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Mytilid mussels: global habitat engineers in coastal sediments

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Abstract Dense beds of mussels of the family Mytilidae occur worldwide on soft-bottoms in cold and warm temperate coastal waters and have usually been considered hot spots of biodiversity. We examined intertidal mussel beds at four distant locations around the globe with the same sampling method, to find out whether this "hot spot" designation holds universally. We studied species assemblages within the matrices of byssally interconnected mussels engineered by *Mytilus edulis* in the North Sea, by mixed *Perumytilus purpuratus* and *Mytilus chilensis* at the southern Chilean coast, by *Musculista senhousia* in the Yellow Sea and by *Xenostrobus inconstans* at the coast of southern Australia. In all cases, species assemblages inside mussel beds were significantly different from those outside with many species being restricted to one habitat type. However, species richness and diversity were not generally higher in mussel beds than in ambient sediments without mussels. In the North Sea (*M. edulis*) and at the Chilean coast (*P. purpuratus*, *M. chilensis*), mussel beds have markedly higher species numbers and diversities than surrounding sediments, but this was not the case for mussel beds in Australia (*X. inconstans*) and the Yellow Sea (*M. senhousia*) where numbers of associated species were only slightly higher and somewhat lower than in adjacent sediments, respectively. In conclusion, although soft bottom mytilid mussels generally enhance habitat heterogeneity and species diversity at the ecosystem level, mussel beds themselves are not universal centres of biodiversity, but the effects on associated species are site specific.

Keywords Ecosystem engineer · Mussel bed · Diversity · Species richness · Soft bottom

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Introduction

Mytilid mussels occur on rocky and sedimentary coasts worldwide (Suchanek 1986). They tend to form dense aggregations by attaching byssal threads to the substratum and conspecifics. These persistent bioaggregates physically change the environment and create unique habitats (Gutiérrez et al. 2003). Therefore, according to the concept of Jones et al. (1994, 1997), mussels are considered ecosystem engineers (Crooks 2002; Gutiérrez et al. 2003). Beds of mytilid mussels are highly structured compared to surrounding areas (Fig. 1) and this entails a specific and

Fig. 1 Mytilid mussels form beds on rocky and sedimentary shores. Soft bottom mussel beds may grade from epibenthic with most mussels lying upon the sediment surface to endobenthic with most individuals lodged in the sediment
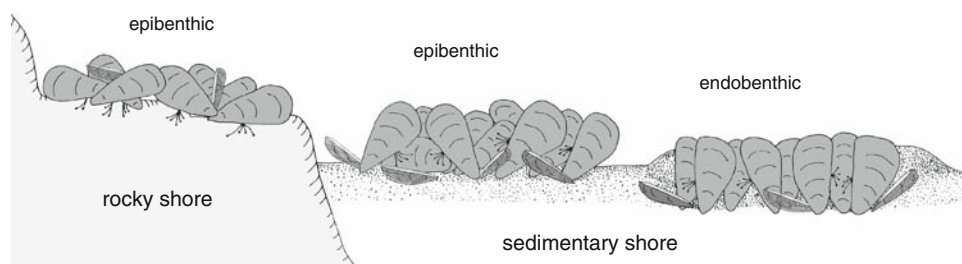
diverse associated species assemblage (e.g. Asmus 1987; Ong Che and Morton 1992; Seed and Suchanek 1992; Peake and Quinn 1993; Lintas and Seed 1994; Seed 1996; Smith et al. 2006; Büttger et al. 2008). Rocky shore mytilid mussel beds are considered biodiversity hot spots because they harbour communities that are generally more diverse than assemblages on surrounding rock without mussels. This pattern occurs in beds of *Mytilus californianus* Conrad on the Pacific coast of North America (Suchanek 1986, 1992), patches of *Mytilus edulis* L. in Japan (Tsuchiya and Nishihira 1985, 1986), aggregations of *Perumytilus purpuratus* Lamarck in Chile (Thiel and Ullrich 2002; Valdivia and Thiel 2006), beds of *Semimytilus algosus* (Gould) in central Peru (Tokeshi 1995; Tokeshi and Romero 1995) and mussel beds of *Brachidontes rodriguezii* (d'Orbigny), *Mytilus edulis platensis* (d'Orbigny) and *Perna perna* (L.) on the Atlantic coast of Uruguay (Borthagaray and Carranza 2007).

Species associated with beds of mytilid mussel on soft-bottoms have received less attention. On sedimentary coasts of the North Sea, Dittmann (1990), Günther (1996) and Ragnarsson and Raffaelli (1999) detected higher macrofaunal species richness in *M. edulis* beds than on surrounding flats. The same was true for soft bottom *M. edulis* beds on the west coast of Sweden (Norling and Kautsky 2007). These North Sea data were obtained from mainly epibenthic mussel beds in which the living individuals are positioned on the sediment surface or only slightly stuck in the mud.

While mussels on rocky surfaces are always epibenthic, soft bottom mussel beds may also be endobenthic, with a diversity of transitions between epibenthic and endobenthic mode (Fig. 1). In endobenthic beds, most individuals are positioned below the sediment surface and only the posterior end with the siphonal apertures projects above the surface (Albrecht and Reise 1994). Endobenthic mussel beds may also be inhabited by a rich associated assemblage of species. For example, on the US Pacific coast, the introduced mussel *Musculista senhousia* Benson in Cantor has facilitating effects on other organisms (Crooks 1998). Densities of macrofaunal individuals and species richness were higher inside than outside these mussel mats. However, studies performed by Commito (1987) and Commito et al.

(2005) on the US Atlantic coast revealed that semi-endobenthic beds of *M. edulis* may have species diversities that are similar or reduced in comparison to the surrounding sedimentary environment. This suggests that mussel aggregations in sedimentary environments may not invariably be diversity hot spots within the ecosystems in which they are found.

Therefore, we propose that the specific modes in which mussels provide hard substratum and shelter, stabilize, accrete and modify sediments and occupy space can have facilitatory on some as well as inhibitory effects on other species. Depending on the coastal system and its species assemblage these effects may result in either enhanced or decreased diversity within mussel beds. Independently of the richness of associated communities, mussel aggregations may provide habitat to species that are otherwise absent or rare in soft bottom habitats (Commito and Dankers 2001). Thus, we go on to propose that mussel beds generally increase biodiversity at the ecosystem level by enhancing habitat heterogeneity, while biodiversity within beds may not be necessarily higher than outside.

