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Subtidal and intertidal mussel beds (*Mytilus edulis* L.) in the Wadden Sea: diversity differences of associated epifauna

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Abstract In 1997 and 1998, surveys were performed to compare species composition, abundance and diversity of non-attached epifauna (>1 mm) in low intertidal and adjacent shallow subtidal zones of three mussel beds (*Mytilus edulis* L.) near the island of Sylt in the North Sea. The community structure was similar when compared within tidal zones: no significant differences in species numbers and abundances were recorded between locations and between years. A comparison between tidal zones, however, revealed higher diversity, species densities and total species numbers in the subtidal (per 1,000 cm²: $H' = 2.0 \pm 0.16$; 12 ± 1 species density; 22 species) than the intertidal zone (per 1,000 cm²: $H' = 0.7 \pm 0.27$; 6 ± 2 species density; 19 species). Abundances significantly dropped with increasing submergence from 2,052 (± 468) m⁻² to 1,184 (± 475) m⁻². This was mainly due to significantly higher densities of both juvenile periwinkles, *Littorina littorea*, and crabs, *Carcinus maenas*, in intertidal mussel beds. However, many less dominant species were significantly more abundant in subtidal mussel beds. This study revealed that in the non-attached epifaunal community of mussel beds the tidal level effect within metres was strong, whilst the spatial variability in a much wider (kilometre) range but the same tidal level was negligible. The high epifaunal diversity in the subtidal zone suggests that the protective measures for mussel beds against the effects of mussel fishery should be extended from the intertidal to the subtidal zone, if the integrity of the mussel bed community in the Wadden Sea National Park is to be maintained.

Keywords Mussel · Epifauna · Diversity · Tidal zone · Spatial variability

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Introduction

The low water mark subdivides the gently sloping shore of the European Wadden Sea into a landward intertidal and a seaward subtidal zone. Due to daily exposure to the terrestrial environment, the intertidal is subject to a wider range of physical factors challenging the physiological adaptability of marine organisms (Newell 1970; Eltringham 1971). Therefore, the number of benthic species is expected to decrease from the subtidal towards the high-tide line. Although this gradient of increasing harshness may be buffered by marine sediments (Peterson 1991), the macro-infauna generally declines in species density and diversity (e.g. McIntyre and Eleftheriou 1968; Sanders 1968; Johnson 1970; Knott et al. 1983; Dexter 1984; Armonies and Reise 2000), whilst the interstitial fauna of a sandy shore (Armonies and Reise 2000) and the benthic diatoms (Asmus 1983) may show a different pattern. An inherent weakness in these studies is that sedimentary composition tends not to be constant perpendicular to the shore, thus obfuscating the effects of tidal zone.

In this paper, the non-attached epifauna is considered, living associated with beds of blue mussels (*Mytilus edulis* L.) which constitute coherent epibenthic patches upon the sediments of the Wadden Sea. The mobile invertebrates were sampled during submergence in both the shallow subtidal and the lower intertidal zone. As they dwell within a complex matrix of mussels interconnected by a mesh of byssal threads, it is not clear whether a vertical difference of 1 m and a difference in mean emergence time of 1 h constitutes an effective environmental gradient to this species assemblage. To evaluate differences, three localities were chosen where mussel beds grade from the shallow subtidal into the lower intertidal zone. Although mussels varied in density and growth rate along the tidal gradient (Buschbaum and Saier 2001), the biogenic structure of the habitat was assumed to be constant between localities and tidal zones.

In spite of the harshness of the intertidal zone, a rich food supply creates high abundances, as first pointed out

by Dahl (1893). Consequently, an increase in dominance is to be expected when faunal assemblages extend from the shallow subtidal into the intertidal zone. As with species richness, this is not easily linked to tidal zone when sediment properties are not constant. Within mussel beds, however, habitat structure remains the same for epibenthic associates between tidal zones.

