ORIGINAL ARTICLE

Werner Armonies · Karsten Reise

Empty habitat in coastal sediments for populations of macrozoobenthos

Abstract Species with wide dispersal are expected to have little empty habitat. This was tested by analysing habitat use in the Wadden Sea near the island of Sylt (North Sea). Sampling covered 222 intertidal sites spread across the Königshafen tidal flats (4.5 km^2, mapping approach conducted once) and 270 subtidal sites along 12 km of a tidal channel system (stratified random sampling in spring and autumn). For any single species, 'suitable habitat' was extrapolated from the ranges of water depth and sediment composition present at the ten sites with the highest frequency or abundance of the species. On average, macrobenthic species actually used less than half of the suitable sites within the scale of local populations; this was far less than expected from a lognormal distribution. In the subtidal, abundance of most species changed between the two sampling seasons. A 50% increase in overall abundance was accompanied by a decrease in empty habitat of only about 25%. Thus, a doubling of abundances would not fill the empty space but just of half of it. The polychaete *Scoloplos armiger* was an exception in occupying almost all of its suitable habitat in the intertidal and subtidal sediments. A distinct patch of high species richness occurred where flood waters persistently form a large gyre which may enhance larval settlement. We suggest that limitations to larval settlement and/or juvenile survival primarily cause the extent of the observed habitat emptiness.

Keywords Benthos · Patchiness · Spatial pattern · Larval supply

W. Armonies (✉) · K. Reise
Alfred Wegener Institute for Polar and Marine Research,
Wattenmeerstation Sylt, 25992 List, Germany
e-mail: warmonies@awi-bremerhaven.de
Tel.: +49-4651-956138, Fax: +49-4651-956200

Introduction

The fraction of localities occupied by a species at any one time increases with migration rate (dispersal) and the density of suitable localities (Andrewartha and Birch 1954). Coastal macrozoobenthos commonly have a large capacity for dispersal, often by pelagic larvae. Where tidal currents keep the coastal waters moving about, individuals may disperse across large areas and any suitable locality within the distributional area may be settled. Furthermore, suitable sedimentary areas occur more or less continuously across wide areas. Therefore, our hypothesis is that all potentially suitable habitats are occupied at any one time. The only exceptions may be habitats with a highly patchy distribution such as mussel beds, and species which lack long-distance dispersal.

However, strong currents may prevent larval settlement to the sediment (Butman 1986; Eckman 1990) resulting in suitable but nevertheless empty habitats. On the other hand, intermittent stagnant conditions (e.g. during slack tides) might facilitate larval settlement and result in local accumulations of the recruits of many species (Gross et al. 1992; Snelgrove 1994; Hsieh and Hsu 1999). Both empty habitat and areas with a higher than average species richness may also develop after larval recruitment (post-settlement processes). Possible causes are local extinctions (e.g. from winter cold or predation pressure) with retarded recolonisation (e.g. because larvae occur seasonally only) or sediment disturbance, for instance by gales. Any of these factors have been shown to affect some benthic species in the Wadden Sea (see Beukema 1992; Posey et al. 1996; Strasser 2000). On the other hand, many benthic animals are highly mobile (see Frid 1989; Shull 1997; Whitlach et al. 1998; Ford et al. 1999) and the migrating specimens diffuse out of local accumulations and may fill empty sites. Thus, mobility tends to equalise effects of patchy settlement as well as of locally differential post-settlement mortality. Similar diffusive effects are expected in species highly sensitive to passive dislocation. The resulting balance between vacancies and crowding has various implications on the

species' performance in its habitat, on the potential variability in community composition and on the invasibility of the Wadden Sea sediments.

The northern Wadden Sea is characterised by strong tidal currents and there are no thermo-haline stratifications throughout the year. The sediments are predominantly sandy and locally blend into mud or gravel. We used two extensive data sets from the Wadden Sea subtidal and intertidal to check for the existence of suitable but empty habitat within spatial scales ranging from 100 m to some 12 km. Throughout this study, the term "empty habitat" refers to areas with (apparently) suitable abiotic conditions but species-specific abundances below a detection level set by the size of the sampling device.

Methods

Field sampling was performed in the List tidal basin in the northern Wadden Sea (North Sea). This bight encloses an area of some 400 km² between the mainland and the islands of Sylt (Germany) and Rømø (Denmark; Bayerl and Köster 1998). Causeways connect both islands with the mainland and separate the bight from the adjoining parts of the Wadden Sea. The tidal inlet 'Lister deep' (2.5 km wide) is the only connection of the bight with the North Sea. The mean tidal range in the bight is 2 m and salinity usually remains close to 30 psu (Backhaus et al. 1998). Tidal flats comprise one third of the bight and deep tidal channels about 10% of the area. The rest belongs to an extensive, shallow subtidal region (Fig. 1).

