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Community dynamics of intertidal soft-bottom mussel beds over two decades

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Abstract Macrozoobenthos communities in the North Sea showed pronounced changes over the past decade in relation to an increasing number of invasive species and climate change. We analysed data sets spanning 22 years on abundance, biomass and species composition of intertidal soft bottom mussel beds near the island of Sylt (German Bight) in the Northern Wadden Sea, based on surveys from 1983/1984, 1990, 1993 and from 1999 to 2005. Mussel bed area and blue mussel biomass decreased, and a change in the dominance structure in the associated community comparing 1984 to mid-1990s with the period from 1999 to 2005 was observed. Coverage of the mussel beds with the algae *Fucus vesiculosus* decreased since the end of the 1990s. Within the study period biomass and densities of the associated community increased significantly. Dominance structure changed mainly because of increasing abundances of associated epibenthic taxa. Apart from the Pacific oyster *Crassostrea gigas* all other alien species were already present in the area during the study period. Community changes already started before Pacific oysters became abundant. An attempt is made to evaluate effects on the observed changes of decreasing mussel biomass, ageing of mussel beds, decreasing fucoid coverage and increasing abundances of

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invader. All four factors are assumed to contribute to changing community structure of intertidal mussel beds.

Introduction

Worldwide, coastal systems have undergone dramatic changes in recent decades, in particular due to eutrophication, climate change and introduced species (Valiela 2005; Philippart et al. 2007). Eutrophication often increases primary production and climate variations may enhance or depress recruitment success (Hagberg et al. 2004; Philippart et al. 2007). Global warming is expected to accelerate the establishment of non-indigenous species in North Sea waters (Stachowicz et al. 2002; Diederich et al. 2005).

Surveys in the Wadden Sea and adjacent North Sea documented major changes of macrobenthic communities in the past decades (Reise 1982, Beukema 1991, 1992). Kröncke et al. (2001) described how climate oscillations influence the occurrence and density of subtidal macrozoobenthos in the southern North Sea, with significant increases in species number, abundance and biomass after mild winters. Franke and Gutow (2004) and Reichert and Buchholz (2006) documented changes of the inter- and subtidal hard-bottom macrozoobenthos community at Helgoland since 1984, recording losses of species as well as the immigration of southern species.

Invasive species contribute significantly to community changes in the Wadden Sea (Nehring and Leuchs 1999; Reise et al. 2005). The introduced Pacific oyster (*Crassostrea gigas*) and the American slipper limpet (*Crepidula*

fornicata) have become abundant on blue mussel beds (*Mytilus edulis*) in the entire Wadden Sea (Thieltges et al. 2003; Diederich 2005; Smaal et al. 2005), particularly in the past 5 years. An increasing number of former mussel beds are now overgrown by oysters forming massive reefs (Diederich 2005, Nehls and Büttger 2007). At the same time, mussel bed area has decreased strongly, because of a lack of recruitment in some areas (de Vlas et al. 2005, Nehls et al. 2006).

Mussel beds are complex entities that provide refuge and suitable habitat for an array of associated organisms (e.g. Suchanek 1980; Tsuchiya and Nishihira 1985, 1986). Blue mussel beds on soft bottoms can be classified as autogenic ecosystem engineers, being a habitat distinctly different from the surrounding tidal flats (Jones et al. 1994; Busch-baum and Saier 2001; Crooks 2002; Gutiérrez et al. 2003). Soft bottom intertidal mussel beds in the Wadden Sea are centers of high diversity (Asmus 1987; Dittmann 1990; Albrecht and Reise 1994), providing substrate for attachment and refuge as well as habitat for many endobenthic species. Biomass and species richness are usually much higher than on surrounding tidal flats. The associated fauna, as well as the mussels themselves, form a rich food source for many predators, such as crabs, starfish and birds (e.g. Beukema 1991; Thiel and Dernedde 1994; Hertzler 1995).

Most field studies and experiments on community structure and dynamics of mussel beds have been short term. Yet, long-term variations and gradual changes in the environment, erratic spatfalls and strong effects of storms or ice cover during winter (Nehls and Thiel 1993; Reise et al. 1994; Strasser et al. 2001) also need to be considered.

In this paper, we present for the first time a long-term study analysing the community structure of intertidal mussel beds in the Wadden Sea, relying on a series of studies from 1983 to 2005.

This data set allowed us to raise the following questions: (1) Did the physical structure of the mussel bed change in terms of area or mussel density and biomass? (2) Did the associated community change in terms of composition and/or abundances? and (3) Did the community respond to structural changes or introduced species?

Methods

Study site

All data analysed in this long-term comparison were obtained in Königshafen, a shallow tidal bay comprising about 4.5 km^2 of intertidal flats near the island of Sylt in the northern Wadden Sea (south-eastern North Sea, German Bight; Fig. 1). The tides are semi-diurnal with an average range of about 2 m. Salinity remains close to 30 psu and mean water temperature is 15°C in summer and