In general, comparisons between subtidal and intertidal zones are scarce because by tradition methods of assessment differ between these two habitats. In this study, however, an identical protocol was followed and both sets of samples were taken during submergence.

In addition to theoretical interest in the question of tidal effects on species diversity and abundance of non-attached epifauna in mussel beds, there is also some practical relevance. The investigated localities are within a National Park where mussel fishery has been restricted to subtidal mussel beds (Ruth 1998). This decision was based on the assumption that mussel beds are the same in the subtidal and intertidal zones but in the latter mussel beds should be strictly protected because these constitute important feeding sites for various shorebirds such as eider ducks (*Somateria mollissima*) and oystercatchers (*Haematopus ostralegus*) (Nehls 1998). This study shows that the low-tide mark subdivides the non-attached epifaunal assemblage of mussel beds with respect to diversity and abundance, and subtidal and intertidal mussel beds should not be assumed to be the same.

Materials and methods

Study area

The study was performed at mussel beds (*Mytilus edulis*) located near Königshafen (55°02'N, 08°26'E), a sheltered tidal bay in the north of the island of Sylt (German Bight, Northern Wadden Sea; Fig. 1). The natural history of the marine life, hydrography, geology and sediments has been described in detail by Wohlenberg (1937), Reise (1985), G. Austen (1994), I. Austen (1994), Bayerl and Higelke (1994) and Reise et al. (1994). The mean tidal range is 1.8 m but considerable variations may occur during onshore and offshore winds. Average salinity is 30 psu and mean water temperature is 15°C in summer and 4°C in winter. The intertidal zone of Königshafen comprises approximately 4.5 km² and is characterized by extensive sandy and muddy flats (about 84%). Seagrass beds occur in the mid-tidal zone and cover another 12% of the area and intertidal mussel beds account for only 1% of the intertidal area (Reise et al. 1994). The three sites studied all included low intertidal mussel beds which stretched continuously into the shallow subtidal within 100 m of horizontal distance (Fig. 1). Mean exposure time of the low intertidal was about 1 h per tide. In this investigation 'shallow subtidal' zones are referred to as areas remaining submerged at spring water low tide and with a maximum water depth of 0.5–1 m at mean low tide. The three localities were similar in mussel community structure (Buschbaum and Saier 2001) but differed in hydrodynamics. Site A was subject to the strongest waves and tidal currents whilst sites B (close to the main tidal channel) and C were more sheltered within 'Königshafen' bight (Behrens et al. 1996). Patches of mussel beds colonized by the seaweed *Fucus vesiculosus* f. *mytili* (Nienburg) harbour a specific faunal assemblage (Albrecht and Reise 1994) and, since these patches only occurred intertidally, they were excluded from this investigation. The same applies to tide pools.