Fig. 1 Sampling sites in List tidal basin (North Sea). *Small dots* represent intertidal (*n*=222) and *large dots* subtidal sites (*n*=270). *Shaded areas* are emergent shoals

Inside the bight, the inlet branches into three main channels. A stratified random design was used to study the macrofauna along 'Lister Ley', the largest of the branches. The strata were position along the north-south axis (five sections), position along the west-east axis (two sections), and depth below low-water mark (three classes: >10 m, 5–10 m, and 0–5 m). Each stratum was sampled by ten replicate box cores (total *n*=270, Fig. 1).

Sampling occurred in September 1996 and the same 270 sites (GPS navigation) were re-sampled in March 1997. During both dates, samples were collected using a 0.02 m² box corer. Depending on sediment composition, the corer penetrated the sediment down to 35 cm. However, on average the sampling depth was 9.2 cm in September and 7.9 cm in March. At some sites with pebbles the box penetrated only 2–3 cm into the sediment. Although this may render insufficient representation of the deeper-living fauna it was decided to use these cores as well to avoid an artificial exclusion of this type of bottom.

The macrofauna was separated by sieving through 1 mm square meshes and fixed in 5% buffered formaldehyde solution. The fauna was determined to the highest possible taxonomic level and counted. Larger epibenthic species such as crabs and shrimps were excluded from data analysis because they are not sufficiently recorded by small box cores (Beukema 1974). A subsample of each of the grabs was used for sediment analysis (dry sieving according to Buchanan 1984). The water depth was measured during sample collection and later adjusted to the tidal phase using data of the water-gauge at List harbour.

The horizontal distance covered by the subtidal sites approximated 12 km in a north–south direction (Fig. 1). Assuming current velocities of 0.5–1.3 ms⁻¹ (Backhaus et al. 1998), organisms drifting with the tidal currents may cross the entire study area within a single tidal cycle. Therefore, larval supply was expected to be rather even across the study area (Hickel 1975) and all sites may have an equal chance of being colonised unless local hydrographic peculiarities will hamper or facilitate spatfall in one area or another. The same applies to the intertidal area of Königshafen, a 4.5 km² bight adjacent to 'Lister Ley'.

This intertidal area was sampled in a different way. It was subdivided into squares of 100×100 m each (*n*=450) and every second one (*n*=222) was studied in August 1989 (completed by a few plots studied in August 1990). At each of the studied squares the sediment from an area of approximately 0.1 m² was excavated with a spade and searched for macrobenthic organisms by hand. The presence of species was noted in a field log and only species that could not be identified in the field were transferred to the laboratory. This sampling procedure was replicated 20 times per square, yielding frequencies of the species in the range of 0 to 20 occurrences per square. The tidal level of each of the squares was read from a topographic map (updated 1992; Higelke 1998) and the sediment composition from maps of a geological survey conducted during the same year (Austen 1992, 1994).

For each of the species the suitable ranges of water depth and sediment composition were extrapolated from the ranges of these factors across the 'top-10 cores' (or squares in the intertidal, respectively), i.e. the ten cores (squares) with the highest abundance or frequency. This was separately done for the subtidal and intertidal sites. For the subtidal sites we used the parameters water depth, percentage dry weight of the sediment of mud (particles <0.063 mm) and gravel (>1 mm), median diameter of sand grains, and the first and third quartile of the cumulative curve of sediment dry weight (all according to Buchanan 1984). For the intertidal sites we used tidal level and the percentages of sediment dry weight of the sieving fractions mud (<0.063 mm), very fine sand (0.09–0.15 mm), fine sand (0.15–0.355 mm), medium sand (0.355- 0.60 mm), and gravel (>1 mm) as well as the modal diameter (Austen 1990, 1992). All of these parameters were used simultaneously, i.e. the suitable range of habitats was defined by the combined ranges (logical AND operation) of these parameters.