To explore these propositions we studied associated species assemblages of soft bottom mussel aggregations in comparison to the surrounding tidal flats without mussels in four coastal systems worldwide. We investigated epibenthic beds of the mussel *M. edulis* in the Northeast Atlantic (North Sea) and mixed aggregations of *P. purpuratus* and *M. chilensis* Hupe 1854 in the Southeast Pacific, while endobenthic beds of the bivalves *M. senhousia* and *Xenostrobus inconstans* (Dunker) were examined in the Northwest Pacific (Yellow Sea) and southern Indopacific, respectively.

Materials and methods

Mussel beds and study sites

Investigations of mussel beds of *M. edulis* and surrounding sand flats were conducted in the northern Wadden Sea near the island of Sylt (54°55′N, 008°20′E) in the Northeast Atlantic (North Sea, German Bight) in August 2002 (Fig. 2). The study area belongs to the cold temperate

Fig. 2 Study areas of mussel beds and surrounding intertidal sediments: epibenthic mussel beds were investigated in the Northeast Atlantic (North Sea, beds of *Mytilus edulis*, **a**) and in the Southeast Pacific (beds of *Mytilus chilensis* and *Perumytilus purpuratus*, **b**). Endobenthic mussel beds were studied in the West Pacific (Yellow Sea, beds of *Musculista senhousia*, **c**) and in the Indian Ocean (beds of *Xenostrobus inconstans*, **d**). Study sites are marked by an *arrow*
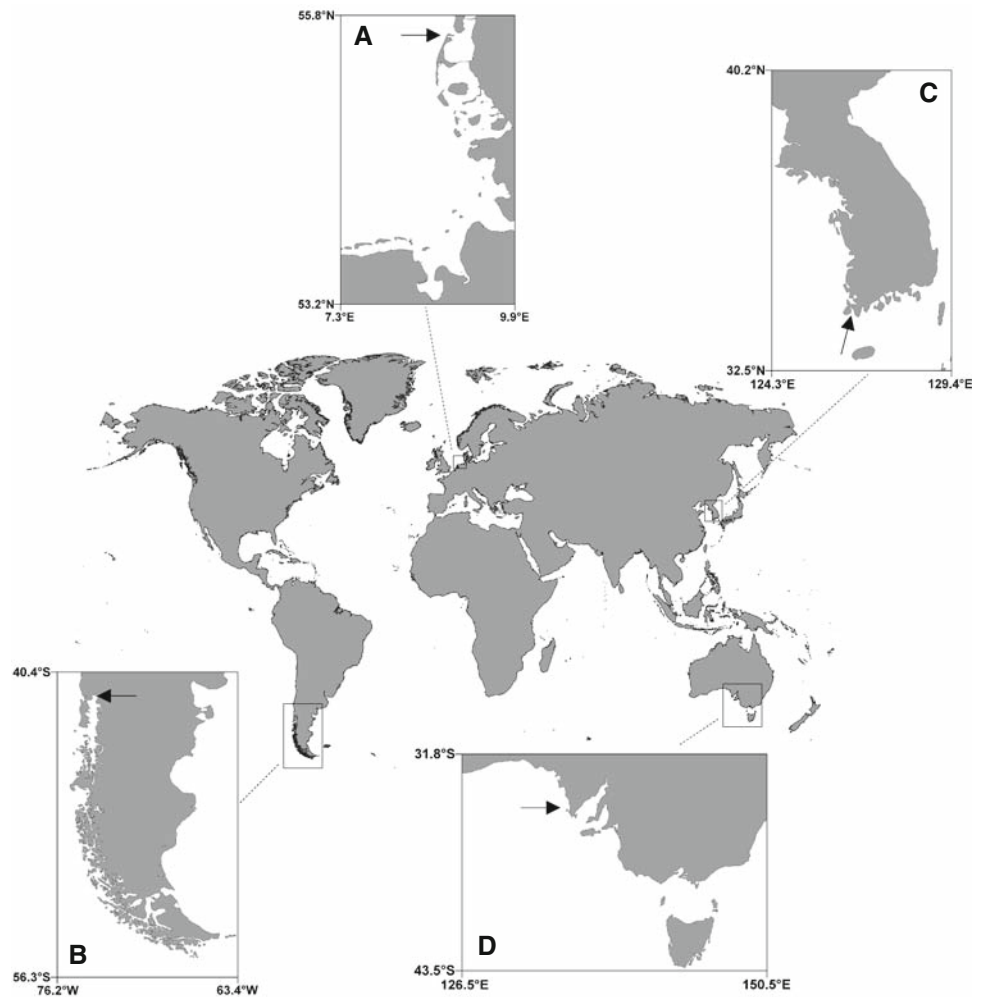
region with a mean annual water temperature of about 9°C, a summer average of 15°C, and a winter average of 4°C. Tides are semi-diurnal (mean range of 2 m) and salinity remains close to 30 psu. For further information on the area see Reise (1985) and Gätje and Reise (1998).

M. edulis is a common mytilid mussel of north European coastal systems where it occurs on both rocky and sedimentary shores (Seed and Suchanek 1992). In the intertidal zone of the northern Wadden Sea, *M. edulis* forms predominantly multi-layered beds on the sediment surface and may achieve densities of about 4,000 ind. m^{-2} (Buschbaum and Saier 2001). These are categorized as epibenthic because most living mussels dwell above the sediment surface.

In March 2003, we studied a second type of epibenthic mussel bed formed by the bivalves *M. chilensis* and *P. purpuratus* at Bahia Cohuin near Puerto Montt (41°29′S, 072°52′W), an intertidal soft bottom area in the fjord region of southern Chile, Southeast Pacific (Fig. 2). Here, the tidal range is close to 5 m (Duarte et al. 2006, Jaramillo et al. 2007). Water temperatures range from 12°C in winter to 26°C during the summer season (Gebauer et al. 2007).

