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ORIGINAL ARTICLE

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Juvenile-adult distribution of the bivalve *Mya arenaria* on intertidal flats in the Wadden Sea: why are there so few year classes?

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Abstract Patchy distribution is frequently observed in benthic marine invertebrates. In order to indentify factors causing spatial patterns in the bivalve *Mya arenaria*, abundances of juveniles and adults, as well as death assemblages, were recorded on a 20-km scale in the intertidal zone of the Sylt-Rømø Bight. Both adults and juveniles exhibited pronounced patchiness. Shell length of juveniles rarely exceeded 2 mm in 1995, which was most likely a consequence of epibenthic predators truncating the size spectrum. Only a few yearclasses dominated the adult population. While the northern part of the Bight was colonized mainly by a 1993-cohort, most *M. arenaria* in the southern part were from the mid-1980s. It is hypothesized that epibenthic predation is a major cause of the lack of dense *M. arenaria* beds from other years. However, examination of the length–frequency distribution of death assemblages revealed that other unidentified causes of mortality exist. High abundances of adults were found in the mid and lower intertidal zone but not in the high intertidal zone. There was no indication that dispersal of *M. arenaria* spat in a landward or seaward direction contributed significantly to the observed distribution pattern, since spat occurred abundantly at all tidal levels except in the high intertidal zone. There was no evidence of negative adult-juvenile interaction. *M. arenaria* was not attracted by seagrass or projecting shell beds – the latter indicating erosion of the sediment – as abundances of adults and juveniles were generally low in these habitats. The effects of sediment type and of the bioturbating lugworm *Arenicola marina* were inconsistent. While adults were more abundant on muddy sand than on sand, recruitment was independent of sediment type. At all high density sites of adults (>50 ind m^{-2}), lugworm densities were below 5 ind m^{-2}, which may indicate a negative interaction. However, lugworm densities >30 ind m^{-2} did not prevent relatively high *M. arenaria* recruitment of >500 ind m^{-2}.

Key words Mya arenaria · Predation · Recruitment · Population dynamics · Patchiness

Introduction

Population structure and dynamics of *Mya arenaria* L. in the European Wadden Sea are characterized by the occurrence of adults in locally restricted dense beds (Kühl 1955) and by a large annual variation in reproductive success (Beukema 1982, 1992). Patchy distribution of adult *M. arenaria* is also reported from the Swedish west coast (Möller and Rosenberg 1983) and the east coast of North America (Brousseau 1978; Emerson et al. 1988). Differential reproductive success in *M. arenaria* may in part be explained by low recruitment after mild winters and heavy spatfall after severe winters (Kühl 1955; Beukema 1982, 1992; Reise 1987). However, low recruitment after the cold winter of 1986 shows that reproductive success cannot be predicted by winter temperature alone (Günther 1992).

In general, distribution patterns of benthic organisms with pelagic larvae are shaped by pre- and post-settlement processes. Concerning pre-settlement processes, Kühl (1981) stated that *M. arenaria* is capable of testing the substrate before settlement. This is supported by a large body of literature in which sediment preferences of *M. arenaria* spat were found. However, these results are inconsistent. For example, silty sediment was preferred in some field studies (Reise 1987; Günther 1992), coarser substrates in others (Brousseau and Baglivo 1988; Beal 1989), or no particular substrate at all (Smidt 1951). Contradicting results were likewise reached on adult-larval interactions. Total bivalve spat was reduced by high numbers of adult *M. arenaria* and *Cerastoderma edule* (L.) in an experimental arrangement on the Swedish west coast (André and Rosenberg 1991), but numbers of *M. arenaria* recruits were not affected by

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dense beds of *M. arenaria* in the Wadden Sea (Kühl 1955; Günther 1992).

Among post-settlement processes, predation has been identified as an important regulator of community structure of infaunal invertebrates including *M. arenaria* (e.g. Pihl 1982; Jensen and Jensen 1985; Reise 1985; Günther 1992). Although young post-larval *M. arenaria* have the potential for dispersal by byssus drifting (Armonies 1994), this was of minor importance for the distribution pattern of *M. arenaria* recruits in the German Bight (Günther 1990). However, on exposed sandy flats, juvenile clams may be dislocated by bedload sediment transport (Emerson and Grant 1991; Armonies 1998). Other physical and biological disturbances may occasionally affect *M. arenaria* populations. *M. arenaria* disappeared from the Danish Wadden Sea after severe winters in the early 1940s (Smidt 1944). Ice scouring reportedly killed *M. arenaria* spat living close to the upper part of the sediment surface, while deeper living adult specimens remained largely unaffected (Kühl 1951). The lugworm, *Arenicola marina* (L.), a dominant bioturbator on the intertidal flats of the Wadden Sea, was found to have an adverse effect on *M. arenaria* recruitment in a field experiment (Flach 1992).