Fig. 1 Study area in the Wadden Sea near the island of Sylt (German Bight). *Inset* shows location of mussel beds, *site 1* (Uthörn Außenwatt) and *site 2* (Odde Watt), in 1989 (*dark grey* = islands and mainland, *light grey* = intertidal, *white* = subtidal areas)
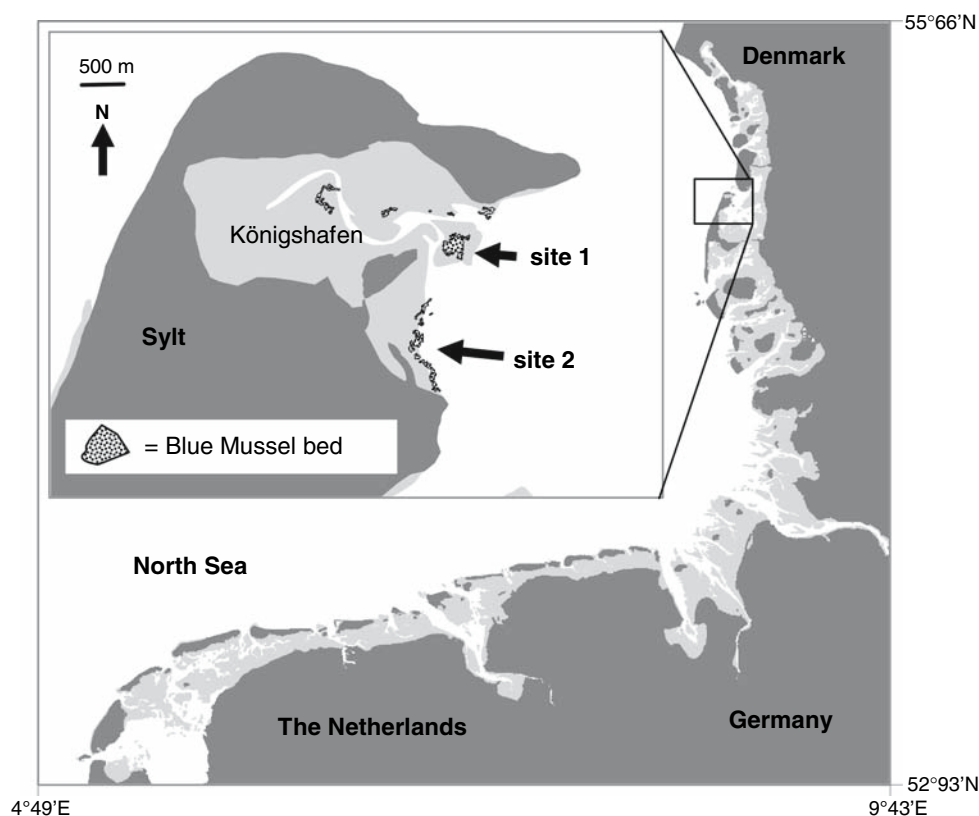
4°C in winter. Detailed information on hydrography, geology, sediments and biota of the area are available from Reise (1985), Austen (1994a, b) and Gätje and Reise (1998). Mussel beds cover up to 5% of the intertidal area of the Königshafen, which is considerably higher than the average of about 1% of the Wadden Sea (de Vlas et al. 2005). Most mussel beds are situated in the outer parts of the Königshafen close to low water line.

Database

Data on mussels and species associated with soft-bottom mussel beds were available from two adjacent beds situated in the eastern part of Königshafen (Fig. 1), which generally were found to be similar in structure, density and biomass of mussels.

This paper is based on four separate studies (Table 1). Sampling was carried out between August and November in each year.

Details in sampling strategy differed between the four studies and mainly relate to the diameter and the depth of the corer and numbers of samples. Corers used by Albrecht (1991) and Hertzler (1995) only reached a sediment depth of 10–15 cm, compared to 30 cm in the other studies; thus a few deeper burrowing endobenthic taxa may be somewhat underrepresented in their samples. However, only very few species occurring on mussel beds in the Wadden Sea burrow deeper than 15 cm, and Albrecht and Reise (1994) did not find living macrofauna below 15 cm. Thus, we regard these methodological differences as less important. Methods used in the first and the most recent study were almost identical, except for the mesh size (Table 1). Since 1999, macrozoobenthos of mussel beds in the study area have been included in a long-term monitoring of blue mussel beds in the Wadden Sea following the standardized methods of the Trilateral Monitoring and Assessment Program (Trilateral Monitoring and Assessment Group 1997). Sample treatment followed common standards in species determination and in measuring biomass as ash-free dry weight. We also used biomass data (Sept 1990, Oct, 1991, April 1992) and densities (Sept. 1990, Oct. 1991) from Nehls and Ketzenberg (2002). Data from 1997 are from Schürmann (1998). Data from both mussel bed sites were pooled.

The mussel beds are located close to the tidal inlet connecting the List tidal basin with the North Sea. Biomass and productivity used to be considerably higher than that in other parts of the Wadden Sea (Asmus 1987; Nehls and Ketzenberg 2002). The structure of the mussel beds analysed in this study was similar in the eighties and nineties, with a mussel cover of 25–30% containing high densities and biomass. Densities and length–frequency distributions were rather similar in the early nineties, when samples were taken on both mussel bed sites (Nehls and Ketzenberg 2002). The mussel bed on site 2 was destroyed by storms in 1998 and last sampled in September 1998, when samples were also taken on site 1. Densities and biomass (live wet weight) in September 1998 were 2,570 ind./m^2 and 12,786 g/m^2 on site 2, and 2,079 ind./m^2 and 13,534 g/m^2 on site 1. *Fucus* coverage was estimated to be about 75% on both sites (G. Nehls, unpubl.). Tidal elevation and sediment characteristics were similar on both sites as well; thus no obvious differences between the sites occurred which could confound changes of associated fauna.

Not all organisms were determined to species level in every year. These inconsistencies required combination of some taxa to ensure consistency. These taxa are Actinaria indet., *Balanus* sp., Cirratulidae indet., *Malacoceros* sp.,

Table 1 Sources of database

Data source	Year of investigation	Mussel bed	Core size (cm^2)	Mesh size of the sieve (mm)	Sample depth (cm)	Sampling method	Data basis
Asmus (1987 and unpubl. data)	1983/1984	Site 2	100	0.5	30	Six sites with five samples each (n = 30)	Mean densities for September to November 1984
Albrecht (1991)	1990	Site 2	500	0.5	15	Six samples within and six outside fucus-covered parts of the mussel bed (n = 12)	Mean densities, samples taken in August 1990
Hertzler (1995)	1993	Site 2	500	1	10–15	Six samples at the edge of the mussel beds, in parts covered with fucus and parts without fucus, respectively (n = 18)	Mean densities, samples taken in August 1993
Mussel monitoring (unpubl. data)	1999–2005	Site 1	113	1	30	Between 1999 and 2002 n = 10 each year, since 2003 n = 25 each year	Mean densities, sampling in September

See Fig. 1 for site location

Nemertea indet., Nephtyidae indet., Neridae indet., *Phyllodoce* sp. and Tellinidae indet.. Data merely given as Spionidae indet., Polychaeta indet. and Phyllodocidae indet. were not included. We did not include Hydrozoa and Bryozoa. Furthermore, we did not incorporate Oligochaeta indet. because of insufficient sampling methods (mesh size) for this group in most years.