During low tide the tidal water assembles in Lister Deep and only a small proportion is exchanged with the North Sea (Backhaus et al. 1998). Because of mixing within Lister Deep the tidal waters do not show any consistent differences in chemical com-

pounds or physical parameters during high tide. Therefore parameters related to the tidal waters cannot be used to characterise suitable habitat. Likewise, in these shallow waters the direction and velocity of the tidal currents strongly depend on the wind direction, and there is no typical pattern at the spatial scale of single sites. Indirectly, however, some of the flow characteristics are included in the local sediment composition, particularly in the percentages of very fine and very coarse particles. Thus, water depth and sediment composition are the only feasible parameters to describe the habitat of a species in this highly dynamic environment.

Because hydrodynamics influence sediment composition across larger spatial scales the sites are not independent of each other and spatial autocorrelation is expected. This was tested by calculating the correlation between the spatial distance and the faunal similarity (Renkonen index) between sites. A priori, we expected a decrease in faunal similarity with increasing distance.

For the subtidal sites the suitable ranges of species were separately calculated for each of the two sampling seasons. However, as the 'preferred' ranges remained very similar for most of the species we used the 'top-10 ranges' from a combined data set to ease comparisons between the two sampling seasons. As an alternative to the 'top-10 ranges' we also estimated suitable habitat from all sites with an abundance higher than twice the overall mean. However, this caused problems in the rare species (overall means <1 core^{-1}) since a value of 1 individual core^{-1} indicated non-suitable habitat while a value of 2 core^{-1} indicated a suitable site. The overall effect was a higher percentage of suitable but empty sites. To be conservative we continued with the top-10 ranges only.

Some 'empty habitat' is expected to occur by mere chance. Its extent was estimated assuming a lognormal distribution of individual species abundances within the suitable sites and calculating the standard scores for x_i=0 (Zar 1996) based on the sites with a non-zero abundance. By multiplying these standard scores by the number of sites within the suitable ranges we got the expected number of empty sites.

Results

Empty habitat

On average, abundant species (defined as ≥100 occurrences/individuals and ≥10 sites occupied) were absent from roughly half of the sites in the subtidal (Table 1). In the intertidal of Königshafen there was an average of one-third of empty suitable sites and even two-thirds of empty subsites (i.e. individual spade samples). In both areas, the number of zero abundances expected from a lognormal distribution was far lower than the observed percentages, about 1% in the intertidal and 2% in the subtidal (Table 1). This difference between both areas may be a consequence of different sampling dates and methods (see Methods section). In rare species, 'suitable

Fig. 2 Sequential estimation of 'suitable habitat' from increasing numbers of sites (*x* axis; arranged according to decreasing abundance). Data from the subtidal sites sampled in September 1996. For further explanations see text
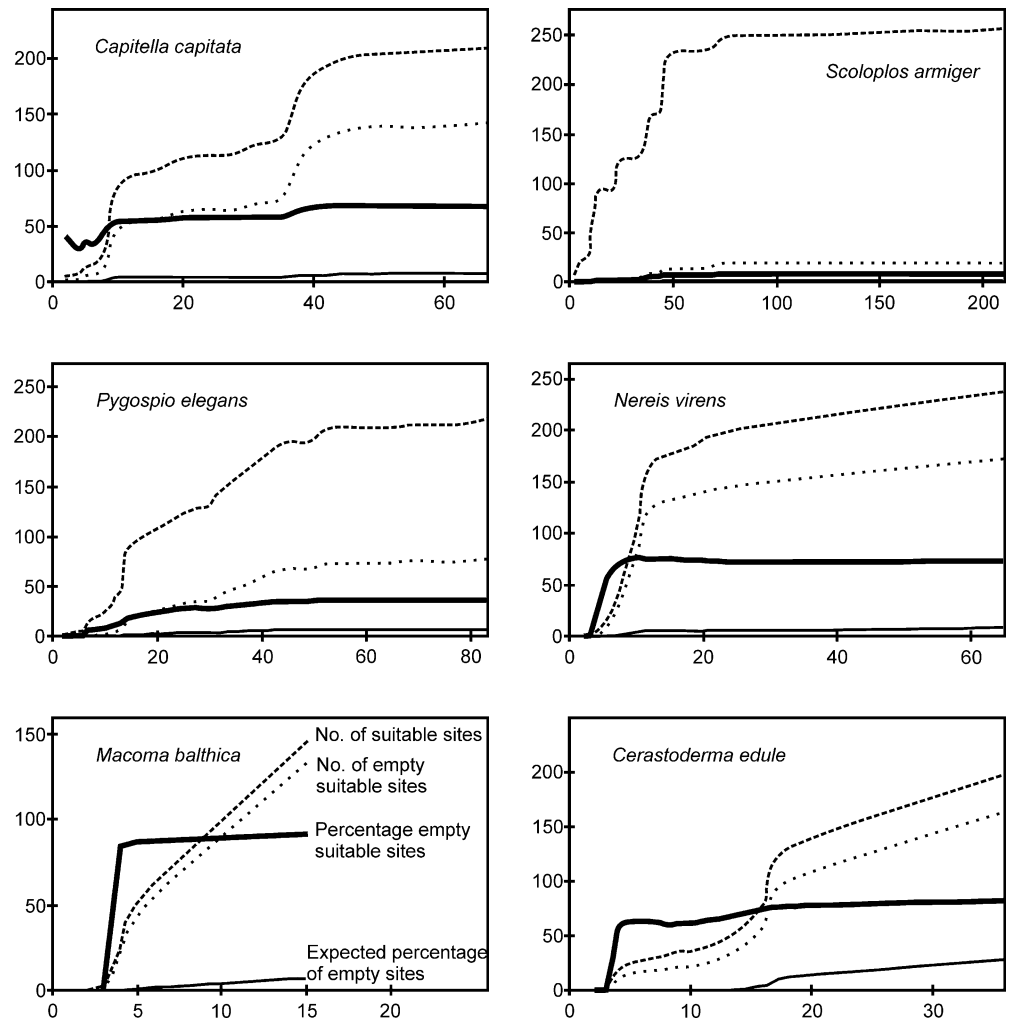
Table 1 Percentages of empty though suitable habitat of abundant (>100 occurences/individuals and ≥10 sites occupied per data set) macrofaunal species in the northern Wadden Sea (tidal migrants excluded). 'Suitable habitat' are the sites characterised by a species-specific combination of physical factors sustaining extraordinarily high densities and 'empty habitat' is the percentage of suitable sites with an abundance below detection threshold. The percentages of zero-abundances expected from a lognormal distribution are given in parentheses. In the subtidal the percentages refer to 270 grabs per date and in the intertidal to 222 sites or 4,440 individual samples (20 per site), respectively. The mean of common species refers to the species occurring both in the intertidal and subtidal