Depending on rainfall, salinity ranges from 25 to 30 psu. In this coastal environment, mussel beds comprise *M. chilensis* and *P. purpuratus*. Mussel beds in the low intertidal zone are dominated by *M. chilensis* while those in the mid intertidal zone are dominated by *P. purpuratus*, which may contribute up to two-thirds of total mussel densities (about 3,500 m^{-2}, M. Thiel, unpublished data). While the purple mussel *P. purpuratus* usually inhabits intertidal hard bottoms (Thiel and Ullrich 2002), in the fjord region it may also form dense aggregations on soft bottoms, similar to those reported for *M. edulis*.

On the west coast of South-Korea (Yellow Sea), about 60 km south of the city of Mokpo near Sanjong/Donghyeon (34°21′N, 126°30′E) we investigated species richness and diversity in mussel aggregations formed by the bivalve *M. senhousia* and in the ambient tidal flats (Fig. 2). Tidal range is about 2.5 m. Studies were done in July 2002. In this year water temperature ranged from 7°C in winter (February) to 25°C in summer (August) while salinity remained close to 32 psu the whole year round (J.-S. Hong, personal communication).

Musculista senhousia is a comparatively small (maximum shell length up to 35 mm) mytilid bivalve with a life span of less than 2 years (Morton 1974). As with other mytilid mussels, *M. senhousia* produces byssal threads and uses them to create byssal bags or cocoons. At high densities of >1,500 m^{-2} it forms a mat on the bottom consisting of a matrix of empty bivalve shells, byssal threads and ambient sediment (Morton 1974, 1992; Crooks 1996; Reusch and Williams 1998). Mussel aggregations form hummocks on the bottom and individuals are lodged within the sediment and only a few individuals pop up at the surface. These mussel beds are categorized as endobenthic.

We investigated beds of *X. inconstans* in Kellidie Bay, a sedimentary bight within Coffin Bay on the southern shore of Australia (34°37′S, 135°30′E, Indian Ocean) in January 2007 (Morton 1992; Dittmann 2007; Fig. 2). The tides in this area are considerably more irregular than in many parts of the world and only semi-diurnal at spring periods. Tidal range is about 2 m, but may be greatly modified by winds. Mean seawater temperatures are about 19°C in summer (February) and 14°C during winter (August). During summer water temperatures of up to 30°C occur in shallow bays or inlets. General information on the hydrography, biota and ecology of south Australian coasts is available in Womersley and Edmonds (1958) and Edgar (2000). As with *M. senhousia*, most *X. inconstans* individuals were lodged within the sediment but they were more crowded, which pushed several individuals above the sediment surface. As these are still a minority, we categorize the Australian mussel beds as endobenthic.

Sampling procedure

All mussel beds and surrounding bare tidal flats without bivalves were sampled with exactly the same procedure to ensure homogeneity of the methods used at all study sites. Mussel beds had a size of >10 m^2 and were at least 2 years old. They were sampled using a corer of 10.5 cm diameter (corresponding to an area of 85 cm^2). Previous investigations indicated that sample sizes between 50 and 200 cm^2 provide representative estimates for species and individual numbers of organisms living associated with mussel beds (Günther 1996; Asmus 1987; Tsuchiya and Nishihira 1985; Commito and Boncavage 1989; Ragnarsson and Raffaelli 1999; Peake and Quinn 1993; Duarte et al. 2006).

The corer was inserted to a depth of 20 cm into the sediment. Then, the mussel mats on top of the samples were carefully separated from the sediment below and washed over a 0.5 mm sieve. Mussels were counted and their lengths measured (maximum anterior–posterior axis) to the nearest 1 mm using vernier callipers. Additionally, all epibionts (macroalgae and invertebrates) attached to the mussels and all mobile organisms remaining in the sieve were

quantified and identified to the lowest taxonomic level possible.

The sediment sample was divided into two sub samples. The upper 5 cm sediment layer was sieved through a 0.5 mm mesh size, and a 1-mm sieve was used for the lower 15 cm sediment layer. This was done because most soft bottom organisms live in the upper 5 cm and individuals <1 mm seldom occur in deeper sediment layers. All live organisms retained in the sieves were counted and identified to the lowest taxonomic level possible.

We classify the associated community into epibiotic species (sessile species that were attached to mussels), epibenthic organisms (mobile species living on the sediment surface and between the mussels) and endobenthic species (living below the sediment surface). These are the three characteristic categories of organisms comprising a mussel bed association (Suchanek 1986; Lintas and Seed 1994).

Samples of the sedimentary areas around mussel beds were taken and handled in the same way. However, as there were no mussels in these samples, no epibenthic layer was treated separately. In all areas investigated we collected 12 mussel bed samples and 12 samples from surrounding tidal flats, respectively. At each study site, samples were haphazardly taken from several mussel beds located in the lower tidal zone and from a large area (1,000 × 1,000 m) of surrounding tidal flats consisting of sandy sediments.

Statistical analyses

Data are presented as arithmetic means with standard deviation (SD). Mussel density differences between mussel beds formed by different mytilid species were tested by a Kruskal–Wallis *H* test (Kruskal–Wallis ANOVA), followed by pairwise Mann–Whitney *U* tests. We analysed mean species number differences inside and outside the mussel beds with *t* tests. *F* tests were used to test for homoscedasticity of variances, and dependent variables were log $(x + 1)$-transformed when variances were heterogenous. Results were considered statistically significant at $P \leq 0.05$ and the Bonferroni correction was applied to multiple comparisons.

Entire communities of mussel beds and surrounding sedimentary areas of the respective study sites were analysed using multivariate, non-parametric ordination techniques including multidimensional scaling (MDS) and analysis of similarities (ANOSIM) based on the Bray–Curtis similarity comparisons in the PRIMER™ software package (Clarke and Warwick 2001). Multivariate analyses were performed on square root transformed data. The PRIMER™ software package was also used for preparing species–sample/area plots. For comparison of species assemblages, two indices were calculated: (1) Shannon Wiener Index $H = -\sum p_i \ln p_i$, where p_i is the proportion of the total number of individuals

(N) made up by specimens of species$_i$ (n_i): $p_i = n_i/N$, and (2) Evenness $e = H/\ln S$, where S is the total number of species.

