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ORIGINAL ARTICLE

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Effects of the severe winter 1995/96 on the benthic macrofauna of the Wadden Sea and the coastal North Sea near the island of Sylt

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Abstract The development of benthic macrofauna in the Wadden Sea and in the coastal North Sea after the severe winter of 1995/96 is compared with the preceding years with mild to moderate winters. In the intertidal of the Wadden Sea, ice-drift and low temperature caused the expected changes in species composition by increasing winter mortality in sensitive species, and by exceptionally high recruitment of some species during the succeeding summer. In the shallow subtidal (10–20 m depth), similar winter effects were observed. However, recovery of many subtidal populations was still incomplete until the summer of 1997. It is suggested that this was due to hydrographic conditions that carried many larvae or drifting juveniles into more distant offshore areas. This may have limited larval supply and may have delayed recovery at the onshore sites. Since in the eastern North Sea severe winters are accompanied by frequent easterly winds, it is not clear whether decreasing winter abundances in some species were due to increased mortality, or to a seaward dislocation of organisms.

Keywords Macrofauna · Wadden Sea · North Sea Winter

Introduction

About a third of the macrobenthic species living on the tidal flats of the Wadden Sea are sensitive to low winter temperature (Beukema 1990). Their overwinter survival and abundance are lower after a severe winter than after normal or mild winters. However, some species recruit exceptionally well after cold winters. In part, this may be due to a higher number of eggs produced, which is likely to result from a lower metabolic energy expenditure during cold winters (Honkoop and van der Meer 1998). On the other hand, after cold winters epibenthic predators such as shore crabs (*Carcinus maenas*) or shrimps (*Crangon crangon*) are less abundant in the intertidal, and they return to the tidal flats with a delay of up to 6 weeks (Beukema 1991, 1992). Meanwhile their prey organisms are partly released from predation pressure, resulting in increased juvenile survival (Reise 1985). Therefore many species may compensate for increased winter mortality during the subsequent summer.

Increasing water depth will suppress short-term temperature extremes and ice formation. Therefore the effects of winter cold are expected to be less pronounced in the subtidal, although some subtidal species such as *Echinocardium cordatum* are sensitive to low temperature as well (Ziegelmeier 1964, 1970; Beukema 1985; Beukema et al. 1988). As winter cold affects the entire Wadden Sea (although with some latitudinal differences), temperature may be a synchronising agent causing common patterns of abundance fluctuations over wide geographical areas (e.g. Beukema and Essink 1986). Therefore the changes observed near the island of Sylt during the severe winter of 1995/96 [see Martens (2001) for a meteorological characterisation] are expected to be representative of the northern Wadden Sea.

Methods

Between 1992 and 1997, the macrozoobenthos of several coastal areas near the island of Sylt was sampled for long-term trends. This included intertidal flats (*Arenicola* sandflats, mussel and seagrass beds in Königshafen, Fig. 1: inset) and three subtidal areas, one in the Wadden Sea (fine sand east of Königshafen, water depth 10 m; Fig. 1) and two in the coastal North Sea (an onshore area 5 km west of Sylt, and an offshore area 20 km west of Sylt; both fine sands, water depth 10 and 20 m, respectively; Fig. 1). Samples (10 box cores of 200 cm^2 intertidally and 24 subtidally per station and date) were collected twice a year in April and September. Intertidal *Zostera* beds were only sampled once annually in July. The sediment was sieved through 1 mm square meshes and the residual organisms determined to species level and counted.