	Intertidal		Subtidal	
	August 1989/1990		September 1996	March 1997
	Samples	Sites	Sites	Sites
Arenicola marina	20	1 (0.0)		
Aricidea minuta			31 (3.0)	45 (0.6)
Autolytus prolifer			84 (0.0)	
Balanus crenatus	74	27 (1.4)		
Bathyporeia spp.			46 (1.8)	27 (2.1)
Bodotria scorpioides			35 (0.0)	52 (0.0)
Corophium arenarium	96	64 (0.7)		74 (6.4)
Capitella capitata	95	66 (1.5)	52 (3.7)	57 (3.2)
Capitella minima			13 (2.6)	24 (1.4)
Cerastoderma edule	21	0 (0.0)	61 (0.4)	72 (0.1)
Crepidula fornicata	92	44 (0.4)		
Carcinus maenas	78	21 (0.7)		
Ensis americanus	90	57 (0.6)	61 (1.3)	75 (1.8)
Eteone longa	95	54 (0.4)	55 (1.1)	57 (0.8)
Electra pilosa	92	59 (1.0)		
Gammarus locusta	98	81 (0.6)		24 (1.9)
Heteromastus filiformis	27	3 (0.0)	63 (2.5)	70 (1.3)
Hydrobia ulvae	40	17 (0.1)	88 (9.3)	75 (10.5)
Lepidochiton cinereus	86	42 (0.0)		54 (0.1)
Lanice conchilega	32	13 (0.0)		
Littorina littorea	56	6 (0.2)		
Littorina saxatilis	94	71 (1.4)		
Lineus viridis	95	50 (0.5)		
Malacoceros spp.	98	85 (0.1)	32 (3.9)	40 (4.5)
Mya arenaria	59	10 (1.3)	55 (6.1)	
Macoma balthica	39	0 (0.0)	86 (4.7)	71 (0.3)
Mytilus edulis	82	35 (1.8)	56 (1.6)	41 (6.1)
Magelona mirabilis	93	55 (3.3)		
Metridium senile	92	59 (1.5)		
Microprotopus maculatus			13 (1.1)	45 (2.5)
Nereis diversicolor	30	7 (0.0)		
Nereis virens	75	37 (0.5)	75 (3.5)	70 (1.3)
Nephtys hombergii	49	3 (0.0)	44 (0.4)	23 (1.0)
Ophelia limacina				29 (1.2)
Polydora spp.	70	27 (0.8)	63 (0.1)	59 (1.7)
Pygospio elegans	43	5 (0.0)	8 (0.2)	25 (2.2)
Phyllodoce mucosa	65	23 (0.1)	12 (2.6)	63 (1.5)
Retusa obtusa	1		53 (1.4)	41 (0.9)
Scoloplos armiger	13	1 (0.0)	0 (0.0)	0 (0.0)
Semibalanus balanoides	91	62 (0.5)		
Scolelepis foliosa	98	87 (1.0)		
Scolelepis squamata	95	79 (0.8)	63 (0.0)	
Spio spp.			20 (1.0)	13 (0.9)
Talitrus saltator	99	91 (0.1)		
Number of species		35	25	26
Mean of listed species	67	38 (0.6)	45 (2.3)	49 (2.0)
Mean of common species	65	33 (0.5)	51 (2.4)	51 (2.3)