Results

Mussel bed characteristics

Mussel size-frequency distribution differed among mussel beds (Fig. 3). Epibenthic beds of *M. edulis* in the Wadden Sea had a wide size distribution of individuals ranging from 5 to 60 mm lacking conspicuous modes. In epibenthic beds consisting of *P. purpuratus* and *M. chilensis* in Chile, most mussels occurred within the size range from 20 to 43 mm with a strong peak around 30 mm.

The size-frequency distribution of endobenthic beds of *M. senhousia* in South-Korea ranged only from 5 to 19 mm and was almost uni-modal, with a peak close to 12 mm. Shell lengths of *X. inconstans* forming endobenthic mussel beds in Australia ranged from 1 to 28 mm and the size-frequency distribution shows two strong modes, with peak frequencies near 8 and 21 mm.

Mussel densities in beds formed by different mytilid species were significantly different (Kruskal–Wallis H test, $P < 0.0001$, $n = 12$), and differed significantly from each other (Mann–Whitney U test, $P < 0.002$, Bonferroni corrected level of significance $P < 0.008$, $n = 12$), except for Wadden Sea *M. edulis* ($1,871 \pm 751$ ind. m^{-2}) and South Korean *M. senhousia* ($1,927 \pm 718$ ind. m^{-2}). Highest mussel density occurred in beds of *X. inconstans* in Australia ($18,393 \pm 5,831$ ind. m^{-2}) while abundances in mussel beds of *P. purpuratus* and *M. chilensis* were intermediate
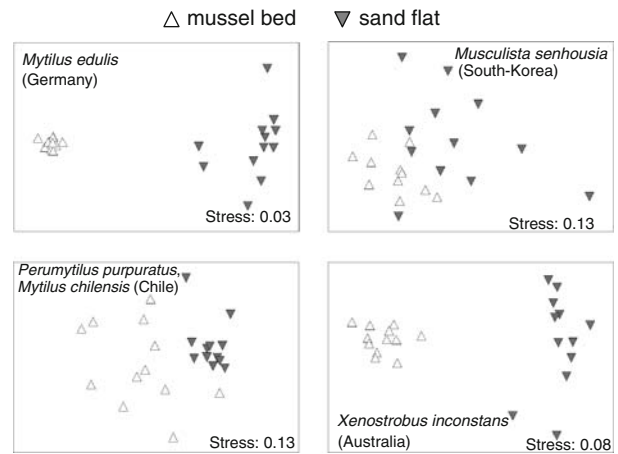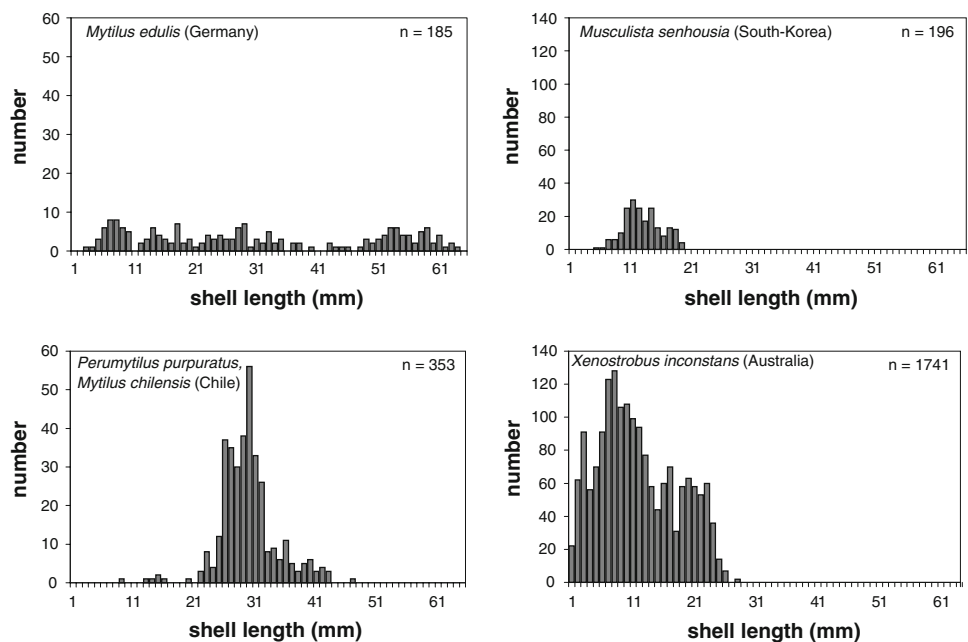
Fig. 4 Multidimensional scaling (MDS) ordination plots of species communities inside and outside mussel beds in four regions of the world (see Fig. 2). Analyses are based on Bray–Curtis similarities using abundance data of species

(total abundance $3,442 \pm 515$ ind. m^{-2}; *P. purpuratus* $2,380 \pm 741$ ind. m^{-2}, *M. chilensis* $1,062 \pm 511$ ind. m^{-2}) on the Chilean coast.

Community analyses

The species communities inside and outside of mussel beds were significantly different in the four coastal systems (Fig. 4). The ANOSIM procedure calculated an R-statistic of 0.997 ($P < 0.001$) for differences among communities of mussel beds (*M. edulis*) and sand flats in the North Sea (Germany) and an R-statistic of 0.507 ($P < 0.001$) for differences among assemblages of mussel aggregations

Fig. 3 Pooled shell length data for all samples of mussels *Mytilus edulis* in the Northeast Atlantic (Germany), *Perumytilus purpuratus* and *Mytilus chilensis* in the Southeast Pacific (Chile) and beds of *Musculista senhousia* in the Yellow Sea (South-Korea) and of *Xenostrobus inconstans* in the Indian Ocean (Australia). Sample size was 85 cm^2 ($n = 12$ samples per area)

(*P. purpuratus* and *M. chilensis*) and surrounding bare areas at the Chilean coast. Communities of mussel beds of *M. senhousia* ($R = 0.333$) and *X. inconstans* ($R = 0.987$) were also significantly different from assemblages inhabiting tidal flats without mussels ($P < 0.001$, respectively).

The Shannon Wiener Index H was higher in mussel beds in the North Sea, Chilean and south Australian coasts, but lower in the Yellow Sea in comparison to sediments without mussels (Table 1). Evenness was higher in mussel beds in the North Sea and on the south Australian coast, but lower at the Chilean coast and in the Yellow Sea compared to surrounding sediments. At all study sites, percentage of species found only in mussel beds was at least 30%, and reached 59% in beds of *M. edulis* in the North Sea (Table 2). Crustaceans, molluscs and polychaetes were the main taxanomic groups in both mussel beds and sand flats in all investigated areas (Table 3).