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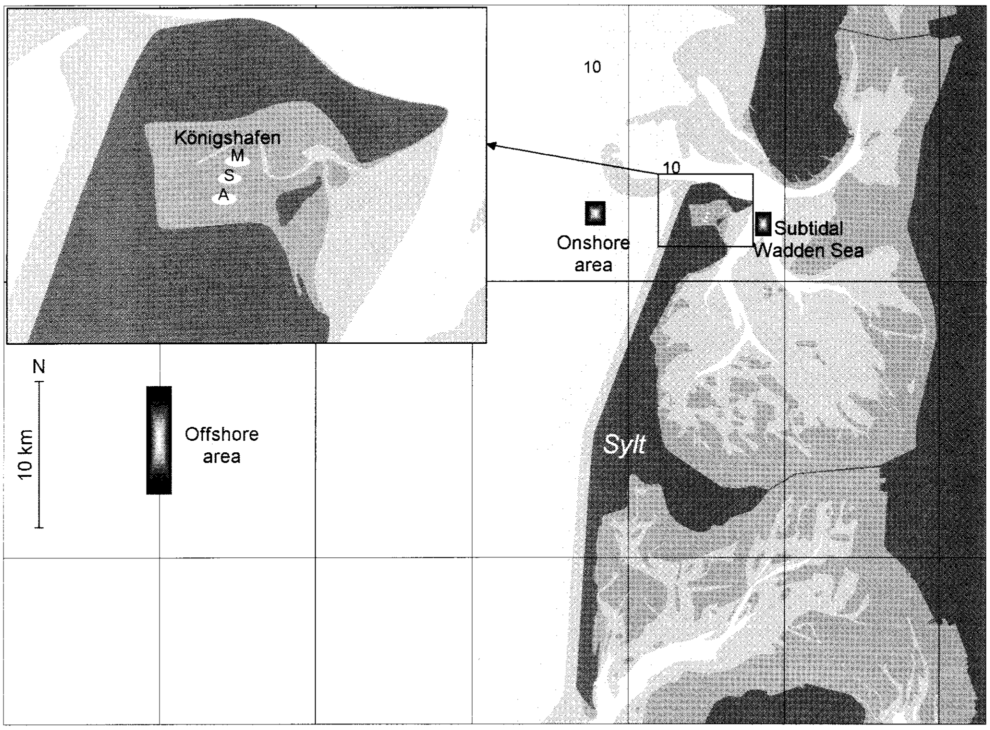

Fig. 1 Areas near the island of Sylt in the eastern North Sea sampled regularly for macrozoobenthos between 1992 and 1996. *M* Mussel bed, *S* Seagrass bed, *A Arenicola* sandflat. Further details in the text