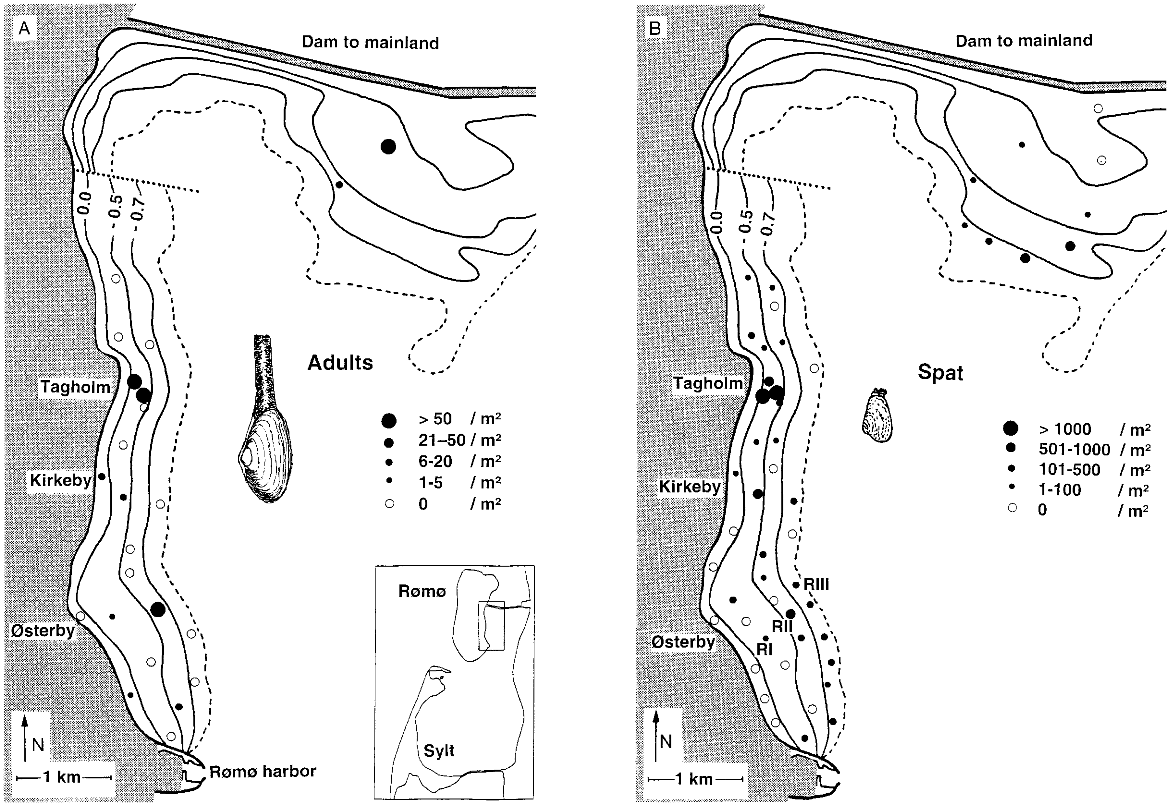
In conclusion, several processes are known to have a strong potential to shape the population structure of *M. arenaria.* Here we examined the relative importance of some of these factors on a large scale (about 20 km). The aim of this study was (1) to determine abundances and distribution of adults and spat, as well as death assemblages, as a prerequisite to investigating whether (2) adult *M. arenaria* beds have an adverse effect on the abundance of spat and whether (3) the distribution patterns of spat and adults of *M. arenaria* are influenced by tidal level, sediment type, *A. marina* density, the presence or absence of seagrass, and projecting *M. arenaria* shells.