Associated species richness

In both epibenthic mussel beds of *M. edulis* (Germany) and mixed beds of *P. purpuratus* and *M. chilensis* (Chile), total species number was about double that in surrounding sand flats (Fig. 5). In endobenthic mussel beds, the pattern was not as clear cut as in epibenthic mussel aggregations. Beds of *M. senhousia* in South-Korea had reduced species numbers in comparison to the bare tidal flat (Fig. 5). In contrast, species richness of *X. inconstans* beds (Australia) was slightly higher inside mussel aggregations than outside.

Species–sample curves of the sites had similar shapes, reaching asymptotes (Fig. 5). This indicates that the respective species communities are representatively sampled and an increase in sampling effort would not have changed results.

The mean species number in mussel beds and surrounding sand flats fitted the pattern for total species number (Fig. 6). In North Sea *M. edulis* beds, mean species number (16.6 ± 2.1 species per sample) was significantly higher (*t* test, $P < 0.0001$) than in areas without mussels (5.1 ± 1.3 species per sample). In Chilean mixed beds of *P. purpuratus* and *M. chilensis* mean species number in mussel aggregations (11.0 ± 1.3 species per sample) was also significantly higher (*t* test, $P < 0.0001$) than on bare tidal flats (7.9 ± 1.2 species per sample).

Table 1 Shannon Wiener Index H and evenness e in mussel beds and surrounding sediments without mussels of the respective study sites

	North Sea		Chilean coast		Yellow Sea		South Australian coast	
	Mussel bed	Sand flat	Mussel bed	Sand flat	Mussel bed	Sand flat	Mussel bed	Sand flat
Shannon Wiener H	1.84	1.06	2.14	1.74	1.70	2.67	2.31	1.52
Evenness e	0.53	0.38	0.69	0.70	0.63	0.90	0.67	0.47

Table 2 Total number of species, species number detected in only one habitat and number of species occurring in both mussel beds and sand flats in the study sites

|	North Sea	Chilean coast	Yellow Sea	South Australian coast
Total no. of species	41	25	29	42
No. of species restricted to mussel beds	24 (59%)	13 (52%)	9 (31%)	16 (38%)
No. of species restricted to sand flats	9 (22%)	2 (8%)	14 (48%)	10 (24%)
No. of species occurring in both habitats	8 (19%)	10 (40%)	6 (21%)	16 (38%)

Numbers of epibiotic, epibenthic and endobenthic species within the dominant taxa are given in parentheses (epibionts/epibenthos/endobenthos)

Table 3 Species number of dominant taxa in mussel beds and surrounding sediments

	North Sea		Chilean coast		Yellow Sea		South Australian coast	
	Mussel bed	Sand flat	Mussel bed	Sand flat	Mussel bed	Sand flat	Mussel bed	Sand flat
Algae	4 (4/0/0)	0 (0/0/0)	0 (0/0/0)	0 (0/0/0)	0 (0/0/0)	0 (0/0/0)	4 (4/0/0)	0 (0/0/0)
Crustacea	6 (3/3/0)	2 (0/2/0)	7 (2/5/0)	2 (0/2/0)	1 (0/1/0)	1 (0/1/0)	6 (1/5/0)	3 (0/3/0)
Mollusca	4 (1/2/1)	2 (0/0/2)	4 (0/3/1)	1 (0/0/1)	5 (0/1/4)	4 (0/0/4)	11 (0/8/3)	13 (0/8/5)
Polychaeta	13 (1/3/9)	11 (0/1/10)	7 (0/0/7)	6 (0/0/6)	8 (0/0/8)	15 (0/1/14)	8 (0/0/8)	9 (0/0/9)
Other species	5 (3/1/1)	2 (0/0/2)	5 (0/1/4)	3 (0/0/3)	1 (0/0/1)	0 (0/0/0)	3 (1/1/1)	1 (0/1/0)

Numbers of epibiotic, epibenthic and endobenthic species within the dominant taxa are given in parentheses (epibionts/epibenthos/endobenthos)