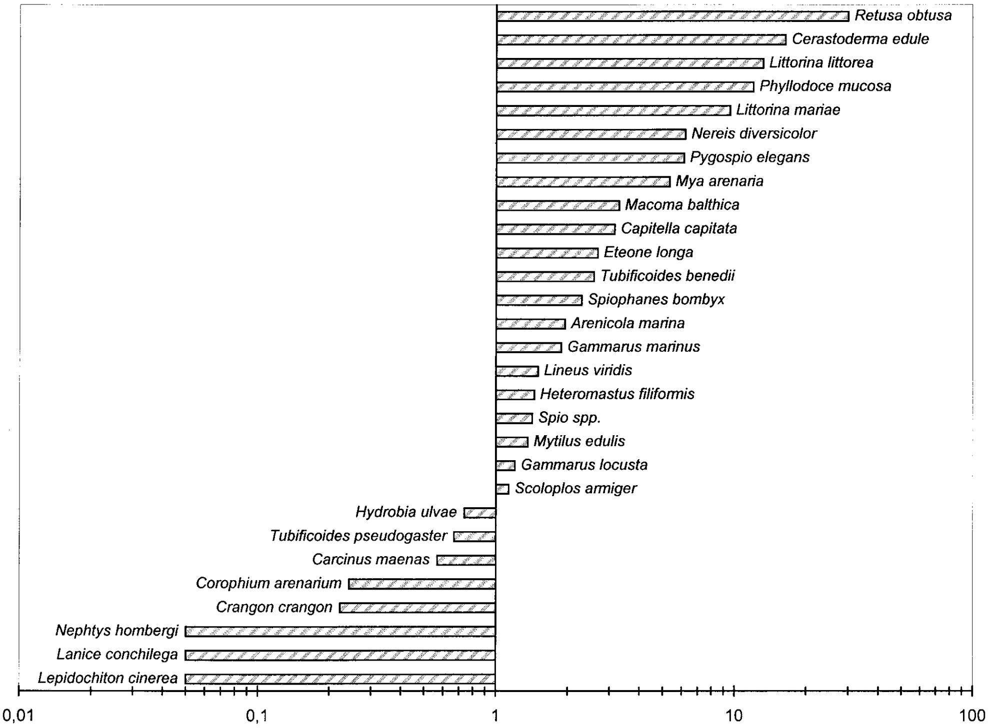

Fig. 2 Relative abundance of macrozoobenthos in the Königshafen intertidal (deviation of the 1996 annual mean from the mean of the 1992–1995 period which was set to unity). The annual means are unweighted averages of all three habitats studied, viz. mussel beds and sand flats (April and September data) and *Zostera* beds (July only), thus combing the effects of winter mortality and following recruitment.

Results

The severe winter of 1995/96 affected the habitats differently. The intertidal sites showed the well known effects on those species sensitive to low temperature. In spring of 1996 the abundance of *Nephtys hombergii*, *Lanice conchilega* and *Lepidochiton cinerea* was down to almost nothing while the abundance of *Corophium arenarium* and *Crangon crangon* was <50% of the 1992–1995 mean (Fig. 2). Other species directly or indirectly profited from the low winter temperature. Apart from *Mytilus edulis* beds which were strongly eroded by drifting ice, the September abundance of molluscs was above the mean of the previous years (Fig. 2). As indicated by age

Table 1 Abundance (m^{-2}) of frequent macrozoobenthic species in a subtidal fine sand community in the Wadden Sea near the island of Sylt during a period with mild to average winters (1992–1995) and after the cold winter of 1995/96

Species	1992–1995	1996–1997	Comments
Polychaeta			
Capitella capitata	13	96	Increased since 1994
Capitella minima	63	52	ns[a]
Magelona mirabilis	39	3	Decreased since 1992
Nephtys spp.	88	2	Sharp decline, slow recovery
Scoloplos armiger	42	92	ns
Spio spp.	51	23	ns
Bivalvia			
Ensis americanus	761	784	ns
Macoma balthica	19	49	Increased recruitment success in 1996

[a] No significant change

Table 2 Abundance (m^{-2}) of frequent macrozoobenthic species in a subtidal fine sand community 5 km west of the island of Sylt during a period with mild to average winters (1992–1995) and after the cold winter of 1995/96

Species	1992–1995	1996–1997	Comments
Polychaeta			
Capitella capitata	7	137	High abundance in September 1996, dropped to background level in 1997
Capitella minima	114	341	High abundance in September 1996, dropped to background level in 1997
Eteone longa	43	36	ns[a]
Eumida sanguinea	45	0	Vanished
Lanice conchilega	156	5	Sharp decrease, slow recovery
Magelona mirabilis	2901	138	Sharp decrease, slow recovery
Nephtys spp.	200	48	Sharp decrease, slow recovery
Pectinaria koreni	107	54	ns
Phyllodoce mucosa	96	90	ns
Scoloplos armiger	451	2072	High abundance in September 1996, dropped to background level in 1997
Spio spp.	141	167	ns
Spiophanes bombyx	1792	345	Decreased since 1994
Amphipoda			
Urothoe poseidonis	74	2	Sharp decrease, no recovery
Bivalvia			
Cerastoderma edule	8	388	High abundance in September 1996, dropped to background level in 1997
Ensis americanus	582	26	No recruitment in 1996 and 1997
Fabulina fabula	806	103	Sharp decrease, slow recovery
Macoma balthica	58	46	ns
Mysella bidentata	32	6	Decreased since 1992
Spisula subtruncata	36	0	Vanished

[a] No significant change

composition, this was due to increased recruitment. Abundance increases of many annelids (e.g. *Phyllodoce mucosa*, *Nereis diversicolor*, *Capitella capitata*) coincided with a low abundance of the epibenthic predators *Carcinus maenas* and *Crangon crangon*. In summary, the severe winter of 1995/96 initially caused a strong decline in many benthic populations in the Königshafen intertidal, but this was compensated for by an exceptional recruitment success until September. As a result, the average abundance of macrobenthos in the Königshafen intertidal (125,000 individuals m^{-2} and 29 species in 1996) was nearly the same as the mean of the preceding years (129,000 m^{-2}, 30 species).