habitat' could not reliably be estimated because of a low number of occupied sites (<10), a low abundance (mean <0.5), or both. In addition, in many of the rare species it was not clear whether they find suitable habitat in the Wadden Sea at all. Therefore rare species were excluded from further analysis.

The unexpectedly high percentage of suitable but empty sites was not an artefact of estimating 'suitable sites' from a fixed number of ten sites. Estimating 'suitable habitat' from other numbers of sites (in the order of decreasing abundances) for some of the more abundant species showed fairly constant percentages of empty habitat (Fig. 2). Starting from the two sites with the highest

abundance, enlarging the 'suitable ranges' according to the physical characters of successively more sites always increased the number of sites that appeared to be suitable ('No. of suitable sites' in Fig. 2). However, the percentage of empty suitable sites increased only initially and rapidly reached a species-specific ± constant level ('Percentage empty suitable sites' in Fig. 2). For all but one of the six species tested the estimates based on ten sites were already in the constant zone. The only exception was the polychaete *Scoloplos armiger*, where a constant level for the 'percentage of empty suitable sites' was only reached after including some 40 sites. Thus, in this species the amount of empty habitat may be underestimated.

Table 2 Multiple regressions between subtidal macrofaunal abundance in the Wadden Sea and some environmental factors (sampled sediment depth, percentage mud, median grain size, quartile deviation and water depth). Regressions were calculated by stepward variable selection including the parameters with statistically significant ($P<0.05$) partial correlations according to their R^2 values. All sites: $n=270$; N number of occupied sites

Species	All sites		Occupied sites			
	September	March	September		March	
	R^2	R^2	N	R^2	N	R^2
Aricidea minuta	0.110	0.201	103	0.300	89	0.469
Bathyporeia spp.	0.225	0.171	85	0.507	112	0.325
Bodotria scorpioides	0.162	0.062	32	0.638	20	0.628
Capitella capitata	0.072	0.036	71	0.298	34	0.258
Capitella minima	0.130	0.173	180	0.248	146	0.360
Cerastoderma edule	0.119	0.033	36	0.428	23	0.355
Corphium arenarium	0.123		20	0.645		
Ensis americanus 0-group	0.070	0.070	64	0.356	33	0.722
Ensis americanus 1+-group	0.048	0.064	14	0.475	24	0.544
Eteone longa	0.195	0.195	72	0.588	79	0.685
Eumida sanguinea	0.061	0.046	7	0.832	10	0.795
Gammarus spp.	0.109	0.039	21	0.573	24	0.297
Heteromastus filiformis	0.059	0.120	31	0.463	19	0.496
Macoma balthica 0-group	0.048	0.118	14	0.755	63	0.518
Macoma balthica 1+-group	0.071	0.047	15	0.826	13	0.791
Magelona mirabilis	0.049	0.065	21	0.696	13	0.973
Malacoceros spp.	0.142	0.128	60	0.304	47	0.387
Microprotopus maculatus	0.135	0.045	41	0.318	29	0.297
Mya arenaria	0.122		47	0.441		
Mytilus edulis	0.159	0.038	86	0.410	93	0.000
Nephtys hombergi	0.266	0.204	84	0.645	96	0.549
Nereis virens	0.173	0.226	65	0.431	57	0.552
Ophelia limacina	0.052	0.152	15	0.000	22	0.557
Phyllodoce mucosa	0.235	0.150	136	0.340	72	0.493
Polydora ciliata	0.091	0.085	35	0.289	20	0.529
Pygospio elegans	0.204	0.079	157	0.262	143	0.151
Retusa obtusa	0.103	0.044	63	0.424	54	0.328
Scolelepis squamata	0.000	0.065	15	0.515		
Scoloplos armiger	0.488	0.562	243	0.543	259	0.592
Spio spp.	0.110	0.172	174	0.228	154	0.374
Tharyx kilariensis	0.040	0.055	71	0.124	37	0.355
Urothoe poseidonis	0.033	0.032	9	0.944	12	0.908