Fucus cover

The percentage of the mussel beds covered by *Fucus vesiculosus* forma *mytili* (hereafter, *Fucus*) was estimated visually in the surveys in 1984 and 1990, and additionally by Parusel (1990) in 1988. Since 1998, the cover has been determined in September each year. This special form of *Fucus* does not possess holdfasts, and mussels attach it with their byssus threads (Albrecht and Reise 1994).

Statistical analyses

Data are presented as mean values with standard deviation ($\bar{x} \pm$ SD). Effects of time and blue mussel densities on the density and biomass of the associated fauna were analysed with the rank correlation after Spearman (r_s). Results for effects of time on densities of single species with less than five data-pairs were not included. Effects were considered statistically significant if $P < 0.05$.

For community analysis the PRIMER Program Package v6 was used (Clarke and Warwick 2001). To analyse changes in community composition between years we used a multi-dimensional scaling plot (MDS-plot), basing on the Bray-Curtis similarity. Fourth root transformation (to downplay the effects of very abundant species) was applied prior to analysis.

To describe changes in diversity, we use a sample-size independent version of the Simpson index: SI = Σ $((n^2 - n))/(N^2 - N)$, where n is the number of individuals of a species (Attrill et al. 2001). The index determines the probability (values between 0 and 1) that any two individuals chosen at random belong to the same species. High values indicate dominance by one or very few taxa. Its complement (1—Simpson index) may be taken as an equitability index.

Results

Mussel bed area

Mussels formed dense beds along the low water line of the Königshafen. Area of site 1 was estimated to about 14 ha in

1992 (Nehls and Ketzenberg 2002). Site 1 reached a maximum area of 16 ha in 2000, when 48% of the mussel bed area was covered by mussels. Mussel patches were clearly distinct from the surrounding area and often elevated by 30–50 cm. Mussel bed area decreased during the study period. In 1998 about 13.5 ha were present, but mussel bed area reached the lowest level of 6.2 ha in 2005. Site 2 was destroyed by storms in 1998. Since then, no strong spatfall occurred that could have re-established losses in mussel bed area. This is the reason why data from 1999 onwards were only available from site 1.

Blue mussel biomass and densities

During the time of the first study in 1984, blue mussel biomass reached $1,208 \pm 207$ g AFDW/m^2. Highest values were found 8 years later in 1992, with 1,838 g AFDW/m^2. In later years, biomass dropped to a third of that found in the beginning of the 1990s (Fig. 2a). Lowest biomass values were obtained in 2000 with 259 ± 170 g AFDW/m^2. Mean biomass of both sites decreased significantly in the study period ($r_s = -0.8$, $P < 0.001$)

Mean mussel densities did not decrease significantly (Table 2). Blue mussel densities were highest in 1990 and in 1997/1998 (Fig. 2b), following a strong spatfall in 1996. No comparable spatfall occurred until 2005.
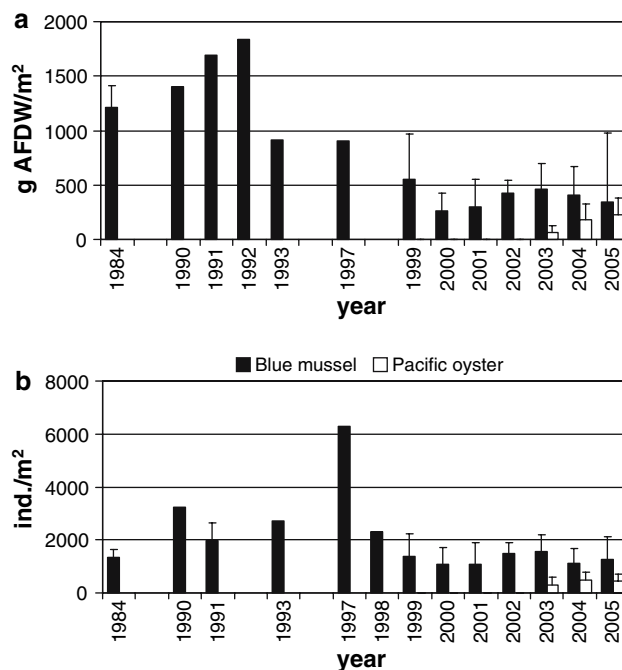

Fig. 2 Mean biomass (+SD) (**a**) and mean densities (+SD) (**b**) of blue mussels *(Mytilus edulis)* and Pacific oysters (*Crassostrea gigas*) on two mussel beds (sites 1 and 2) in Königshafen from 1984 to 2005. SD not available for all years
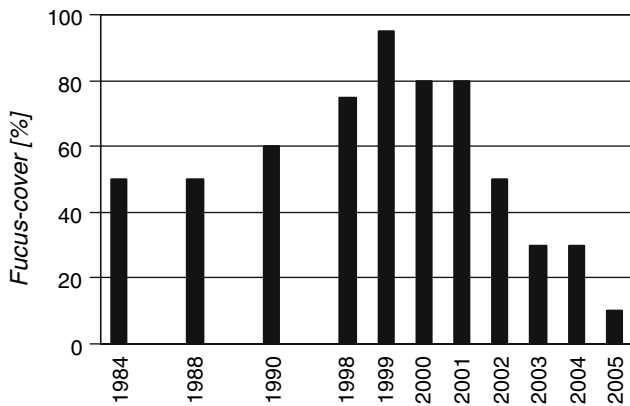
Fig. 3 Changes of *Fucus*-cover (% of the mussel bed area)

Fucus-cover

Considerable parts of the mussel beds were covered by a dense layer of *Fucus*. About half of the mussel bed was covered in the 1980s, and the cover increased in the late 1990s. In 1999 cover was estimated at 95%. Dry mass of the algae was about 730 g/m^2. Since then *Fucus* has decreased with only 10% cover remaining in 2005 (Fig. 3).