There was no unusual change in the macrozoobenthos of the subtidal Wadden Sea area (fine sand, 10 m depth) during the winter of 1995/96 (Table 1). This area is rather exposed to currents, and in the long run, abundance and the species composition seem to be more affected by hydrography than by temperature. In part, this may be due to the dominance of rather large sized and long living species such as razor-clams, *Ensis americanus*. Amphipods, on the other hand, had a low abundance

Table 3 Abundance (m^{-2}) of frequent macrozoobenthic species in a subtidal fine sand community 20 km west of the island of Sylt during a period with mild to average winters (1992–1995) and after the cold winter of 1995/96

Species	1992–1995	1996–1997	Comments
Nemertini			
Tubulanus linearis	556	81	Sharp decline, slow recovery
Phoronida			
Phoronis muelleri	6775	0	Vanished
Polychaeta			
Capitella capitata	0	133	High abundance in September 1996, vanished again in 1997
Capitella minima	21	170	High abundance in September 1996, dropped to background level in 1997
Chaetozone setosa	73	67	ns[a]
Eteone longa	50	69	ns
Eumida sanguinea	336	31	Strong decline
Lanice conchilega	131	1926	High abundance in September 1996, dropped to background level in 1997
Magelona mirabilis	1384	68	Decreased continuously since 1992
Nephtys spp.	105	20	Sharp decline, slow recovery
Owenia fusiformis	447	0	vanished
Pectinaria koreni	14	1442	High abundance in September 1996, dropped to background level in 1997
Phyllodoce mucosa	42	114	High abundance in September 1996, dropped to background level in 1997
Polydora pulchra	87	6	Sharp decrease
Scoloplos armiger	66	953	High abundance since September 1996
Spio spp.	592	17	Vanished, slow recovery in 1997
Spiophanes bombyx	104	395	High abundance in September 1996, dropped to background level in 1997
Amphipoda			
Bathyporeia guilliamsoniana	119	15	Decreased since 1993
Pariambus typicus	32	0	Increased until 1994, then decreased again
Urothoe poseidonis	113	44	Sharp decline, slow recovery
Gastropoda			
Lunatia nitida	33	0	Vanished
Bivalvia			
Ensis americanus	2	628	High abundance in September 1996, dropped to background level in 1997
Fabulina fabula	219	128	Sharp decrease, recovery in 1997
Spisula subtruncata	34	0	decreased since 1993
Echinodermata			
Echinocardium cordatum	40	50	Sharp decrease, 1996 recruitment not successful
Ophiura ophiura	49	100	ns

[a] No significant change

throughout 1996 and did not reach the level of previous years until September. It is not clear, however, whether their low abundance was really caused by winter cold (see below).

In the coastal North Sea ('onshore area', 5 km west of the island) abundance and species density of macrozoobenthos showed long-term minima in 1996. However, this had already been preceded by unusually low values in the previous autumn. The percentage winter decrease in abundance was in the same order of magnitude as in previous years. However, dominance changed. In some bivalves (*Ensis americanus*, *Fabulina fabula* and *Spisula subtruncata*) over-winter survival was low, as was recruitment in summer 1996 (Table 2). At the same time, cockles (*Cerastoderma edule*) showed an exceptionally high recruitment in this area (>1,000 m^{-2}). Since cockles were very rare in the previous years, it is suspected that either larvae, or byssus-drifting postlarvae, were imported into this area from the Wadden Sea. This implies a high recruitment in the Wadden Sea (as was actually observed, Fig. 2) and a hydrographic situation facilitating a seaward transport of specimens in early summer. The latter seems to be corroborated by benthic development in the offshore area (Table 3) showing exceptional recruitment of species that were rare in previous years but had been abundant in the onshore area (i.e. *Lanice conchilega*, *Pectinaria koreni* and *Ensis americanus*).