Fig. 5 Species–sample curves for mussel beds (*left panels*) and surrounding sand flats without mussels (*right panels*) in four regions of the world (see Fig. 2)
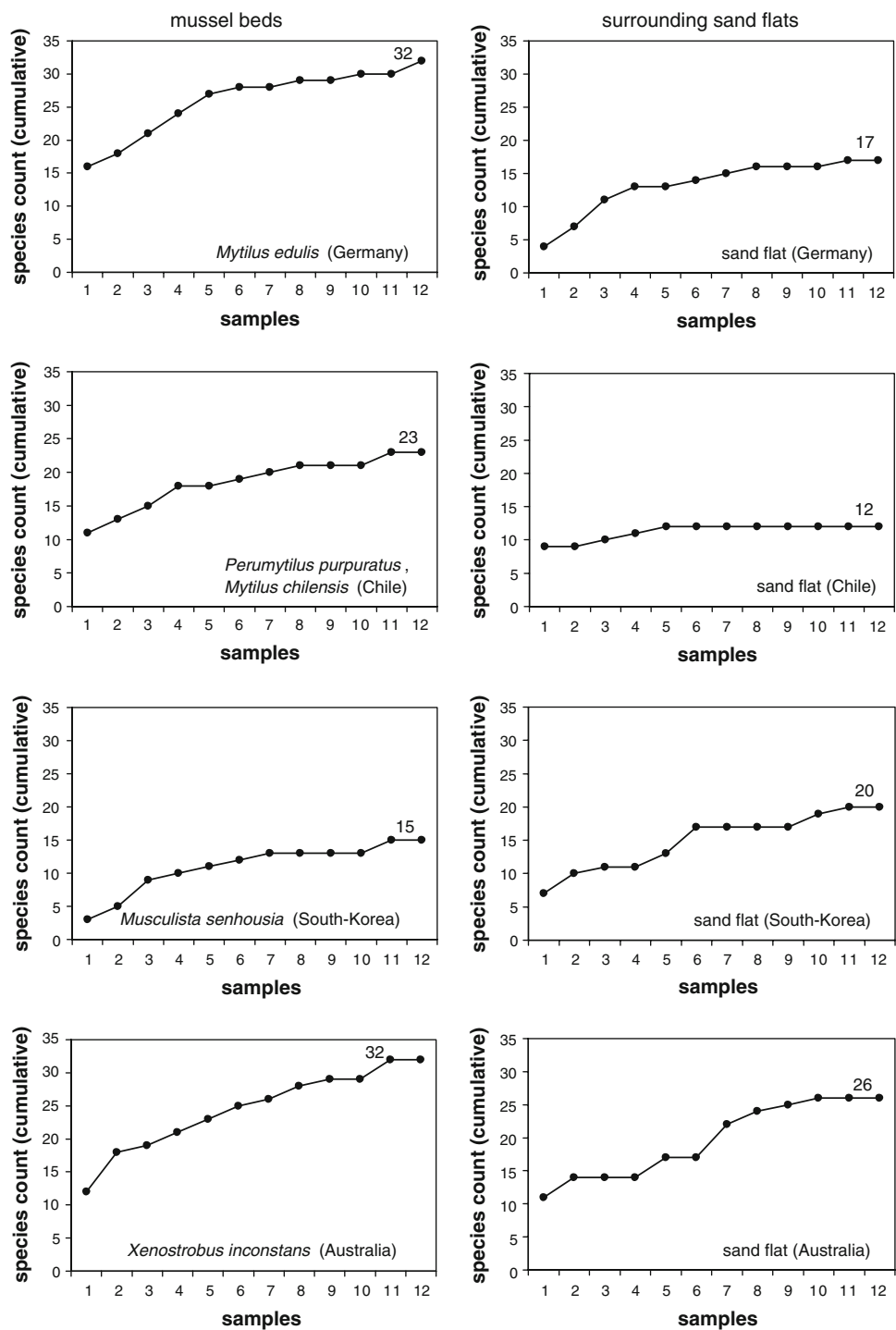
In contrast, in Korean beds of *M. senhousia*, mean species number (2.6 ± 1.3 species per sample) was lower in comparison to samples without mussels (4.0 ± 1.8 species per sample; t test, $P < 0.05$) while Australian beds of *X. inconstans* showed an increased mean species number (13.3 ± 1.4 species per sample) compared to surrounding tidal flats (9.4 ± 2.1 species per sample; t test, $P < 0.0001$).

Occurrence of epibionts, epibenthic and endobenthic species

Epibionts were not encountered on sand flats because of the lack of epibenthic structures (Fig. 7). The total number of epibenthic species (without epibionts) was similar in mussel beds of Germany (*M. edulis*) and Chile (mixed *P. purpuratus* and *M. chilensis*) and much higher than in areas

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Fig. 6 Mean species number
per sample (+SD, *n* = 12) in
epibenthic mussel beds (beds of
M. edulis in Germany and mixed
beds of *P. purpuratus* and
M. chilensis in Chile) and
endobenthic mussel beds (beds
of *M. senhousia* in South Korea
and *X. inconstans* in Australia)
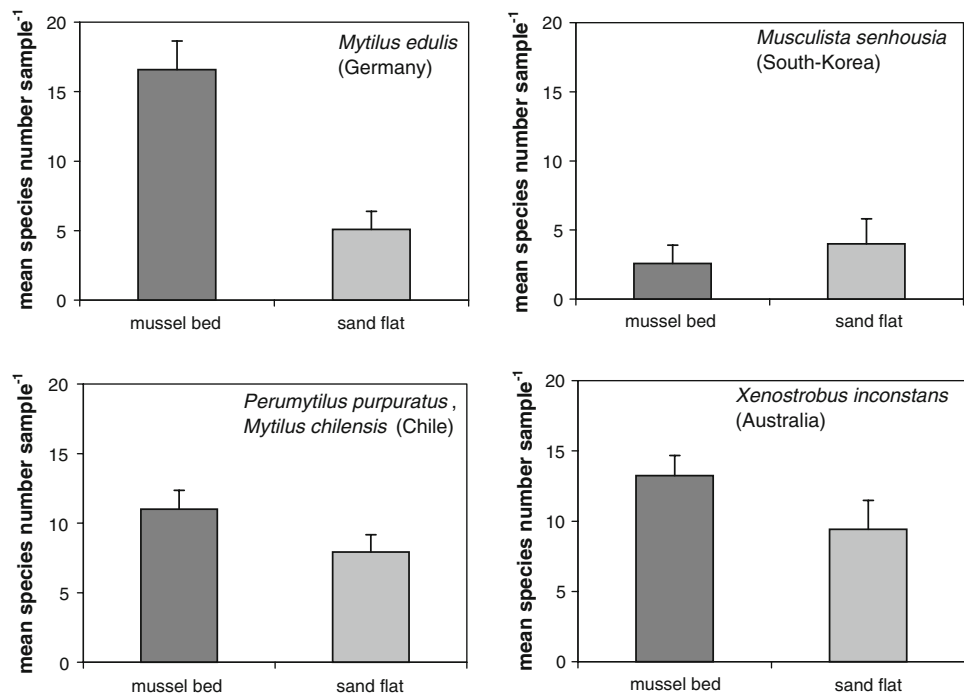in comparison to bare tidal flats
without mussel aggregations