Species richness, diversity and patterns of single associated taxa

A total number of 65 taxa were found at least once during the mussel bed surveys (Table 2). The total number of taxa was lower in the first two years (1984 and 1990), with 23 and 25 respectively, whereas 45 taxa were recorded in 2003. In addition to the blue mussels themselves, 12 taxa (*Capitella capitata*, *Heteromastus filiformis*, *Nereididae* indet., *Malacoceros* sp., *Carcinus maenas*, *Jaera albifrons*, *Actinaria* indet., *Littorina littorea*, *Nemertini* indet., *Lepidochitona cinereus*, *Balanus* sp. and *Cirratulidae* indet.) occurred in all years. Records of 13 taxa in single years (with low mean densities) can be considered as rare.

Twenty-nine taxa which were not recorded in the first three surveys appeared between 1999 and 2005. Thirteen of these were found in 1 year only and at low densities. Another 11 of these 29 taxa occurred in 2 or 3 years in low densities and are regarded as rare as well. *C. gigas* was abundant in all surveys since 2002. Five taxa, H*armothoe imbricata*, *Polynoidae* indet., *Spio filicornis*, *Gammarus locusta* and *Gammarus oceanicus* have occurred since 1999 in at least 4 years, with variable abundances.

Within the study period, no characteristic mussel bed species vanished. Densities of *Chaetogammarus marinus*,

known to be closely associated with fucoid algae on which it is feeding, and *G. locusta* declined significantly ($r_s = -1$, $P = 0$ and $r_s = -0.88$, $P = 0.01$; Table 2). Three polychaete species (*Kefersteinia cirrata*, *Eumida sanguinea* and *Arenicola marina*) which were found in low densities in 1984, 1990 and 1993, have not been recorded since 1999 and are regarded not to be typical for mussel beds.

Examining the number of all taxa determined to species level (Table 2), species richness was lowest in 1984 with 26 species found between September and November. Yet, in total, Asmus (1987) found 38 species during the whole year of his investigation (December 1983–November 1984). Species richness was also low (33 species) in 1990 (10 samples only), but highest (51 species) in 2003 (25 samples). Although richness estimates will be influenced by the variable numbers of samples taken in the different studies, the doubling of species from autumn 1983 (90 samples of 100 cm^2) to 2003 (25 samples of 78.5 cm^2) may indicate an increase.

The Simpson-index (*M. edulis* and *C. gigas* were not included) increased from 0.17 in 1984 to 0.76 in 2005. The values fluctuated slightly between 1999 and 2005, but they were always above 0.5, and clearly higher than in 1984, 1990 and 1993. This reflects an increasing dominance by a few species, and equitability declined respectively.

Biomass and densities of associated fauna

Overall, mean density of associated macrozoobenthos showed a significant positive trend over time ($r_s = 0.87$, $P < 0.001$). Mean densities were comparatively low in 1984 and high since 2002, apart from 2004 (Fig. 4). This density increase came along with a biomass increase ($r_s = 0.78$, $P < 0.05$). Densities of the associated community did not correlate with mussel densities ($r_s = 0.03$, $P = 0.47$).

Abundances of the associated community increased due to epibenthic species ($r_s = 0.87$, $P < 0.001$, Fig. 4b). Densities of endobenthic species did not show a significant trend, but were highest in 2003 with high abundances of Polychaeta, mainly of Cirratulidae indet., Nereididae indet. and (most importantly) *Polydora* sp. (see Table 2 for Spearman rank correlation). Barnacles were largely responsible for the overall increase in abundance by epibenthic species, and showed a significant positive trend ($r_s = 0.92$, $P < 0.001$). Densities of barnacles were highest in 2002 with 22,768 ind./m^2 and they formed by far the highest proportion of all individuals.

Regarding those surveys which provided abundance data for different species of barnacles, the temporal patterns of densities differed among species. *Balanus crenatus* and *Semibalanus balanoides* were found in all years.

Table 2 Taxa and their mean densities (ind./m^2) found in the 10 surveys considered, using combinations on a higher taxonomic level if necessary (see text)

Phylum	Class	Scientific name	1984	1990	1993	1999	2000	2001	2002	2003	2004	2005	r_s (t)	r_s (M. e.)
Cnidaria	Anthozoa	Actiniaria indet.		4.5	22.3	17.7	123.8	114.9	17.7	176.8	526.7	109.6	0.63, P = 0.04	NS
Nemertea	Nemertini	Nemertini indet.	41.4	56.5	62.7	79.6	44.2	26.5	44.2	58.9	415.2	84.9	NS	NS
Mollusca	Polyplacophora	Lepidochitona cinereus (L.)	40.0	12.0	5.7	17.7	8.8	88.4	44.2	55.3	61.5	49.5	0.66, P = 0.02	NS
	Gastropoda	Acmaea sp.				17.7			26.5				n < 5	n < 5
		Crepidula fornicata (L.)	60.0		4.0	8.8		26.5	114.9	353.7	242.2	74.3	0.69, P = 0.03	NS
		Hydrobia ulvae (Pennant)		8.5				362.5		110.5	3.8	10.6	NS	NS
		Littorina littorea (L.)	270.0	1720.0	825.7	97.3	265.3	150.3	371.4	324.2	419.0	339.5	NS	NS
		Littorina mariae/obtusata (L.)	30.0	3.5	78.0					29.5	11.5		NS	NS
		Littorina saxatilis (Olivi)							132.6	7.4		10.6	n < 5	n < 5
		Patella vulgata L.					44.2						n < 5	n < 5
	Bivalvia	Tellinidae indet.							17.7	14.7	3.8	7.1	n < 5	N < 5
		Angulus tenuis da Costa											n < 5	n < 5
		Cerastoderma edule (L.)		11.5	1.3			8.8		40.5		3.5	NS	NS
		Crassostrea gigas (Thunberg)								305.8	484.4	442.1	n < 5	n < 5
		Ensis sp.									7.7		n < 5	n < 5
		Macoma balthica (L.)		16.5	7.0	8.8	26.5		8.8	25.8	61.5	7.1	NS	NS
		Mya arenaria L.	0.1	1.3	1.3	8.8				11.1		7.1	NS	NS
		Mysella bidentata (Montagu)								11.1	10.6	14.1	n < 5	n < 5
		Mytilus edulis (L.)	1355.3	3560.0	1362.3	1379.3	1078.7	1069.9	1503.1	1551.0	1114.9	1255.6	NS	–
		Petricola pholadiformis Lamarck									7.7		n < 5	N < 5
Annelida	Polychaeta	Ampharete acutifrons Grube 1860	5.7	13.5	37.7	8.8			17.7	23.1	23.1	17.7	NS	NS
		Arenicola marina Linnaeus 1758	0.1										n < 5	N < 5
		Bylgides sarsi (Kinberg)			1.3	17.7				14.7	3.8	17.7	NS	NS
		Capitella capitata Fabricius 1780	350.0	164.5	374.0	88.4	194.5	79.6	61.9	95.8	80.7	180.4	NS	NS
		Cirratulidae indet.	40.0	42.0	21.0	26.5	97.3	132.6	176.8	103.2	11.5	17.7	NS	NS
		Eteone flava (Fabricius)							26.5				n < 5	n < 5
		Eteone longa (Fabricius)			8.3	17.7						10.6	n < 5	n < 5
		Eulalia viridis (L.)	0.1			8.8	8.8	8.8	17.7	3.7			NS	NS
		Eumida sanguinea (Oersted)	0.1		2.7					14.7			n < 5	n < 5
		Gattyana cirrosa (Pallas)				26.5		8.8	53.1				n < 5	n < 5
		Harmothoe impar Johnston				8.8				3.7	10.6		n < 5	n < 5
		Harmothoe imbricata (L.)				8.8		8.8	53.1	62.6	38.4	7.1	NS	NS
		Heteromastus filiformis (Claparède)	450.0	540.0	178.0	114.9	61.9	459.8	159.2	196.1	100.5	70.7	NS	NS
		Kefersteinia cirrata (Keferstein)	0.1	5									n < 5	n < 5
		Lanice conchilega (Pallas)		12.0	44.2	44.2	8.8	159.2	212.2	114.2	101.1	77.8	NS	NS