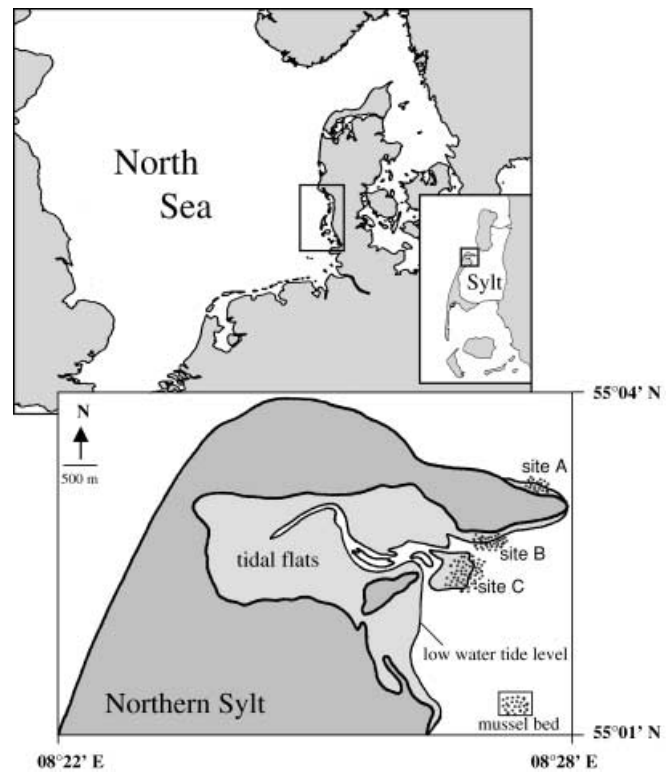


Fig. 1 Investigation area in the Wadden Sea near the island of Sylt, North Sea, Germany. *Above* overview of North Sea and location of the island of Sylt. *Below* tidal flats of northern Sylt with distribution of investigated mussel beds (dotted) near the low water tide mark in 1997 and 1998

Sampling procedure

Using a stratified random sampling procedure, six samples per tidal level per site were taken during tidal submergence in August 1997 (site B) and 1998 (sites A, B and C) by diving. A hand-held metal box corer (1,000 cm²) with a sharpened edge was manually pressed through the mussel layer to a sediment depth of 12 cm. The sediment cores were subsequently transferred to linen bags. In the laboratory, the contents were washed through 1 mm meshes and non-attached epifauna separated from mussels and identified to species level. If the whole sample could not be analysed immediately, parts were fixed in 4% buffered formaldehyde for later identification. Due to their locomotory capabilities the anthozoans *Metridium senile* and *Sagartiogeton undatus* were also included (Wahl 1985a, b).

Data analysis

Abundances and species densities are presented as arithmetic means (rounded values) with standard deviation ($\bar{x} \pm SD$) on a 1,000 cm² basis and two-factor analysis of variance (ANOVA) was used to test for the significance of effects of tidal zone and location or year, respectively. Variances were homogeneous (Cochran's test) and no transformations were required to make data fit to the assumptions of the analysis. Differences in abundances of single species in intertidal and subtidal mussel beds were analysed by Mann-Whitney *U*-tests. Diversity was calculated according to Shannon-Wiener: $H' = -\sum p_i \cdot \ln p_i$, with p_i being the portion of a species' (n_i) number of individuals based on the total number (N): $p_i = n_i/N$. Significant interannual differences of diversity indices were tested with a two-way ANOVA.

Table 1 Spatial variability of total and mean species numbers (SD in parentheses) per box core (1,000 cm²), mean abundances m⁻² (SD in parentheses), diversity H' (SD in parentheses) and even-

	Intertidal				Subtidal			
	Site A <i>n</i> = 6	Site B <i>n</i> = 6	Site C <i>n</i> = 6	All sites <i>n</i> = 18	Site A <i>n</i> = 6	Site B <i>n</i> = 6	Site C <i>n</i> = 6	All sites <i>n</i> = 18
Total species no.	15	15	16	19	18	18	17	22
Species density	6 (2)	6 (2)	8 (2)	6 (2)	12 (1)	12 (1)	12 (1)	12 (1)
Abundance	2118 (352)	2285 (593)	1753 (302)	2052 (468)	1320 (447)	1036 (216)	1198 (687)	1184 (475)
Diversity H'	0.59 (0.13)	0.52 (0.06)	1.0 (0.29)	0.7 (0.27)	1.99 (0.13)	2.1 (0.05)	1.92 (0.21)	2.0 (0.16)
Evenness	0.20	0.22	0.40	0.26	0.77	0.74	0.76	0.74

Since variances remained heterogeneous despite transformation, I used the H -test (Kruskal-Wallis), followed by pairwise Mann-Whitney U -tests to test for significant differences between diversity indices of tidal zone and location in 1998. Evenness ($J' = H'/\ln S$) expressed the distribution of individuals over the species, with S being the total number of species. Renkonen's index ($R = \sum p_i$, with p_i being the portion of animals in the site where species i is less abundant) was applied to compare dominance and one-way ANOVA tested for significant differences. Faunal similarity between stations was expressed with Sørensen's index S_{2G/S_A+S_B} , with G being number of co-occurring species at sites A and B and S_A and S_B the number of species at sites A and B, respectively. H -test and pairwise U -tests were used to test for the significance of differences. Effects were considered statistically significant if $P < 0.05$. The Bonferroni procedure was applied for multiple comparisons of data.