Fig. 7 Total numbers of epi-
bionts, epi- and endobenthic spe-
cies occurring in epibenthic
mussel aggregations (*M. edulis*
beds in Germany and mixed *P.
purpuratus* and *M. chilensis*
beds in Chile) and endobenthic
mussel beds (beds of *M. senhou-
sia* in South Korea and *X. incon-
stans* in Australia) in
comparison to surrounding bare
sand flats
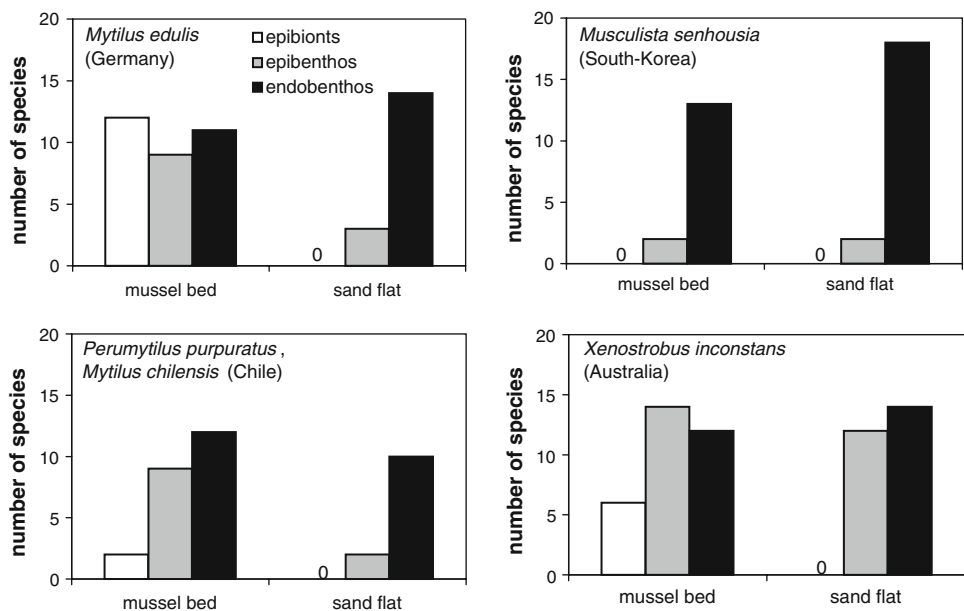
without bivalves. In both systems, the total number of
endobenthic species was similar in mussel beds and sur-
rounding sand flats.

In *M. senhousia* beds (Yellow Sea, South-Korea), no
epibiontic species were detected whereas six epibiontic
species were identified in *X. inconstans* beds in Australia.
In both South-Korea and Australia, total epibenthic species
number was similar in mussel beds and areas without
bivalves, although there were many times more of such
species in Australia. Total endobenthos species number in
M. senhousia beds was lower than in bare sand flats in

South Korea, while number of endobenthic species was
similar in *X. inconstans* beds and sand flats in Australia.

Mean number of epibenthic organisms per sample was
significantly higher in mussel beds in Germany and Chile in
comparison to areas without mussels (*t* test, *P* < 0.0001,
respectively) while no significant differences existed in
mean numbers of endobenthic organisms in mussel beds
and surrounding sand flats (*t* test, *P* > 0.05, respectively,
Fig. 8).

In beds of *M. senhousia* mean species numbers of epi- and
endobenthic organisms showed no significant difference

Fig. 8 Mean species number per sample (+SD, $n = 12$) of epibionts, epi- and endobenthic organisms occurring in epibenthic mussel beds (beds of *M. edulis* in Germany and mixed beds of *P. purpuratus* and *M. chilensis* in Chile) and endobenthic mussel beds (beds of *M. senhousia* in South Korea and *X. inconstans* in Australia) compared to tidal flats without mussel aggregations
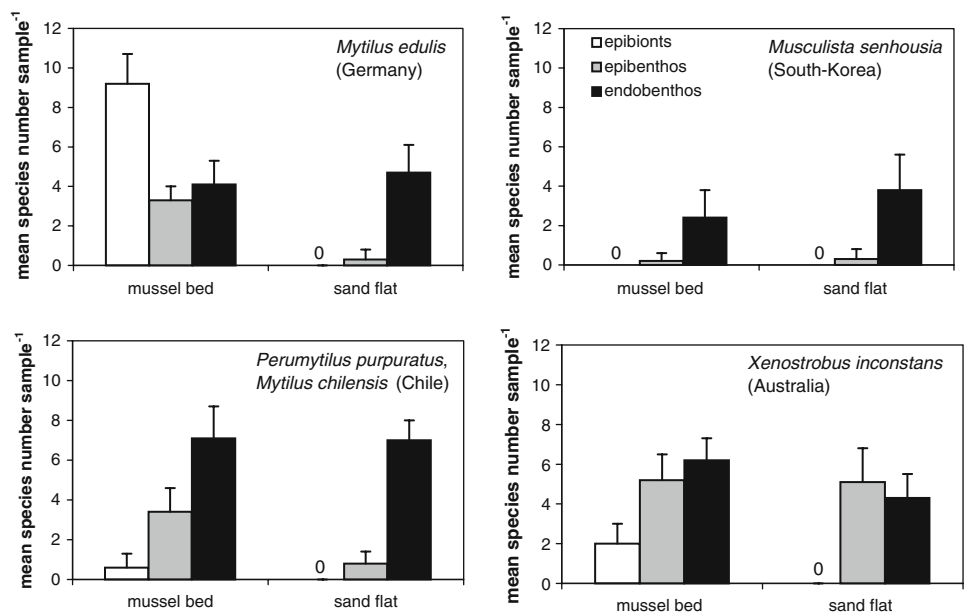
(t test, $P > 0.05$, respectively). In addition, there was no difference in mean number of epibenthic species between mussel aggregations and bare tidal areas in Australia (t test, $P > 0.05$). Mean number of endobenthic species was significantly higher in beds of *X. inconstans* (t test, $P < 0.001$).

Discussion

We investigated the species community of four kinds of soft bottom mussel beds generated by different mytilid species and compared the associated organisms with the species assemblage of surrounding sediments in four sedimentary coastal systems worldwide. We recognize that these four sites are hardly representative for all kinds of mussel beds in sedimentary environments. However, given the scarcity of data sets obtained with the same method, time has not yet come for a comprehensive meta-analysis. Our pioneer approach serves to build hypotheses which may stimulate and direct further studies in the infant field of global coastal ecology.

In all regions, species assemblages within mussel aggregations were different from the community occurring in bare sand flats without mussels, which is concordant with other studies on soft bottom mussel beds (e.g. Ragnarsson and Raffaelli 1999; Commito and Dankers 2001; Duarte et al. 2006). Many species were confined to one habitat type and at least 30% of total species number found within one study site was restricted to mussel beds. Although soft bottom mussel beds often cover less than 1% of tidal area in coastal systems (Büttger et al. 2008), they provide an additional habitat with a unique species assemblage that would otherwise not occur. Norling and Kautsky (2007) argue that

the physical structure properties of a soft bottom mussel bed are the main factor responsible for biodiversity of associated species and that biological activities may have an additional positive effect on diversity due to the increased supply of mussel deposits and organic matter as a food source. Therefore, ecosystem engineering mytilid mussels may conspicuously enhance biodiversity by increasing habitat heterogeneity in a sedimentary coastal system.