Table 2 continued

Phylum	Class	Scientific name	1984	1990	1993	1999	2000	2001	2002	2003	2004	2005	r_s (t)	r_s (M. e.)
		Lepidonotus squamatus (L.)		4.5	5.3	17.7	44.2	35.4		7.4		3.5	NS	NS
		Malacoceros sp.	120.0	964.0	376.6	0.0	26.5	132.6	97.3	320.5	64.3	49.5	NS	NS
		Manayunkia aestuarina (Bourne)				8.8							$n < 5$	$n < 5$
		Nephtyidae indet.		1.5	4.3	17.7		17.7		11.1	19.2		0.81, P = 0.02	NS
		Nereididae indet.	87.6	6.0	56.3	114.9	17.7	70.7	327.2	294.7	441.4	300.6	0.85, P < 0.05	NS
		Ophelina acuminata (Oersted)										3.5	$n < 5$	$n < 5$
		Pectinaria koreni Malmgren			1.3							3.5	$n < 5$	$n < 5$
		Pholoe baltica Oersted				17.7			8.8	7.4			$n < 5$	$n < 5$
		Phyllodoce sp.		1.5	2.7	8.8	8.8	132.6	70.7	29.5	34.6	28.3	0.67, P = 0.02	NS
		Polydora sp.	0.1		5.7	61.9	168.0	123.8	1476.6	4572.0	218.9	802.8	0.85, P < 0.05	NS
		Polynoidae indet				61.9	8.8		8.8	26.9	7.7	53.1	NS	NS
		Proceraea cornuta (Agassiz)								3.7			$n < 5$	$n < 5$
		Pygospio elegans Claparède			22.7		53.1	97.3		18.4	19.2	24.8	NS	0.82, P = 0.02
		Scoloplos armiger (O. F. Müller)	11.4	1.5	2.7			17.7				14.1	NS	NS
		Spio filicornis (O. F. Müller)				26.5	114.9	35.4		3.7			$n < 5$	$n < 5$
		Spiophanes bombyx (Claparède)				8.8					7.4	10.6	$n < 5$	$n < 5$
		Spiophanes kröyeri Grube								3.7			$n < 5$	$n < 5$
	Oligochaeta	Oligochaeta indet.	2382.9		2424.0	3236.2	2944.4	4306.0	4783.5	8031.4	6543.1	8014.4	–	–
Arthropoda	Cirripedia	Balanus sp.	849.9	1847.0	2429.3	4916.1	6498.8	9284.1	22768.0	18730.2	10214.4	19303.8	0.92, P < 0.001	NS
	Malacostraca	Carcinus maenas (L.)	150.0	551.0	225.3	371.4	194.5	495.1	504.0	736.8	438.3	417.3	NS	NS
		Chaetogammarus marinus Leach		570.0	460.0	185.7	79.6	44.2	26.5	14.7	7.7		–1, P = 0	NS
		Gammarus locusta (L.)				35.4	8.8	8.8	8.8	3.7	3.8		–0.88, P = 0.01	NS
		Gammarus oceanicus Segerstråle				168.0	26.5	17.7	44.2	73.7	26.9		NS	0.83, P = 0.02
		Idothea balthica (Pallas)				17.7							$n < 5$	$n < 5$
		Jaera albifrons Leach	100.0	17.0	46.0	26.5	61.9	61.9	44.2	23.1	19.2	10.6	NS	NS
		Pagurus bernhardus (L.)							8.8		3.8	3.5	$n < 5$	$n < 5$
	Pycnogonida	Nymphon sp.									3.8		$n < 5$	$n < 5$
		Pygnogonum littorale (Strøm)				8.8							$n < 5$	$n < 5$

Table 2 continued

Phylum	Class	Scientific name	1984	1990	1993	1999	2000	2001	2002	2003	2004	2005	r_s (t)	r_s (M. e.)
Echinodermata	Stelleroidea	*Asterias rubens* (L.)	0.1		7.0	17.7	17.7	8.8	26.5	36.8	19.2	7.1	NS	NS
Chordata	Ascidiacea	Ascidiacea indet.								22.1			$n < 5$	$n < 5$
		Number of taxa	23	25	31	39	29	30	34	45	37	38		
		Number of determined species[a]	26 (38[b])	33	39[c]	47	35	41	41	51	41	44		

Columns r_s (t) and r_s (M. e.) show results of the correlation (Spearman rank correlation) between densities of each taxa and (t) time and (M. e.) blue mussel densities, respectively