Results

Effects of tidal level and location

In 1998 a comparison of non-attached epifauna of the three mussel beds revealed significant differences between tidal zones. However, within each tidal zone the species densities (two-way ANOVA, $F_{1,30} = 1.317$, $P = 0.282$) and abundances (two-way ANOVA, $F_{1,30} = 0.954$, $P = 0.396$) did not significantly vary over the three locations (Table 1). Except for the intertidal site C, diversity H' (H -test, followed by pairwise Mann-Whitney U -tests; $P > 0.05$) and evenness J' were also similar within tidal zones. Furthermore, comparisons of the species composition revealed a higher degree of similarity (Sørensen's index) and dominance (Renkonen's index) within intertidal and subtidal sites than between them (Table 2). A significant difference was recorded in the comparison of dominance between tidal zone (one-way ANOVA, $F_{2,12} = 30.4940$, $P < 0.001$). Intertidal mussel beds were characterized by a strong dominance of a smaller number of species.

When data from the three locations were pooled to compare between the tidal zones, this revealed a much higher diversity H' in the shallow subtidal zone (2.0 ± 0.16) of the mussel beds than intertidally (0.70 ± 0.27). Whilst total species numbers were similar in both tidal zones, with 22 species of non-attached epifauna occurring subtidally and 19 intertidally (Table 3), the average number of species per box core (1,000 cm²)

ness at low intertidal and adjacent shallow subtidal zones of three mussel beds in the north of Sylt

Table 2 Similarity (Sørensen's index) and dominance (Renkonen's index) for six intertidal (I) and six subtidal (S) localities presented as absolute or mean values with standard deviation (SD). \times = compared with

Locality	Similarity	Dominance
I: site A \times site B	0.93	0.96
I: site A \times site C	0.84	0.78
I: site B \times site C	0.84	0.91
S: site A \times site B	0.83	0.7
S: site A \times site C	0.8	0.66
S: site B \times site C	0.91	0.68
All intertidal sites (I)	0.87 (0.05)	0.88 (0.09)
All subtidal sites (S)	0.85 (0.06)	0.68 (0.02)
All I \times all S	0.75 (0.1)	0.36 * (0.12)

*Significant difference

was significantly higher subtidally (12 ± 1) than intertidally (6 ± 2) (two-way ANOVA, $F_{1,30} = 140.984$, $P < 0.0001$). In contrast, abundances were significantly higher at intertidal ($2,052 \pm 468$ m⁻²) than subtidal localities ($1,184 \pm 475$ m⁻²) (two-way ANOVA, $F_{1,30} = 31.479$, $P < 0.0001$). This was mainly due to periwinkles, *Littorina littorea*, and crabs, *Carcinus maenas*, which dominated and accounted for 97% of all intertidal specimens (Fig. 2). *L. littorea* had an average density of $1,586 (\pm 539)$ m⁻² in the intertidal zone and were almost exclusively juveniles (≤ 13 mm shell height). In the adjacent shallow subtidal zone, *L. littorea* abundance was significantly lower (223 ± 105 m⁻²) (Mann-Whitney U -test, $P < 0.01$; Table 3) and dominated by adults. Similarly, crabs, *C. maenas*, were significantly more abundant in the intertidal (359 ± 116 m⁻²) than the subtidal zone (144 ± 54 m⁻²; Mann-Whitney U -test, $P < 0.01$; Table 3). Juvenile crabs (< 10 mm carapace width) accounted for about 90% of all specimens in both tidal zones.