Among species the intensity of habitat use varied widely. Roughly half of the species used less than 50% of their suitable habitat. On the other hand, *Scoloplos armiger*, *Arenicola marina*, *Cerastoderma edule* and *Macoma balthica* occupied the highest percentages of suitable habitat in the intertidal and *S. armiger* also in the subtidal. In these species the percentage of empty habitat observed was similar to the percentages expected from a lognormal distribution (Table 1). Generally, however, the observed percentages of empty habitat were one to two orders of magnitude higher than expected from the lognormal distributions (Fig. 2; Table 1).

As a consequence of a high percentage of empty though suitable habitat, regression analyses of species abundance on environmental factors in most species gave rather poor results, explaining a very small part of variance only (Table 2). The only exception was *S. armiger*, which used its niche almost completely. However, restricting these regression analyses to the sites that were actually occupied yielded high coefficients ($R^2>0.5$) in many species (Table 2). Thus, the presence of empty though suitable space masked the potential importance of these environmental factors.
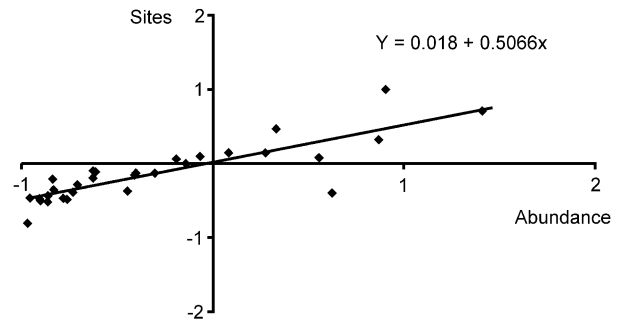

Fig. 3 Relative change in the number of occupied subtidal sites of abundant macrobenthic species versus the relative change in their abundance

Seasonal changes of abundance and habitat use

In the subtidal, abundance of most species changed between the sampling dates. This also affected the number of sites occupied (sign test on a common trend in the changes of abundance and number of occupied sites, $P<0.001$, $n=31$). However, abundance changed to a greater extent than the number of occupied sites (Fig. 3). On average over all abundant species, the percentage

change in the number of sites was only half the percentage change in abundance (linear regression, $R=0.84$, $r^2=0.705$, $t=8.189$, $df=30$, $P<0.0001$). Thus, based on an average of 50% of empty though suitable habitats (Table 1), a doubling of abundances might still leave 25% of empty habitat while a four-fold increase in abundances might still leave about 12% of empty habitat. However, at least in part, this relation may be brought about by a rather small grab used to estimate abundance. Habitat may have appeared to be empty because abundance was below the grab-specific detection threshold. However, regardless whether these sites were really empty or simply had a low abundance, this means that the species were well below carrying capacity at the spatial scale of the entire bight, since other sites with the same physical quality were densely populated.

Scales in the spatial pattern of species

Both in the intertidal and in the subtidal, empty and occupied sites were not randomly distributed across the suitable area. Cockles *Cerastoderma edule*, for example, attained highest subtidal abundances ($>10,000$ m^{-2}) in an area east of Königshafen (Fig. 4). Within that area it was extraordinarily abundant at all sites. Outside this field there was only a single other patch containing cockles (some 3,000 m^{-2}) while all other patches of suitable habitat were virtually empty (Fig. 4). In the intertidal of Königshafen, cockles occurred in 79% of all subsites (i.e. spade samples) in the suitable range. However, based on sites (i.e. the 20 replicate spade samples combined), it actually used all of the sites within its suitable range.

Such cases of aggregated occurrence of species may lead to spatial autocorrelation. In the subtidal, sites that were <1 km apart displayed highest faunal similarity (Fig. 5) but there was no significant change in average faunal similarity of sites that are 1–8 km apart. Only when the distance between sites exceeded 8 km did faunal similarity decrease. This spatial autocorrelation was statistically significant (χ^2-test, $P<0.001$) but explained almost nothing ($r^2=0.021$). In the intertidal of Königshafen, faunal similarity rather steadily decreased with increasing distance between sites (χ^2-test, $P<0.001$; Fig. 5), but as before the explanatory power was negligible ($r^2=0.044$).