However, when comparing species richness and diversity inside and outside the investigated mussel beds the pattern was variable. Total species number in mussel beds in the North Sea (*M. edulis*) and at the Chilean coast (*P. purpuratus* and *M. chilensis*) were enhanced, but lower in mussel aggregations in the Yellow Sea (*M. senhousia*) and similar in beds at the south Australian coast (*X. inconstans*) compared to sand flats without mussels. In contrast to our study, Crooks (1998) found higher species richness inside mats of *M. senhousia* on the North American Pacific coast and Commito et al. (2005) demonstrated a decreased diversity in *M. edulis* beds in comparison to sand flats without mussels on the North American Atlantic coast. Species richness within mussel beds may be enhanced but also decreased compared to bare sand flats, depending on the respective ecosystem. Thus, diversity of mussel beds seems to be less dependent on mytilid species and the question arises:

When does a soft bottom mussel bed function as hot spot of diversity?

Our investigations included both the associated species assemblage of epibenthic (North Sea, Chilean coast) and endobenthic mussel beds (Yellow Sea, south Australian

coast). For epibenthic mussel beds, diversity of associated organisms was enhanced, but this was not the case in endobenthic beds.

In sedimentary coastal environments, mussel beds provide the only major hard substratum available, which is especially true for epibenthic beds with most mussels lying on the sediment surface (Dittmann 1990; Albrecht 1998). These are often used by sessile algae and invertebrates, e.g. in mussel beds of *M. edulis* in the North Sea where we detected a high number of organisms attached to the mussels (12 species). However, in epibenthic beds of *M. chilensis* and *P. purpuratus* at the Chilean coast, we detected a comparatively low number of epibionts (two species), which was also lower than in endobenthic beds of *X. inconstans* in Australia (six species). This indicates that epibenthic beds are not generally inhabited by a high number of epibiotic species.

In both epibenthic mussel beds investigated, we detected an enriched epibenthos community (mobile species living predominantly on the sediment surface, not including epibionts) compared to surrounding sediments. These organisms may profit from the structural complexity of mussel aggregations on the bottom which provides refuges from competition, predation and disturbance (e.g. Commito and Dankers 2001; Norling and Kautsky 2007). This pattern is consistent with other studies on species diversity in epibenthic mussel beds (Dittmann 1990; Günther 1996) and high species number of epibenthos was clearly responsible for enriched diversity in this mussel bed type. This may lead to the assumption that epibenthic soft bottom mussel beds have a higher diversity than surrounding sand flats and can, therefore, be considered biodiversity hot spots. However, we investigated only two epibenthic beds and the studies by Dittmann (1990) and Günther (1996) supporting this assumption were also performed on *M. edulis* mussel beds in the North Sea. Thus, further investigations on epibenthic mussel in different coastal systems are necessary. They should include experimentally arranged epi- and endobenthic mussel beds of one mytilid species to enable direct comparisons of diversity within a study area.

That epibenthic mussel beds do not necessarily have a rich associated community is clear from the low numbers of epibionts attached to epibenthic mussel beds on the Chilean coast. Therefore, at the present state of knowledge, a generalisation of the structural function of epibenthic soft bottom mussel beds for associated organisms must be considered tentative.

That mussel beds cannot generally be considered biodiversity centres is supported by our investigations on endobenthic beds in the Yellow Sea and at the south Australian coast. Woodin (1976) predicted that densely packed suspension feeding bivalves may prevent successful larval settlement of associated organisms through intensive filtration activity and ingestion of free swimming larvae. Additionally, she stated that recently settled larvae are suffocated in produced faecal material where conditions for many animals are harmful due to low oxygen and high sulphide concentrations. This would result in decreased species richness and abundance in beds with high mussel densities. In endobenthic mussel beds in Australia, *X. inconstans* attained densities of about 18,000 ind. m^{-2}, which was ninefold higher than in mussel beds of *M. senhousia* in the Yellow Sea. Despite high mussel densities in Australian beds, total species number of infauna was similar and mean number of infaunal species per sample was about twice as high as that in beds of *M. senhousia*. Furthermore, associated epi- and endobenthic species numbers in *X. inconstans* beds were similar to surrounding sedimentary areas without mussels, and most of the endobenthic organisms within mussel beds were polychaete worms (Dittmann and Buschbaum in preparation). These results suggest that high mussel densities do not prevent a rich and diverse associated community of infaunal organisms. On the other hand, beds with reduced mussel densities may not be inhabited by a rich associated community, as we have shown for the Yellow Sea. These findings are in concordance with results obtained by Jaramillo et al. (2007) and contradict Woodin's hypothesis which was also questioned by Commito (1987), Commito and Boncavage (1989) and Commito and Dankers (2001).

Hence, the question of whether a mussel bed is highly diverse seems to be less dependent on the mytilid species, the density and epi- versus endobenthic traits.

Site-specific character of soft bottom mussel beds

We suggest that the degree of diversity may depend strongly on the regional spectrum of species and the ability of these species to adapt to the engineered conditions within mussel beds. Soft bottom mussel beds may constitute physically similar habitats throughout the world but the responses of other benthic species may not be the same, and thus the arising mussel bed communities arise by site-specific rules. Future research will need to include the species pools of habitats in the respective regions which are the main sources to the species colonizing mussel beds.

The non-deterministic effects of mussel beds on associated communities may serve as an analogue to the limitations of predicting the effects of alien species invasions. Particularly, mussels have been introduced across oceans many times with both, facilitating and inhibiting effects on species in recipient ecosystems (e.g. Branch and Steffani 2004; Crooks 1998; Crooks and Khim 1999; Rilov et al. 2004; Robinson et al. 2007). Apparently, we cannot derive the effects directly from the properties of mussel species. They unfold their effects by interactions with the respective physical and biotic environment, including feedbacks

operating over long time scales. In conclusion, our study supports the non-deterministic nature of ecological networks by recognizing a site-specific pattern in mussel bed communities over the world.

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