On the other hand, many less dominant species occurred in significantly higher abundances at subtidal sites (Fig. 3). In order of decreasing total abundance these included slipper limpets (*Crepidula fornicata*), anthozoans (*Metridium senile* and *Sagartiogeton undatus*), polychaetes (*Harmothoe imbricata* and *Harmothoe impar*, *Polydora ciliata*, *Lepidonotus squamatus*), seastars (*Asterias rubens*), the nudibranch *Aeolidia papillosa* and sea urchins (*Psammechinus miliaris*).

Table 3 Mean and standard deviation (SD) of species abundances (ind. m⁻²) of non-attached epifauna (>1 mm) in intertidal and subtidal zones of three mussel beds in the north of Sylt in August 1998

	Intertidal			Subtidal	
	Mean	SD		Mean	SD
Coelenterata					
<i>Metridium senile</i>	8	14	**	161	157
<i>Sagartiogeton undatus</i>	7	13	**	95	111
Mollusca					
<i>Lepidochitona cinereus</i>	14	19		31	32
<i>Littorina littorea</i>	1586	539	**	223	105
<i>Crepidula fornicata</i>	36	114	**	203	241
<i>Buccinum undatum</i>	0	0		1	5
<i>Onchidoris bilamellata</i>	0	0		2	5
<i>Aeolidia papillosa</i>	0	0	**	34	49
Polychaeta					
<i>Harmothoe impar</i>	3	5	**	29	16
<i>Harmothoe imbricata</i>	7	11	**	87	52
<i>Lepidonotus squamatus</i>	1	5	*	11	15
<i>Phyllodoce mucosa</i>	2	4		4	9
<i>Eulalia viridis</i>	1	2		6	14
<i>Nereis diversicolor</i>	7	10		4	8
<i>Nereis succinea</i>	1	3		1	2
<i>Nereis virens</i>	1	2		1	2
<i>Polydora ciliata</i>	2	4	*	12	12
<i>Neoamphitrite figulus</i>	1	5		0	0
Crustacea					
<i>Jaera albifrons</i>	3	5		0	0
<i>Gammarus locusta</i>	1	5		1	2
<i>Carcinus maenas</i>	359	116	**	144	54
<i>Pagurus bernhardus</i>	0	0		3	5
Echinodermata					
<i>Asterias rubens</i>	12	15	**	125	86
<i>Psammechinus miliaris</i>	0	0	*	8	11
Total species number	19			22	
Total abundance	2052			1184	

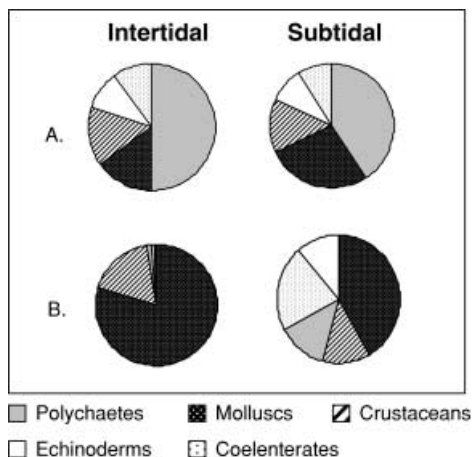


Fig. 2 Taxonomic composition of non-attached epifauna in low intertidal and adjacent shallow subtidal zones of mussel beds, based on the individual sum of 18 samples per zone. A Species, B individuals