Materials and Methods

Sampling took place in the Sylt-Rømø Bight, a shallow tidal basin in the North Sea, 54°50’–55°10’ N ; 8°20’–8°40’ E. The Bight is bound on two sides by two barrier islands, and their respective causeways to the mainland. The water exchange between the Bight and the North Sea is confined to a narrow tidal inlet between the islands. Here, maximum tidal current velocities are about 1.3 m s^{-1}. The Sylt-Rømø Bight encloses 404 km^2, of which one third belongs to the intertidal zone. This zone consists largely of sand flats (72%) and to a lesser extent of muddy sand (25%) and mud flats (3%). The low water volume of the Bight is about 570×10^6 m^3 and is doubled at high tide to a volume of about 1120×10^6 m^3. The tides are semi-diurnal with a mean tidal range of about 2 m. Salinity normally remains close to 30 psu. Mean annual water temperature is 9 °C with a summer average of 14 °C and a winter average of 5 °C. Localized water circulation patterns are generated by the flood and ebb tides in combination with changing wind conditions. More about the area is given in Gätje and Reise (1998).

Spat, adults, and death assemblages of *M. arenaria* were sampled along the east coasts of the islands Rømø (northern part of

Fig. 1A,B Mean abundance of *Mya arenaria* in the intertidal zone north of Rømø harbor, northern Wadden Sea, in 1995. For better visualization of the sampling sites the intertidal zone *below the dotted line* is enlarged by 110%. **A** Adults. **B** Juveniles. At permanent sites (*RI*, *RII*, *RIII*) abundances are averaged over five sampling dates between July and September 1995



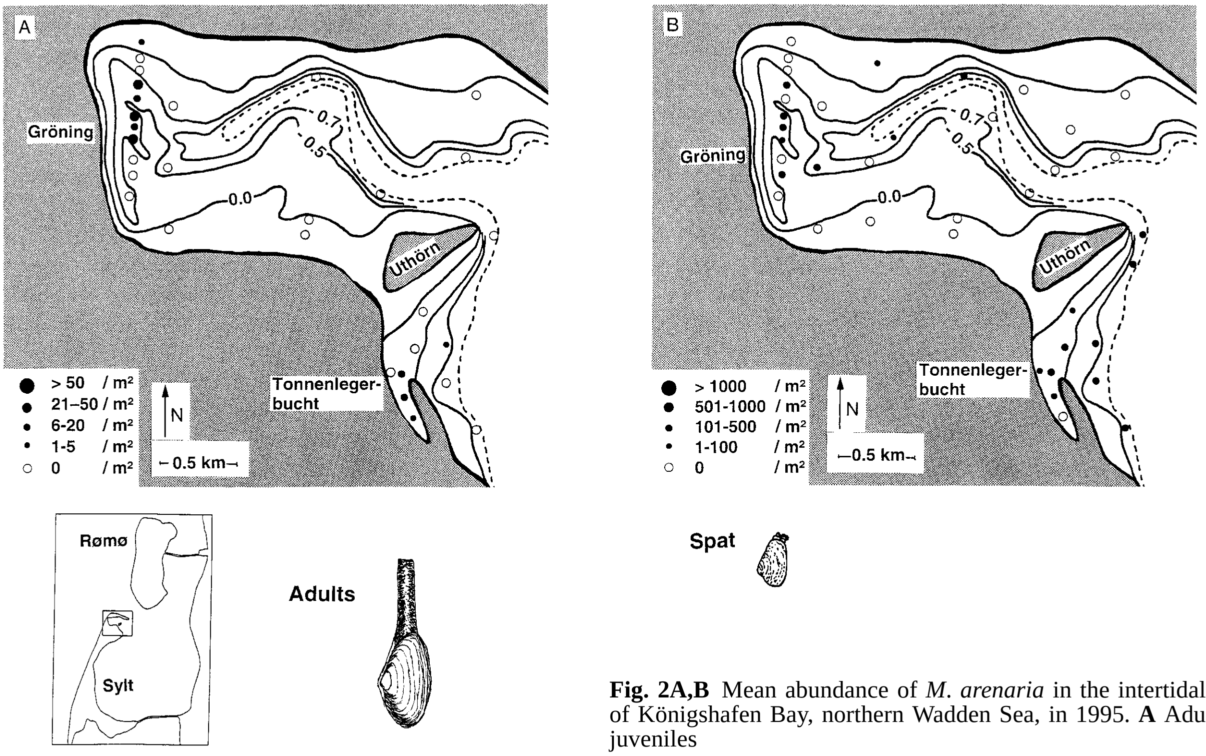


Fig. 2A,B Mean abundance of *M. arenaria* in the intertidal zone of Königshafen Bay, northern Wadden Sea, in 1995. **A** Adults; **B** juveniles

the Bight) and Sylt (southern part of the Bight). The two areas differed both in size and environmental conditions:

1. The northern part (Fig. 1) is dominated by muddy sand. In addition, an extensive mud flat is situated in the corner between Rømø and the causeway. This mud was too soft to walk across and was spared from sampling. The sampling area comprised about 5.0 km^2.
2. The southern part is dominated by sand and muddy sand. The intertidal zone of Königshafen Bay (Fig. 2) covers an area of about 4.0 km^2. Sand flats make up 88% of this area. Muddy sand and mud flats are only encountered in two small areas. The area from List harbour to Munkmarsch (Fig. 3) consists of sand flats to the north and muddy sand to the south. With about 11.3 km^2, the intertidal zone here was larger than the other two areas combined.

Sampling of *M. arenaria* adults, death assemblages and bivalve spat

Between 24 May and 29 June 1995 a total of 98 sites on the intertidal flats of Sylt and Rømø were sampled once for adults of *M. arenaria*. A few sites were sampled again in August 1996 and July 1997. At most sites, empty shells still in living position (death assemblages) were also recorded. The same sites plus another 67 (resulting in a total of 165) were sampled for spat between 11 July and 12 September 1995. All sites were visited once except for six permanent sites (three at Rømø, three at East Sylt), sampled fortnightly (around full and new moon) from 11 July until 12 October 1995. In 1996 150 sites were sampled again for spat between 18 September and 10 October. A global positioning system (Garmin GPS 50) was used to locate sampling positions. Permanent sites were marked with iron stakes.

Selection of sampling sites

The intertidal flats were divided into three locations (see Figs 1–3) and four tidal levels: (1) high intertidal zone: above 0.0=mean tidal level (MTL), (2) mid-intertidal zone: –0.5 to 0.0 MTL, (3) upper low intertidal zone: –0.7 to –0.5 MTL, (4) lower low intertidal zone: below –0.7 MTL.

The sites were selected using a stratified random sampling procedure. The uneven number of sites at tidal levels and locations (Table 1) roughly reflects the areal proportions in the Sylt-Rømø Bight. For practical reasons, 11 sites in the western part of Königshafen Bay were sampled in a straight line (Fig. 2). Because these sites were situated at different tidal levels and on different sediments, they are treated as random samples. At each sampling site the following parameters were recorded: (1) sediment type: sand (0 –10% of the particle fraction <0.063 mm) or muddy sand (10–50% of the particle fraction <0.063 mm) according to the map of Bayerl et al. (1998); (2) *A. marina* densities based on number of casts per square metre (<5 ind m^{-2}, 5–30 ind m^{-2}, >30 ind m^{-2}); (3) presence or absence of seagrass (*Zostera* spp.); (4) presence or absence of projecting *M. arenaria* shells (distinct areas where empty shells of *M. arenaria* in living position project out of the sediment).

Sampling technique and size measurement

Adults and death assemblages of M. arenaria

At each site the sediment below 0.1 m^2 was sampled using a metal frame (50 cm long, 20 cm wide, 20 cm deep). The frame was pushed into the sediment and its contents excavated down to 35 cm with a fork. Live clams and shells were separated from the sediment by hand. At sites where *M. arenaria* signalled its presence by distinct oval siphon holes at the sediment surface, unbiased samples were obtained by throwing the frame a few metres with eyes closed. Between three and five parallels, 1–3 m apart, were taken per site. The death assemblages were obtained from the first subsample only. In the laboratory, live clams and empty shells were counted and the maximum shell length of the left valve measured to the nearest millimetre with a vernier caliper.