NS not significant, $n < 5$ = less than five data-pairs

[a] Number of all determined species within each survey are given

[b] Asmus (1987) found 26 species between September and November 1984, but 39 species during the whole year of investigation

[c] Three species of barnacles were included here that are mentioned by Hertzler (1995) in the text, but which have not been distinguished for abundance-data
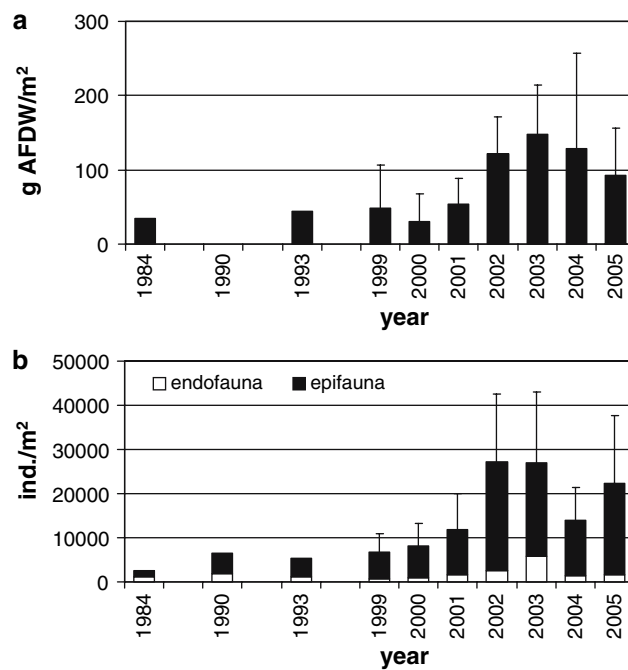
Fig. 4 Mean biomass (+SD) (**a**) and mean densities (divided in endofauna and epifauna, +SD is given for total mean densities) (**b**) of the associated macrozoobenthos on two mussel beds (sites 1 and 2) in the outer Königshafen from 1984 to 2005. *Mytilus edulis*, *Crassostrea gigas* and Oligochaeta indet. are not included. SD not always available

B. crenatus was most abundant in 2002 (12,387 $\pm$ 12,463 ind./m^2), but densities decreased afterwards. *S. balanoides* occurred with maximum densities in 2003 (8,282 $\pm$ 8,805 ind./m^2), but they were lower in 2004 (1,096 $\pm$ 1,040 ind./m^2) and 2005 (1,316 $\pm$ 1,541 ind./m^2). *Balanus improvisus* always occurred in low densities. This barnacle was found for the first time in 1999 with 106 $\pm$ 228 ind./m^2 and in 2003 with 335 $\pm$ 768 ind./m^2. Densities were highest in 2005 (742 $\pm$ 2,995 ind./m^2). *Elminius modestus* reached high densities, especially in 2005 with 11,565 ($\pm$10,986) ind./m^2. This species occurred in 2000 for the first time in high numbers (114 $\pm$ 306 ind./m^2).

Apart from barnacles, few taxa showed increasing abundances. Although Oligochaeta were not included in the analysis, it is worth to mention that their abundances increased significantly ($r_s = 0.932$, $P < 0.001$) from 1984 (2,383 ind./m^2) 2005, with more than 8,000 ind./m^2 and slightly lower densities in 2003 (6,543 ind./m^2).

High biomass in 2002 and in the following years was mainly due to the species *B. crenatus* (between 18.4 $\pm$ 15.6 g/m^2 and 43.6 $\pm$ 32.1 g/m^2), *S. balanoides* (between 8.2 $\pm$ 7.9 g/m^2 and 31.8 $\pm$ 21.9 g/m^2), *L. littorea* (between 17.2 $\pm$ 19.6 g/m^2 and 31.7 $\pm$ 28 g/m^2) and *C. maenas* (between 5.4 g/m^2 $\pm$ 5.6 and 33.8 $\pm$ 121.2 g/m^2).

Development of alien species

We found several species likely to have been introduced (*Tharyx killariensis*, *Aphelochaeta marioni*, *E. modestus*, *B. improvisus*, *C. fornicata*, *C. gigas*, *Ensis americanus*, *Petricola pholadiformes* and *Mya arenaria*) associated with mussel beds in Königshafen. With the exception of the Pacific oyster and the barnacle *B. improvisus*, all introduced species were already present on the mussel beds in the first investigations performed in the 1980s and 1990s. The polychaete *T. killariensis* (first record 1972 in the Wadden Sea, Nehring and Leuchs 1999) and *A. marioni* (first record in the Wadden Sea 1967, Nehring and Leuchs 1999) were pooled with *Chaetozone* cf. *setosa* for the analysis as *Cirratulidae* indet. Densities did not change significantly (Table 2).

The occurrence and development of the barnacles *E. modestus* (introduced in the Wadden Sea 1943, Nehring and Leuchs 1999) and *B. improvisus* (introduced in 1858 in the Wadden Sea, Nehring and Leuchs 1999) is described above.

The American slipper limpet *C. fornicata* (1934 first record in the Lister Deep, Nehring and Leuchs 1999) prefers shallow subtidal areas. Therefore, density estimates of *C. fornicata* could be strongly influenced by the sampling procedure across the mussel beds. Our database shows increasing densities until 2003 (354 ind./m^2) while the densities in the following years decreased again.

The American razor clam *E. americanus* (first record in 1978, Nehring and Leuchs 1999), and the bivalve *P. pholadiformes* (first record in 1896, Nehring and Leuchs 1999) were found in single years and with low densities.

The clam *M. arenaria* has occurred since at least 1860 in the German Wadden Sea (Nehring and Leuchs 1999), and was found at low densities in the mussel bed (our database).

Although the first feral Pacific oyster *C. gigas* was sighted at site 2 earlier in 1991 (Reise 1998), oysters did not occur in the samples before 2003. Mean oyster densities in 2003 to 2005 were about 400 ind./m^2.

By 2005, about 54% of all macrofaunal individuals (including blue mussels, except Oligochaeta indet.) on the mussel beds were represented by introduced species (including *C. gigas*). The numerically most important species were *E. modestus*, followed by *B. improvisus* and *C. gigas*. In 1984, alien species represented only 3% of all individuals.