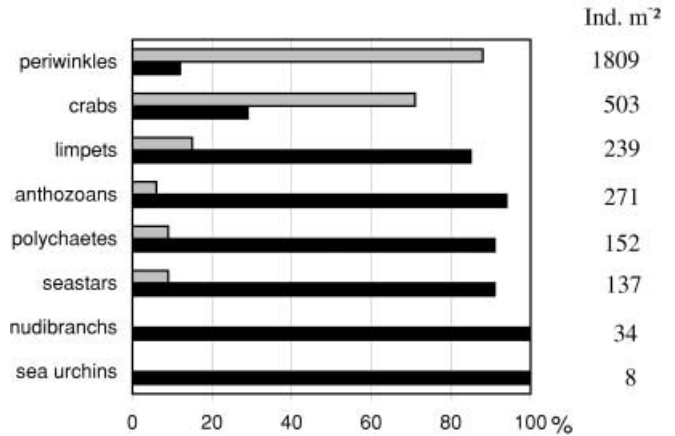


Fig. 3 Relative abundance of non-attached epifauna (>1 mm), differing significantly between intertidal (grey) and subtidal (black) zones of mussel beds. Means ($n=18$) and total numbers (ind. m⁻²), corresponding to 100%

Effect of tidal level and year

At site B (see Fig. 1), a comparison of species numbers and abundances of non-attached epifauna between 1997 and 1998 also revealed significant differences between tidal zones. Within each tidal zone, the species densities and abundances did not significantly vary between years. In 1997, the average species number per box core (1,000 cm²) was similar to 1998 (two-way ANOVA, $F_{1,20}=0.028$, $P=0.868$) and significantly higher in the subtidal zone (11 ± 1) than intertidally (7 ± 1) (two-way ANOVA, $F_{1,20}=119.350$, $P<0.0001$). Abundances were significantly higher in the intertidal ($1,835\pm 560$ m⁻²) than the subtidal mussel bed (624 ± 291 m⁻²) in 1997 (two-way ANOVA, $F_{1,20}=24.720$, $P<0.0001$) and there was no significant difference compared to 1998 (two-way ANOVA, $F_{1,20}=3.836$, $P=0.064$). In 1997 diversity H' was significantly higher in the shallow subtidal (1.8 ± 0.2) than the intertidal (0.6 ± 0.2) zone of site B (two-way ANOVA, $F_{1,20}=402.7276$, $P<0.0001$) but not significantly different between 1997 and 1998 (two-way ANOVA, $F_{1,20}=2.5642$, $P=0.125$). Moreover, individuals were more evenly distributed over the species in subtidal (evenness $J'=0.74$) than intertidal ($J'=0.25$) mussel beds in 1997.

The comparison between 1997 and 1998 revealed interannual differences in the species composition of low intertidal and adjacent shallow subtidal zones. In 1997, only periwinkles, *Littorina littorea*, and anthozoans (*Metridium senile* and *Sagartiogeton undatus*) showed significant differences between intertidal and subtidal sites (Mann-Whitney U -test, $P<0.01$) and occurred in the following respective densities: *L. littorea*: $1,610\pm 558$ m⁻² and 248 ± 192 m⁻²; *M. senile*: 3 ± 8 m⁻² and 237 ± 182 m⁻²; *S. undatus*: 17 ± 41 m⁻² and 138 ± 117 m⁻². These abundances were similar to 1998 (see Table 3). In contrast to 1998, juvenile crabs occurred in similar abundances in intertidal (52 ± 33 m⁻²) and subtidal zones (78 ± 36 m⁻²) in 1997 (Mann-Whitney U -test, $P>0.05$)

and the same was true for many less abundant species, for example slipper limpets, polychaetes, seastars and sea urchins: no significant differences were detected between intertidal and subtidal sites in 1997, but the trends were the same, i.e. in both years towards a higher abundance in the subtidal zone.

At subtidal sites, abundances of juvenile seastars (*Asterias rubens*) and *Crepidula fornicata* significantly increased in 1998: 266 (± 166) m⁻² seastars and 160 (± 102) m⁻² limpets occurred in comparison to only 43 (± 40) m⁻² and 18 (± 20) m⁻² in 1997 (Mann-Whitney *U*-test, $P < 0.01$).