Species interactions

The survival of a species at a single site may be influenced by other species in a variety of ways. Therefore, we checked for statistically significant correlations of abundances between pairs of species. From the subtidal data set we got 223 statistically significant ($P<0.01$) correlations for September (total number of comparisons = 1,081) and 163 for March (1,300 comparisons). All except three (September) and one (March) were positive

Fig. 4 Spatial pattern of cockles *Cerastoderma edule* along Lister Ley in September 1996, and in the intertidal of Königshafen in August 1989. *Empty dots* represent samples without cockles and *filled dots* occupied sites
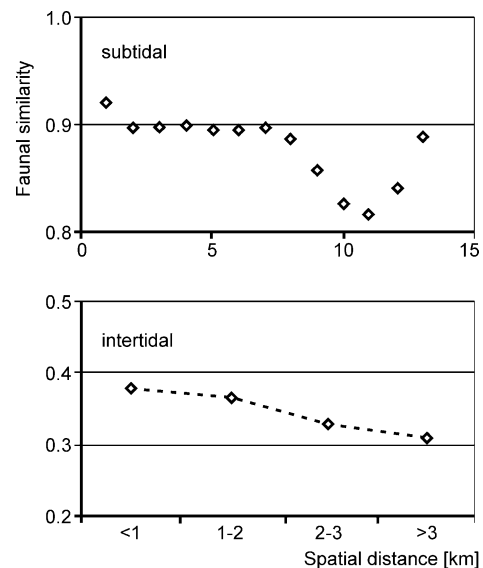

Fig. 5 Relationship between faunal similarity and the spatial distance of sampled sites (1 km distance classes) in the subtidal of Lister Ley (September 1996) and in the intertidal of Königshafen (August 1989)

ed to the prevalence of positive correlations between species over negative ones.

Discussion

Amount of empty space

During the study period, macrobenthic abundances and species richness were in the same order of magnitude as during the preceding years (Armonies et al. 2001) and presumably higher than several decades ago (Reise et al. 1989, 1994). Therefore, the existence of empty though suitable habitat is not due to an intermittently low abundance of macrobenthos. However, since abundances of single species vary considerably between years (e.g. Beukema et al. 1993) this may not be the case for all of the species. In particular, many species in shallow waters suffer heavy mortality during exceptionally cold winters (e.g. Beukema 1992). Recolonisation may take several years, for instance because larvae run in short supply after cold winters (e.g. Strasser and Pieloth 2001). However, this does not contradict our estimates of actual habitat use but constitutes one of the causes for the existence of empty habitat. In the subtidal sites these effects of a cold winter may even have caused underestimation of the amount of empty space because the winter preceding the study period was exceptionally cold, and some temperature sensitive species like *Lanice conchilega* did not show up in our samples at all. Thus, we should have added some '100% empty though suitable space' for these species. On the other hand, bivalves are known to recruit exceptionally well after cold winters (e.g. Beukema 1992; Strasser et al. 2001) but nevertheless, all of them used less than half of the suitable subtidal sites during this study (Table 1). Beukema et al. (1983) reported differential variability in time and space of the numbers in suspension and deposit feeding benthic species. Concerning habitat use a difference between suspension and deposit feeding species is not apparent (Table 1).

Spatial patterns

The spatial distribution of species richness (Fig. 6) as well as the overwhelming superiority of positive correlations between species over negative ones indicate that the species tend to aggregate in some patches and leave others barely exploited. We suggest that local hydrodynamics may be a prominent reason for these aggregated patterns. Although it is basically the same water body that covers the various sites, at times, the scope for settlement of larvae may vary over sites (Gross et al. 1992; Snelgrove 1994; Hsieh and Hsu 1999). In the study area, highest species richness occurred in the shallow waters east of Königshafen (Fig. 6). This area is part of a large gyre system emerging in the flooding waters and often lasting until high tide, depending on the wind direction (Behrens et al. 1997). Similar gyres may also emerge in other parts of the

Fig. 6 Spatial pattern of species richness in the subtidal of Lister Ley (September 1996, species per 0.02 m² box core) and intertidal of Königshafen (August 1989, species per 0.1 m² spade sample). The *lines* were drawn according to linear interpolation between adjoining sites

correlations. This was different in the intertidal. Here we obtained 705 significant correlations out of 4,465 pairs of species, but the share of negative correlations (76) was ten times higher than in the subtidal. These negative correlations were associated with a few species which may be indicative for the major habitats, viz. *Arenicola marina* (sandy tidal flats), *Hydrobia ulvae* (muddy flats), and *Mytilus edulis* (mussel banks). Species associations such as these intertidal ones did not show up in the subtidal. As a consequence, the similarity between sites of the faunal composition was higher in the subtidal than in the intertidal (see Fig. 5).