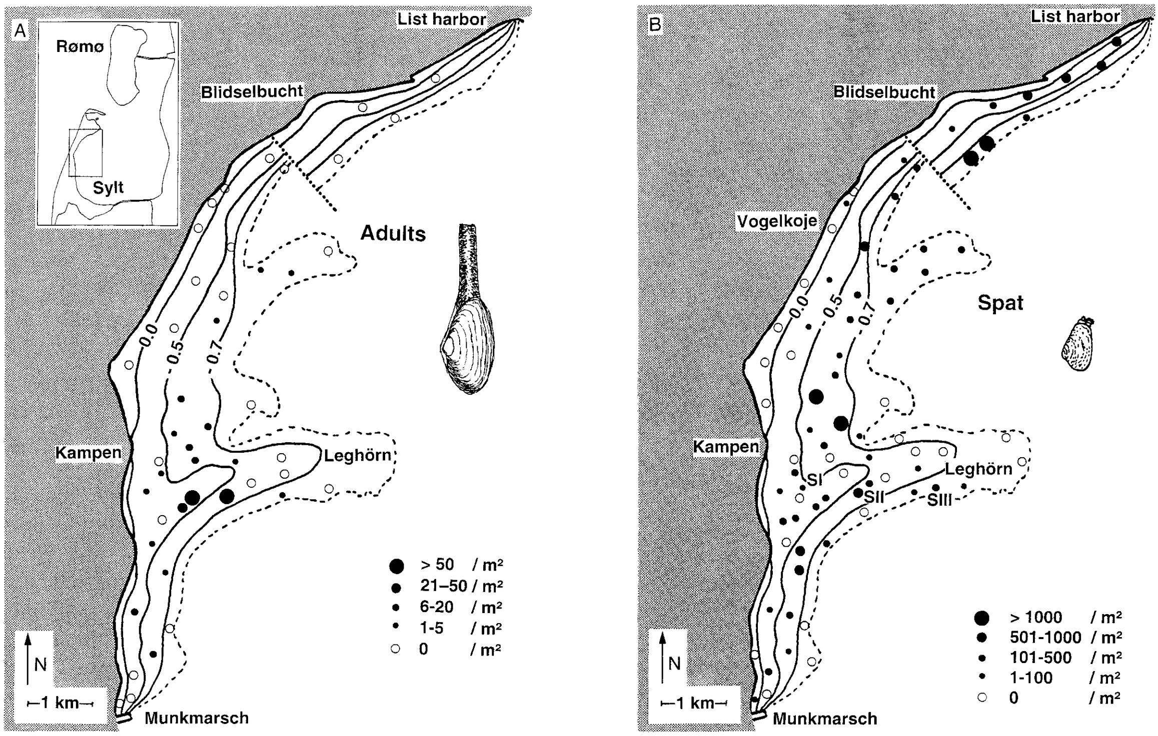


Fig. 3A,B Mean abundance of *M. arenaria* in the intertidal zone of East Sylt, northern Wadden Sea, in 1995. For better visualization of the sampling sites the intertidal zone *below the dotted line* is enlarged by 50%, above the dotted line by 200%. **A** Adults; **B** juveniles. At permanent sites (*SI*, *SII*, *SIII*) abundances are averaged over five sampling dates between July and September 1995

Table 1 Distribution of sampling sites among tidal levels and locations. 165 sites were sampled for *M. arenaria* spat and in parentheses, 98 sites were sampled for adult *M. arenaria*

Tidal level	Location			Total
	Rømø	Königshafen Bay	East Sylt	
High	9 (3)	6 (4)	9 (5)	24 (12)
Mid	16 (11)	14 (12)	23 (15)	53 (38)
Upper low	3 (6)	9 (8)	22 (15)	44 (29)
Lower low	12 (3)	10 (6)	22 (10)	44 (19)
Total	50 (23)	39 (30)	76 (45)	165 (98)

Bivalve spat

At each site, six sediment cores of 20 cm²×3 cm depth were collected randomly within a 9 m² area using a Perspex tube. At the permanent sites nine or ten cores were taken. Juvenile molluscs were separated from the sediment using a shaking-decantation procedure originally developed for meiofauna (Armonies and Hellwig 1986). Initial sieving through a 0.25-mm screen in July 1995 indicated a minimum spat length of 0.8 mm. Therefore a 0.5-mm screen was used. Sorting, identification and counting of the bivalves were done under a dissecting microscope (×8–80 magnification). The maximum shell length of *M. arenaria* was measured with a calibrated ocular micrometer. For all statistical computations the program STATISTICA (Statsoft 1994) was used.