Discussion

Effect of tidal level

In the European Wadden Sea, investigations of the epifaunal species composition of mussel beds were either restricted to intertidal (e.g. Dittmann 1990; Obert and Michaelis 1991; Albrecht and Reise 1994; Günther 1996; Albrecht 1998) or subtidal mussel beds (e.g. Dekker 1989; Dankers and Zuidema 1995). Comparisons between both tidal zones were not performed along rocky shores, where predators, in particular seastars, may set sharp boundaries to the distribution of mussels towards the adjacent subtidal (Kitching and Elbling 1967; Seed 1969; Paine 1974; Suchanek 1978). Within the rocky intertidal, however, the fauna associated with *Mytilus edulis* revealed increasing species richness and diversity towards the low-tide mark (Lintas and Seed 1994). This trend was also shown for macro-invertebrates of sedimentary environments (e.g. McIntyre and Eleftheriou 1968; Sanders 1968; Johnson 1970; Knott et al. 1983; Dexter 1984; Armonies and Reise 2000) and, according to Sanders (1968), may be due to increased physical stability in the subtidal zone. Most of these sedimentary shore studies, however, did not unambiguously reveal tidal effects because habitat structure was rarely kept constant perpendicular to the shore. Knott et al. (1983) recognized the low water mark as a distinct boundary between tidal and subtidal invertebrate assemblages but pointed out that the numerical dominants were widely distributed throughout the subtidal and intertidal zones.

The present study also showed that the low water mark subdivides the non-attached epifaunal assemblage of intertidal and subtidal mussel beds with respect to species diversity and abundance. At all locations and in both years, diversity was lower at intertidal than subtidal sites within the investigated mussel beds. This was due to the strong dominance of two species in the intertidal zone and many less abundant species which were unable to establish themselves on tidal mussel beds. For instance, the common whelk *Buccinum undatum* (L.), nudibranch molluscs, hermit crabs and sea urchins were confined to the shallow subtidal zone. The absence of several species from intertidal sites is considered to be due to a lack of physiological tolerance against desicca-

tion, heat stress and reduced oxygen during tidal emergence (Wolff 1983). Despite the buffering capacities provided by the complex habitat structure of mussel beds (Seed and Suchanek 1992), physiological stresses may control the upper distributional limits of associated species. The effect of low-tide physiological stress is well documented for sessile organisms living at high shore levels on rocky shores (Raffaelli and Hawkins 1996) and there is also experimental evidence for the importance of physical factors in setting distributional limits of marine invertebrates in sedimentary environments (e.g. Peterson and Black 1987, 1988).

The major differences resulting from this comparison of intertidal and subtidal mussel beds were due to different abundances of the associated epifauna. In particular, juvenile periwinkles, *Littorina littorea*, and juvenile shore crabs, *Carcinus maenas*, occurred in significantly higher numbers at the intertidal sites. Both species may find refuges from predation (Thiel and Darnedde 1994) and characterize intertidal mussel beds to be important nurseries (Reise 1985; Saier 2000).

In the case of *L. littorea*, high intertidal densities were considered to be due to a combined effect of intertidal recruitment, the presence of an additional biogenic structure provided by barnacle epibionts and crab predation (Saier 2000). For *C. maenas*, mussel beds in the Wadden Sea are well known settlement and recruitment sites (Reise 1985; Albrecht and Reise 1994; Günther 1996) and there is no evidence that young crabs perform tidal migrations during the summer months (Klein Breteler 1985; Thiel and Darnedde 1994). The structural heterogeneity of densely layered intertidal mussels may provide spatial refuges from predators (Thiel and Darnedde 1994; Moksnes et al. 1998). These include cannibalistic adults, preferentially inhabiting the subtidal parts of the Wadden Sea and adjacent North Sea (Reise and Bartsch 1990; Buhs and Reise 1997). In turn, predation by juvenile *C. maenas* and birds (e.g. gulls, oystercatchers, turnstones) may have pronounced effects on the survival of associated intertidal species such as polychaetes (Reise 1977; Scherer and Reise 1981). Thus, higher abundances of *Harmothoe* spp., *Polydora* and *Lepidonotus* in the subtidal zones of the investigated sites may in part be due to high abundances of juvenile crabs on intertidal mussel beds. Furthermore, physical stress might contribute to limit the upward spread of non-tube-building worms, sea anemones and molluscs without external shells and continuous food availability may account for higher subtidal abundances of filter feeders such as slipper limpets, *Crepidula fornicata*, or *Metridium senile* and its mollusc predator *Aeolidia papillosa*. Since barnacles occur in significantly higher numbers on lower intertidal than shallow subtidal *Mytilus edulis* (Buschbaum and Saier 2001), this additional structural component may enhance zonation of resident species by biological interactions. *C. fornicata*, for instance, may additionally benefit from a relief from competition for space.