The paucity of negative correlations between species in the subtidal gives no hint about biotic interactions affecting the spatial structure of the populations (on a kilometre scale). Nevertheless, areas with high and low species richness displayed distinct spatial patterns both in the intertidal and in the subtidal (Fig. 6). Lowest species richness (<6 species per box core) was generally found along the tidal creeks in >10 m water depth while the sites with a high species richness (>18 species per box core) formed four distinct patches in medium to shallow waters. These patches may have substantially contribut-

tidal channel system, some of which were densely populated with many species during this study and others not. However, unlike the large gyre east of Königshafen the latter ones only emerge during particular combinations of wind direction and wind velocity, hence are more variable and less persistent (Behrens et al. 1997). Possibly the gyres enhance larval settlement by increasing the pool of competent larvae supplied to the underlying sediment. In this case, larvae settling to the sediment during the same period of time should initially concentrate in the same area. That is exactly the pattern we observed in bivalve larval settlement (Armonies 1996) and during this study abundances of 0-group *Macoma balthica*, *Cerastoderma edule*, and *Mya arenaria* correlated particularly well with each other (r=0.48–0.79, all P<0.001).

The patchy distribution of specimens across suitable sites does not fit previous assumptions of a well-mixed water body (Hickel 1975) with a similar chance of planktonic larvae to settle anywhere in the bight. Indeed, current studies of plankton dispersion across the List tidal basin indicate 'clouds' of polychaete larvae rather than a random distribution (J.A. Rodríguez-Valencia and N.A. Hernández-Guevara, unpublished results). In addition, these clouds of larvae do not move randomly with the tidal currents but the larvae seem to be able to keep a position close to the adult sites until recruitment. Thus, besides the hydrographic conditions, larval behaviour is another aspect deciding which of the suitable habitats may actually be occupied during larval settlement.

After initial settlement the spatial patterns are likely to change because of species interactions and mobility. The term 'mobility' includes the active dispersal capabilities of larvae and later stages as well as passive redistribution of benthic stages. The latter may occur during sediment disturbance with consecutive bedload transport (e.g. Thiébaut et al. 1996; Olivier and Retière 1998; Armonies 2000). Both migrations and bedload transport of resuspended organisms at least partly depend on the tidal currents. However, the frequency of migrations (with trial and error search for a suitable habitat) and the susceptibility of the specimens to resuspension will divide the fauna into 'strong' and 'weak' secondary dispersers. Weak dispersers will stay in the area of initial settlement if they are capable of surviving there. Strong dispersers, on the other hand, may change the spatial distribution several times and thus distribute across a higher percentage of suitable habitat and leave non-suitable sites. Indeed, the species known to be highly mobile such as the bivalves *Macoma balthica* and *Cerastoderma edule*, and lugworms *Arenicola marina* used higher than average percentages of suitable habitat (Table 1). However, the same was true for some species that are not known to be strong dispersers, e.g. the polychaetes *Pygospio elegans* and *Scoloplos armiger*. In *P. elegans* this may be brought about by fast reproduction within suitable sites and in *S. armiger* by a very wide niche (however, recent studies indicate that *S. armiger* is a sibling species with significant genetic differences between inhabitants of the subtidal and the intertidal; Kruse et al. (2002).

Conclusions

In spite of a wide dispersal in many macrozoobenthic species, there is apparently a problem of settlement and survival during the early post-settlement phase (<1 mm in size), preventing the occupation of many suitable sites, and keeping populations well below carrying capacities. To some extent our results will certainly depend on the physical conditions during the study period and some variations between years are expected. However, although the degree of variation is unknown, it is clear that both empty habitat and areas with a higher than average species richness may strongly affect our perception of the environment, for instance in monitoring programmes. Sites that are close together with the same ranges of water depth and sediment composition may differ in hydrographic conditions and, therefore, accessibility for recruits. Thus, sites that look the same may strongly differ in their ecosystem functions and cannot replace each other. This needs to be taken into account in conservation measures and environmental management.

The mesoscale crowding of populations may be important for mating or external egg fertilisation. Patches of high species richness may provide opportunities for species interactions. The spacious empty habitats offer plenty of room for interannual variability in abundances and spatial patterns, as well as for change in the composition of local species assemblages and the invasibility of the benthic community in the Wadden Sea.

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