic, Dordrecht, pp 83–92
- Beukema JJ (1992) Expected changes in the Wadden Sea benthos in a warmer world: lessons from periods with mild winters. *Neth J Sea Res* 30:73–79
- Bourget E (1983) Seasonal variations of cold tolerance in intertidal mollusks and relation to environmental conditions in the St. Lawrence Estuary. *Can J Zool* 61:1193–1201

- Dörjes J (1980) Auswirkungen des kalten Winters 1978/79 auf das marine Makrobenthos. *Nat Mus* 110:109–115
- Figge K, Köster R, Thiel H, Wieland P (1980) Schlickuntersuchungen im Wattenmeer der Deutschen Bucht – Zwischenbericht über ein Forschungsprojekt des KFKI. *Küste* 35:187–204
- Hardwick-Witman MN (1985) Biological consequences of ice rafting in a New England salt marsh community. *J Exp Mar Biol Ecol* 87:283–298
- Hertzler I (1995) Nahrungsökologische Bedeutung von Miesmuschelbänken für Vögel (Laro-Limikolen) im Nordfriesischen Wattenmeer. Master's thesis, University of Göttingen, Germany
- Jepsen U (1965) Die Struktur der Wattbiozönosen im Vormündungsgebiet der Elbe. *Arch Hydrobiol* 29 [Suppl]:252–370
- Kristensen I (1957) Differences in density and growth in a cockle population in the Dutch Wadden Sea. *Arch Neerl Zool* 12:351–453
- Kühl H (1951) Über die Siedlungsweise von *Mya arenaria*. *Verh Dtsch Zool Ges* 25:385–391
- Martens P (2001) Effects of the severe winter 1995/96 and the biological oceanography of the Sylt-Rømø tidal basin. *Helgol Mar Res* 55. DOI 10.1007/s101520100078
- Muus BJ (1967) The fauna of Danish estuaries and lagoons. *Medd Dan Fisk Havunders* 5:1–316
- Nehls G, Thiel M (1993) Large-scale distribution patterns of the mussel *Mytilus edulis* in the Wadden Sea of Schleswig-Holstein: do storms structure the ecosystem? *Neth J Sea Res* 31:181–187
- Obert B, Michaelis H (1991) History and ecology of the mussel beds (*Mytilus edulis* L.) in the catchment area of a Wadden Sea tidal inlet. In: Elliott M, Ducrotot J-P (eds) *Estuaries and coasts: spatial and temporal intercomparisons*. Olsen and Olsen, Fredensborg, pp 185–194
- Rasmussen E (1973) Systematics and ecology of the Isefjord marine fauna (Denmark). *Ophelia* 11:1–507
- Reise K (1985) *Tidal flat ecology*. Springer, Berlin Heidelberg New York
- Reise K, Lackschewitz D (1998) Benthos des Wattenmeeres zwischen Sylt und Rømø. In: Gätje C, Reise K (eds) *Ökosystem Wattenmeer, Austausch-, Transport- und Stoffumwandlungsprozesse*. Springer, Berlin Heidelberg New York, pp 55–64
- Reise K, Herre E, Sturm M (1994) Biomass and abundance of macrofauna in intertidal sediments of Königshafen in the northern Wadden Sea. *Helgol Meeresunters* 48:201–215
- Riecke W (1998) Lufttemperatur. In: Nationalparkamt Schleswig-Holsteinisches Wattenmeer and Umweltbundesamt (eds) *Umweltatlas Wattenmeer, vol 1*. Ulmer, Stuttgart, pp 64–65
- Smidt ELB (1944) The effects of icewinters on marine littoral faunas. *Folia Geogr Dan* 2(3):1–36
- Smidt ELB (1951) Animal production in the Danish Waddensea. *Medd Dan Fisk Havunders (Ser Fisk)* 11:1–151
- Spiegel F (1998) Volumina von Tidebecken im nordfriesischen Wattenmeer. In: Nationalparkamt Schleswig-Holsteinisches Wattenmeer and Umweltbundesamt (eds) *Umweltatlas Wattenmeer, vol 1*. Ulmer, Stuttgart, pp 46–47
- Strasser M, Walensky M, Reise K (1999) Juvenile-adult distribution of the bivalve *Mya arenaria* on intertidal flats in the Wadden Sea: why are there so few year classes? *Helgol Mar Res* 53:45–55
- Strasser M, Hertlein A, Reise K (2001) Differential recruitment of bivalve species in the northern Wadden Sea after the severe winter of 1995/96 and of subsequent milder winters. *Helgol Mar Res* 55. DOI 10.1007/s101520100080
- Strübing K (1996) The ice winter of 1995/96 on the German coasts between Ems and Oder, with a survey of the entire Baltic area. *Dtsch Hydrogr Z* 48:73–87
- Theede H (1965) Vergleichende experimentelle Untersuchungen über die zelluläre Gefrierresistenz mariner Muscheln. *Kiel Meeresforsch* 21:153–166
- Theede H, Lassig J (1967) Comparative studies on cellular resistance of bivalves from marine and brackish waters. *Helgol Wiss Meeresunters* 16:119–129
- Ziegelmeier E (1964) Einwirkungen des kalten Winters 1962/63 auf das Makrobenthos im Ostteil der Deutschen Bucht. *Helgol Wiss Meeresunters* 10:276–282