In summary, between tidal zones, a vertical difference of only 1 m and a short mean emergence time of about 1 h

strongly affected the non-attached epifaunal community of intertidal and subtidal sites within mussel beds. Hence, the effect of tidal level was not compensated for by the complex mussel bed structure. Whatever factors produced the observed zonation within intertidal and subtidal mussel beds, both physiological stress and biological processes such as predation or larval settlement interact to set distribution patterns (Raffaelli and Hawkins 1996).

Effect of location

The present study also revealed that the effect of tidal level was a stronger determinant of the community composition than the spatial variability among the three locations separated by approximately 2 km in horizontal distance and with differences in hydrodynamics, indicating that the combined effects of larval supply and post-settlement factors may be similar at a kilometre scale with respect to epifauna. This is surprising and in contrast to the surrounding sand flats where the infaunal community composition showed highly variable large-scale (kilometre) distribution pattern (e.g. Armonies and Hellwig-Armonies 1992; Zühlke and Reise 1994; Armonies 1996).

By creating structurally complex reefs, soft-bottom mussel beds modify the physical environment which in turn shapes the associated community by providing habitat space, outcompeting other surface dwellers and creating a sedimentary environment high in organic material and low in oxygen, thus favouring some species and eliminating others (Jacobi 1987; Seed and Suchanek 1992; Denny et al. 1998; Commito and Rusignuolo 2000). In particular, mussel beds may alter water flow, which can influence the recruitment of macrofauna including the settlement of larvae as well as redistribution of settled individuals (Commito and Rusignuolo 2000; Snelgrove and Butman 1994). For instance, studies that have measured water flow over *Mytilus edulis* beds demonstrated that roughness elements may play an important role in controlling a number of ecologically important processes, including biodeposition and erosion rates (Widdows et al. 1998), food regulated growth and vertical gradients of particulate organic material (Fréchette and Bourget 1985a, b; Fréchette et al. 1989; Fréchette and Grant 1991), and removal of individuals by current-induced dislodgement (Dolmer and Svane 1994). However, specific mechanisms which may explain the small spatial variability within intertidal and subtidal sites of the three mussel beds remain unclear and need further study.

Conclusions

The different diversity of associated epifauna between intertidal and subtidal mussel beds was mainly caused by differences in juvenile abundances of *Littorina littorea* and *Carcinus maenas* and by higher subtidal species numbers. Intertidal abundances of both species may fluctuate interannually (Beukema 1991; Buschbaum 2001)

and, therefore, the differences between intertidal and subtidal species assemblages resulting from this study may become less pronounced in other years. Nevertheless, diversity increased in the adjacent subtidal zones regardless of the assumed fluctuations in juvenile abundances and, therefore, intertidal and subtidal mussel beds should not be considered the same.

Based on this finding, the current National Park policy which sets aside the intertidal mussel beds for nature conservation whilst subtidal mussel beds are left to the partial exploitation of the mussel fishery, needs to be re-considered. Monitoring of mussel stocks and community structure (Nehls 2000) should no longer be confined to the intertidal mussel beds but should include those of the subtidal zone as well. If conservation attempts to cover all biotic components of the Wadden Sea within the National Park, wild subtidal mussel beds with their high diversity cannot be entirely sacrificed to the fishery.

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The experiments comply with current laws.

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