Results

Distribution of abundances in adults and spat

Adults

The abundance of adult *M. arenaria* ranged from 0 to 243 ind m^{-2} with a mean of 11.8 ind m^{-2}. A coefficient of variation (calculated as standard deviation/mean) of 3.1 expresses their pronounced patchy distribution (cf. Figs 1–3A). At 59 sites (60%) no live *M. arenaria* were found. At six sites (6%), the abundance of adult *M. arenaria* exceeded 50 ind m^{-2}. Two of these sites were located on the flat called Leghörn at East Sylt (Fig. 3A) and four high density sites were located at Rømø (Fig. 1A) – one near the causeway, two near Tagholm, and one near Østerby. Out of 552 *M. arenaria* collected from 98 sites, 69% were from these six sites alone.

Spat

In 1995 *M. arenaria* spat occurred at an average abundance of 235 ind m^{-2}, ranging from 0 to 2917 ind m^{-2}. The coefficient of variation of 1.8 indicates an aggregated distribution (cf. Figs 1–3B). At 60 sites (36%) no *M. arenaria* were found, while abundance exceeded 1000 ind m^{-2} at 6 sites (4%). Two of these sites were situated near Tagholm, Rømø (Fig. 1B), two in Blidselbucht and two near Kampen, East Sylt (Fig. 3 B). In each case, two of these sites were located in direct proximity to each other which may be a consequence of high spatfall on a scale larger than intersite distances.

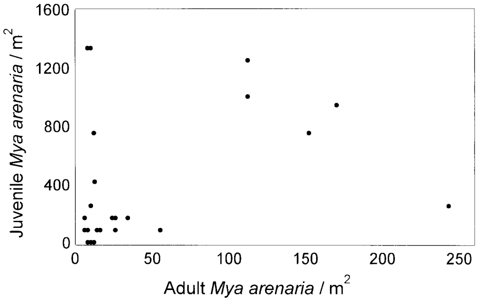


Fig. 4 Abundance of juvenile versus abundance of adult *M arenaria* per square metre, considering all sites with more than 5 adults m^{-2}. Correlation is not significant (Spearmans *R*=0.287, *n*=25, *P*>0.05)

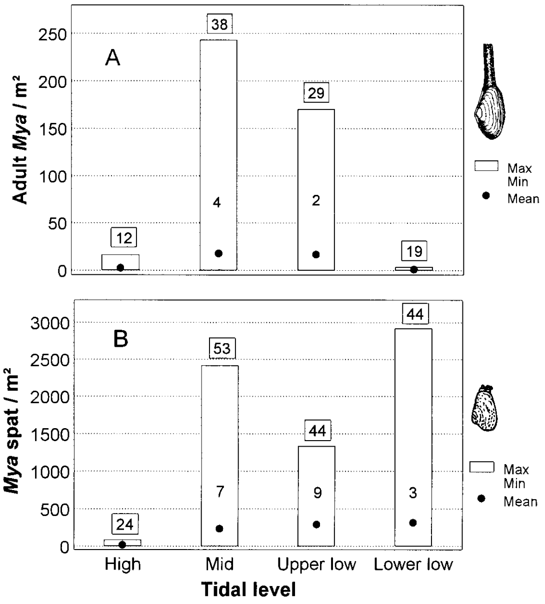


Fig. 5A,B Abundance of *M. arenaria* in relation to tidal level. Indicated are mean (*middle point*) and minimum/maximum values (*box*). Number of sampling sites is given over each box. **A** Adults; number of high density sites (>50 ind m^{-2}) is given inside each box. **B** Spat; number of high density sites (>500 ind m^{-2}) is given inside each box

Comparison of abundances of adults and spat

The coefficient of variation (CV) as a rough measure of patchiness shows that adult *M. arenaria* (CV=3.1) were more aggregated than *M. arenaria* spat (CV=1.8). Considering all sites with abundances >5 adults m^{-2} there was no significant correlation (Spearmans *R*=0.287, *n*=25, *P*>0.05) between adults and spat (Fig. 4). The positive Spearmans *R* was caused by relatively high abundances of spat (750–1250 ind m^{-2}) found at 4 sites with dense beds of adults (112–170 ind m^{-2}). Three of these sites were located at Rømø: two near Tagholm and one near Østerby (Fig. 1). The other site was situated on Leghörn, East Sylt (Fig. 3).