Community structure and changes of functional groups

Multi-variate analyses indicate a major shift in community composition between the early and late 1990s (Fig. 5).
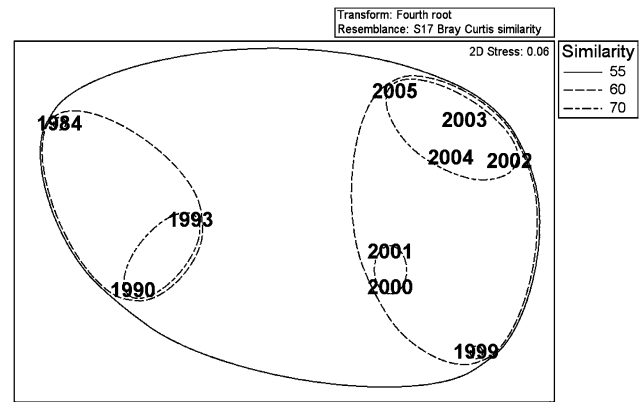

Fig. 5 Non-parametric multi-dimensional scaling plot (fourth root transformed, Bray-Curtis-similarity) for the macrozoobenthos community (between 1984 and 2005) on mussel beds in the outer Königshafen (Sylt, Germany). Additional similarity over all years with 55, 60 and 70% are given (indicated with the *closed* and *dashed lines*) arbitrarily chosen from a cluster analysis (not shown)

Community compositions in 1990 and 1993 were similar to 1984, and in 1999 to 2001 also more similar to each other than in the surveys since 2002.

Between 1984 and 1990/1993, changes reflect fluctuation in species composition and an increase of epibenthic species abundances. Later, community structure shifted mainly because of increasing abundances, notably by barnacles. Barnacles were treated in the analysis as one taxonomic group (see Methods). However, a shift from native to introduced barnacle species was apparent (see above).

Because of the strong increase in densities of barnacles, the absolute abundance of suspension feeders increased as well (Fig. 6) while the other functional groups showed less temporal fluctuation. Despite a marked qualitative change in dominant species, the community remained primarily a filter feeder assemblage.

Discussion

The results of the study revealed a shift from high to low biomass of mussel beds and from low to high abundances of the associated community which also changed in composition. However, there are also peaks of mussel density and of fucoid cover at an intermediate phase of the two decades of observation.

Mussel beds may form very stable and long-lived structures in the Wadden Sea, if losses from factors like hydrodynamic forces, storm events or predation are balanced by recruitment (Nehls and Thiel 1993, Dankers et al. 1999; Nehls and Ketzenberg 2002). Over recent years, the mussel bed area has been declining in many parts of the Wadden Sea as a result of recruitment failures (de Vlas
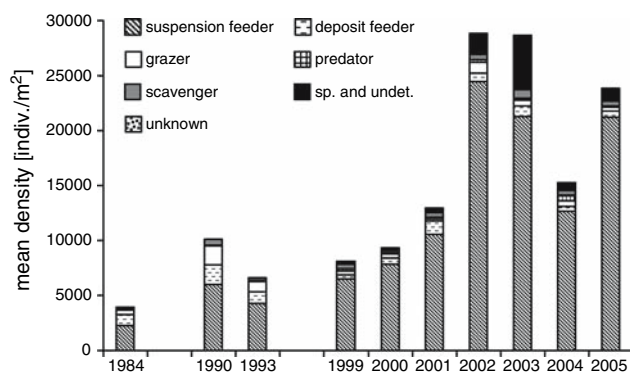
Fig. 6 Mean densities of functional groups between 1984 and 2005 (*Mytilus edulis* and *Crassostrea gigas* are included, Oligochaeta indet. were not considered)

et al. 2005, Nehls and Büttger 2007), thus the development in our study area is not a local phenomenon. The last massive recruitment in the northern Wadden Sea occurred in 1996 following a severe winter. Therefore, recruitment failure might be related to mild winters, whereas increasing summer temperatures facilitate oyster proliferation in the Wadden Sea (see details in Diederich et al. 2005; Nehls et al. 2006; Nehls and Büttger 2007).

We suggest that several processes have interacted and that invading species are not the only driving force that take advantage of changing mussel beds. Four changes in the mussel bed structure have to be considered: (1) a decrease in mussel biomass, (2) ageing of mussel beds, (3) decrease of *Fucus* cover since 2001, (4) increasing abundances of non-native species.

A decrease in mussel biomass

Although mussel densities did not decrease significantly, mussel biomass did, indicating a decline in large-sized mussels which in general dominate the biomass (Nehls and Ketzenberg 2002).

Reduced mussel biomass within the patches may well play a role in changing communities. Densely packed mussel patches which store high mussel biomass may enhance the accretion of the mussel beds by accumulating faeces and pseudofaeces and layers of dead shells, which might enhance the numbers of associated endofauna (Commito and Boncavage 1989, Ragnarsson and Raffaelli 1999). In contrast, experiments of Beadman et al. (2004) revealed an inverse relation between mussel cover on the one hand and species richness and abundance of associated infauna on the other hand. In our study, densities of endofauna (excluding Oligochaeta) increased since 2000 until 2003, whereas total density and biomass of blue mussels was lowest in this period. Dense mussel patches in

the study area with high biodeposition have been found to harbour lower densities of Polychaeta (Dittmann 1990). In our study, densities of some polychaetes increased as mussel biomass decreased (Table 2) but no general trend appeared.

After 2003, mussels were partly replaced by Pacific oysters, which fulfil a similar ecological function from an infaunal point of view (as they also accumulate faeces and pseudofaeces). With the co-occurrence of blue mussels and oysters, total bivalve density and biomass increased since 2003 (Table 2).

We did not find any correlation between mussel density and the total densities of the associated epi- or endofauna. Increasing abundances of the associated community in our study were largely dominated by epibenthic species, especially barnacles. Mussels actively change their positions from bottom to top layers (Okun 1999). When they are on the bottom of the stack, survival of epifauna may be reduced. More detailed research on the interactions between mussel densities and associated epifauna is recommended.