Discussion

In the intertidal of the Wadden Sea the cold winter of 1995/96 resulted in the expected changes in species composition as caused by ice-drift, low temperature, and exceptional recruitment of some species during the following summer (also see Strasser et al. 2001b). Some species sensitive to low temperature vanished while others increased in abundance. Presumably, the latter took advantage of the low abundance of epibenthic predators. This is exactly what occurred in the western part of the Wadden Sea after cold winters in previous years (e.g. Beukema and Essink 1986). In the Königshafen intertidal, the bivalves *Macoma balthica* and *Mya arenaria* recruited to a higher abundance than the average of the 1992–1995 period (Fig. 2). However, this was not generally the case. Considering a larger area (i.e. the western part of the Sylt-Rømø Bight) the 1996 recruitment of both species was lower than average (Strasser et al. 2001a).

Despite the damping of temperature extremes by a large volume of water, the effects of winter cold were comparable in the subtidal sites. Some species showed a sharp decline in abundance or even vanished from our samples (e.g. *Phoronis muelleri*, *Eumida sanguinea*, *Owenia fusiformis*, *Polydora pulchra*, *Lunatia nitida* and *Fabulina fabula*), while others showed temporary increases in the summer of 1996 but mostly fell to background level in 1997 (e.g. *Capitella capitata*, *Pectinaria koreni*, *Lanice conchilega* and *Ensis americanus* in the offshore area, and *Cerastoderma edule* in the onshore area). The same occurred after previous cold winters (Ziegelmeier 1964, 1970). Finally, some species seemed to be virtually unaffected by winter cold (e.g. *Chaetozone setosa* and *Eteone longa*).

The unusually high recruitment of *Pectinaria koreni* and *Ensis americanus* in the offshore area was accompanied by an unusually low recruitment of the same species in the onshore area. Offshore currents might have transported the larvae of both species towards the deeper water areas. Indeed, the March of 1996 was characterised by a rather stable weather situation with easterly winds inducing superficial currents in a north to north-westward direction. Though the wind direction varied until June, residual currents kept a north or westward direction during most of that time (MURSYS 1996). The North Atlantic Oscillation index (NAO), as an index orchestrating hemispheric-scale climatic fluctuations centred over the northern Atlantic, was negative until May as well (as was the case during the preceding winter). This indicates that the wind onto Europe had a relatively weak westerly component and, in turn, a relatively strong easterly (continental) one. Therefore larval transport in an offshore direction seems a plausible explanation for the observed patterns. Likewise, Ziegelmeier (1964) observed *Macoma balthica* recruiting unusually far seaward after the cold winter of 1962/63.