Ageing of mussel beds

A second possible reason for the observed changes could be the ageing of mussel beds. The last strong spatfall of blue mussels in the study area occurred after the cold winter of 1995/1996 (Hertlein 1997) and led to mussel beds with several thousands of young mussels per square meter. Subsequently, although densities declined, biomass remained constant over several years as decreasing mussel numbers were counteracted by the larger sizes of the mussels (Guinez 2005). Older mussel beds become more heterogeneous in physical structure (Tsuchiya and Nishihira 1986; Günther 1996; O'Connor and Crowe 2007), because of an increasing number of dead shells, and higher densities of associated species than young mussel beds (such as barnacles, see Buschbaum 2001). In addition young mussels are able to clean their shell with their foot, and shells of young *M. edulis* have a slick surface with a closed and uneroded periostracum (inhibiting epifaunal settlement) that is lost as older mussels abrade them (Theisen 1972; Fig. 7). Older blue mussels thus offer much better opportunities for settling epifauna. Increasing oyster densities since 2003 also facilitate settling of epifauna.

Decrease of *Fucus* cover

Reasons for the up- and downward trends in *Fucus*-cover on mussel beds in the outer Königshafen are unclear. *Fucus* cover positively enhances the occurrence of some

Fig. 7 A young mussel bed (*top*), an older mussel bed (*middle*) and an oyster dominated bed (*bottom*) to illustrate structural differences

epibenthic species, such as *Littorina mariae, Jaera albifrons* and *Gammarus* sp., while other species, especially barnacles and *L. littorea* are depressed beneath *Fucus*-cover (Albrecht and Reise 1994). As *Fucus* acts as sediment trap, the sediment of the mussel beds gets muddier. This often results in decreasing mussel densities and attached

epifauna. Decrease in *Fucus* cover is thus likely to be an important factor for the increase of epibenthic species, especially barnacles. On the other hand, the decrease of species as *J. albifrons* and *Chaetogammarus marinus* is also considered to be a result from loss of this seaweed. These species are most closely linked to the *Fucus* 'canopy' on the mussel beds, which offers shelter against predators and against desiccation at low tide. *J. albifrons* and *C. marinus* rarely occur outside the algal cover. Densities of *Ch. marinus* decreased significantly until 2004 (Table 2) and no individuals were found in 2005. To judge if these species have disappeared from this mussel bed or not data of the following years associated with information about the occurrence of the fucoid algae are needed.

Increasing abundances of non-native species

In two decades covered by the data set, diversity decreased (Simpson index), indicating the dominance of a few species. Together with Pacific oysters, American slipper limpets and some others, alien species have achieved numerical dominance on the mussel beds. Among alien species, only the Pacific oyster is a recent inhabitant of the mussel beds. All other alien species were already present during our first study in Königshafen or were detected decades before in the Wadden Sea (Nehring and Leuchs 1999). Thus, introductions did not contribute to an increase in species richness within the period considered here.

However, the introduced Pacific oyster plays a special role as it increasingly takes in the place of the blue mussel as a habitat builder. Individuals of the Pacific oyster were first recorded in 1991 on intertidal mussel beds in the List Tidal Basin (Reise 1998). Low densities (3.9 oysters/m^2) were found from 1999 until 2002 (Diederich et al. 2005), followed by several years of good spatfalls leading to rapidly increasing oyster densities and biomass (Nehls and Büttger 2007; 314 ± 200 ind./m^2 in 2003, Fig. 2). After 2003, the mussel bed turned into an oyster reef with tightly packed oysters standing vertically (Fig. 7). Oyster densities and biomass reported in Fig. 2 are likely to be underestimated, as large oysters and clumps were difficult to sample using a corer. Separate oysters sampling yielded higher densities (about 1,800 indiv./m^2 in 2007; Nehls and Büttger, unpublished, compare Nehls and Büttger 2007). Like mussel beds, oysters offer a heterogeneous physical structure which serves as a habitat for many associated species, and also act as ecosystem engineers (Jones et al. 1994; Commito and Dankers 2001; Crooks 2002; Palomo et al. 2007). Although competition for limited space and probably also for food is anticipated to be important at a small scale at least, there is still no evidence that oysters have displaced mussels (Nehls et al. 2006; Nehls and Büttger

2007). Whether or not the spread of the Pacific oysters has promoted the increase of other alien species such as *Balanus improvisus* or *Elminius modestus* cannot be concluded from our data. Like in native barnacles, their spread is considered to be facilitated by decreasing *Fucus* cover. Additionally, the barnacle *E. modestus*, in particular, is expected to take advantage of mild winters (Harms 1998). This introduced species competes for space with the native *S. balanoides* (Nehring and Leuchs 1999; Franke and Gutow 2004). This shift in dominance seems to be induced by climatic factors and supported by structural factors, and oysters are assumed to offer more surface for settlement when they grow tightly packed in vertical position (compare Markert 2006). Increasing abundances of the non-native *C. fornicata* were facilitated by mild winters (Nehls et al. 2006). Since oysters became more abundant, densities of *C. fornicata* decreased probably due to the fact that the American slipper limpet was not observed in higher densities on densely packed oysters. Additionally this species preferentially occurs below low water line (Thieltges et al. 2003) rather than on elevated oyster patches. All other non-native species did not show clear trends of their abundances.

Alien species thus play an important role in species turnover of the mussel bed community. Decreasing mussel biomass followed by increasing oyster densities was apparently facilitated by climatic factors (Diederich et al. 2005) and supported increasing densities of the associated community and structural changes in the study period.

Conclusions and outlook

All four factors discussed earlier are assumed to contribute to changing community structure of intertidal mussel beds. Two of them are considered as common processes in Wadden Sea mussel beds; ageing of mussels and self-thinning of mussel beds (Guinez 2005) probably lead to a natural succession of the associated community. In the following years after the spatfall, as shown in this study, the stability of the mussel beds was lost; they deteriorated and were partly taken over by invading oysters. With the background of a very fast increasing population in the entire Wadden Sea, oysters are set to take over the role of mussels as ecosystem engineers. The effects of *C. gigas* on the benthic communities in the Wadden Sea will be composed of direct structural attributes and species interactions, and further modulated by climate change and changing of *Fucus* cover.

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