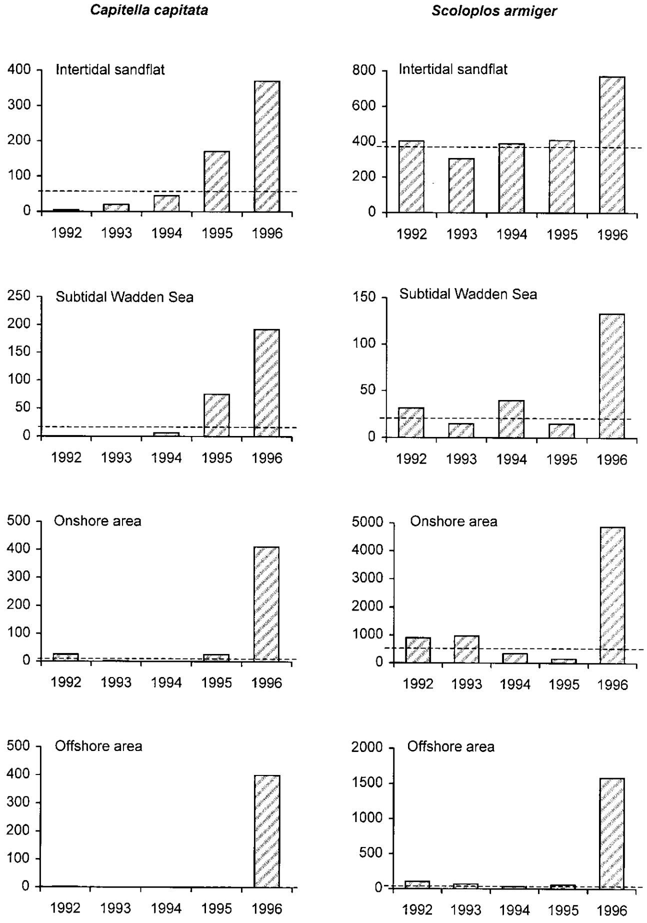

Fig. 3 Abundance (m^{-2}) of the polychaetes *Capitella capitata* and *Scoloplos armiger* in four areas near the island of Sylt, September 1992 to September 1996. The *dashed lines* indicate the mean of the 1992–1995 period with mild to moderate winter temperatures.

Offshore currents may also have caused high imports of *Cerastoderma edule* from the Wadden Sea into the coastal North Sea. However, once offshore currents are evoked to explain unusual imports of larvae, the same currents may have exported some species towards deeper waters by benthic drift. In particular, some amphipods such as *Bathyporeia* spp. or *Urothoe poseidonis*, vanished from the coastal area during the summer of 1996 and did not, or only in a very reduced abundance, return in 1997. Thus, decreasing abundances must not exclusively be attributed to winter cold, but might partly be explained by offshore organism transport. In addition, during cold winters, some species might swim actively towards the deeper and warmer offshore waters. However, many benthic species may not be able to cover large horizontal distances by active swimming. In the Sylt area, for example, the 10 and 20 m isobaths are about 20 km apart, on average.

During the summer of 1996 the polychaetes *Capitella capitata* and *Scoloplos armiger* attained a higher abundance in all of the four areas studied (Fig. 3). However, compared with other polychaetes, their abundance increases were rather low in the intertidal. Both species showed a stronger increase of abundance in the subtidal Wadden Sea and the degree of abundance increases amplified in the seaward direction in the coastal North Sea (Fig. 3). Considering offshore currents, could this pattern similarly have derived from transportation of organisms? This might explain why both species benefited to such a low degree from the low abundance of predators in the intertidal during the summer.

In conclusion, we suggest that the hitherto known ‘typical effects of severe winters’ may be a complex mixture of temperature effects on the one hand and hydrographic peculiarities on the other. Both factors are causally linked by large-scale atmospheric fluctuations. Thus, easterly (continental) wind during winter may decrease the populations of sensitive species either by increasing mortality, or by offshore dislocation with offshore currents, or both. Concerning recovery, the hydrographic situation during spring is likely to be a key factor (Belgrano and Dewarumez 1995; Belgrano et al. 1995). Studying a limited area we may find ‘unusually low recruitment’ if the currents carry the larvae beyond the studied area, while recruitment may be ‘exceptionally high’ if the currents tend to concentrate the larvae, or result in imports of larvae from elsewhere. Because the species vary both in the duration and the seasonal timing of the larval stage, the hydrographic influence on the spatial distribution of larvae will vary with species. Accordingly, recovery from winter losses will vary over species as well, and there is no single common spatial pattern of recruitment.

Until now, neither the direction nor the horizontal distance of organism dislocations with the tidal currents can be precisely predicted. This is because both are strongly influenced by the behaviour of the drifting organisms, particularly with respect to vertical migrations in the water column (Hill 1991a, b). Thus, while offshore wind may result in offshore transports of specimens residing close to the water surface, near-bottom compensatory currents may, at the same time, lead organisms residing close to the sediment in an opposite direction. In order to predict the direction and distance of transportations we need both a detailed knowledge on the vertical position of the organisms in the water column and a 3-dimensional hydrographic model of the region under study. Then we may not only be able to separate the 'true' effects of winter cold from the effects of hydrography but also predict larval supply and the large-scale spatial pattern of benthic organisms.

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