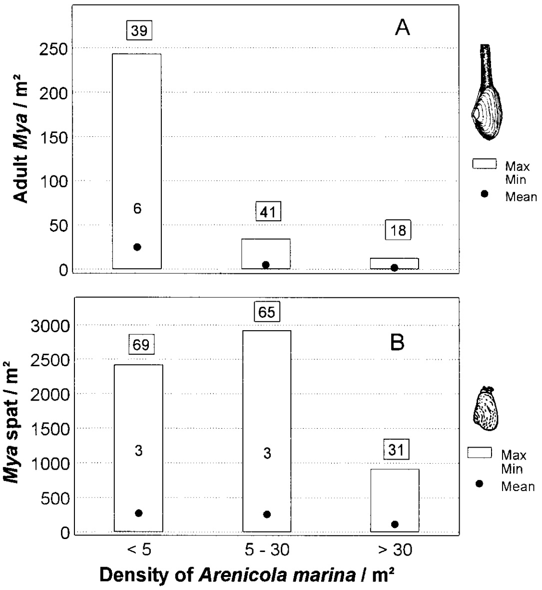


Fig. 6A,B Abundance of *M. arenaria* in relation to three different density classes of *Arenicola marina* casts. **A** Adults; number of high density sites (>50 ind m^{-2}) is given inside each box. **B** Spat; number of high density sites (>1000 ind m^{-2}) is given inside each box. For further explanations, see Fig. 5

Tidal level

Abundances of adult *M. arenaria* differed significantly between tidal levels (H-test, *P*<0.001). The reason for this difference was a higher abundance in the upper low intertidal zone compared with that in the high intertidal (U-test, *P*<0.05) and in the lower low intertidal zone (*P*<0.001). High density patches (>50 ind m^{-2}) were found in the mid and upper low intertidal zone but not in the high intertidal and the lower low intertidal zone (Fig. 5 A). It cannot be ruled out that the low number of sampling sites at these tidal levels was responsible for the absence of high density patches. However, projecting shell beds – proof of dense *M. arenaria* beds in the past – were found at all tidal levels except in the high intertidal zone.

Abundance of *M. arenaria* spat also differed significantly according to the tidal levels (H-test, *P*<0.001). Mean values increased toward the low tide mark, but a significant difference was only found in the high intertidal zone compared with all other tidal zones (U-test, *P*<0.001). Likewise, abundances exceeding 500 ind m^{-2} were found at all tidal levels but not in the high intertidal zone (Fig. 5B). In the mid intertidal zone, the upper low intertidal zone, and the lower low intertidal zone abundances exceeded 500 ind m^{-2} at least at three sites. So, the low number of sampling sites in the high intertidal zone cannot account for the observed differences in abundance.

Densities of A. marina

Abundances of adult *M. arenaria* showed no significant difference in relation to densities of *A. marina* (H-test,

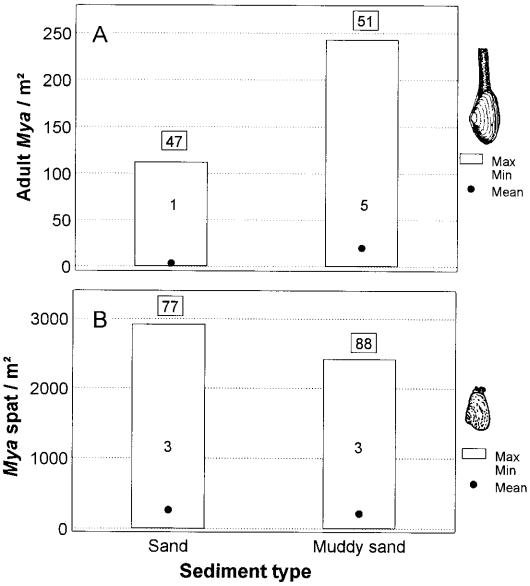


Fig. 7A,B Abundance of *M. arenaria* on sand and muddy sand. **A** Adults; number of high density sites (>50 ind m^{-2}) is given inside each box. **B** Spat; number of high density sites (>1000 ind m^{-2}) is given inside each box. For further explanations, see Fig. 5

$P>0.05$). However, all high density patches (>50 ind m^{-2}) coincided with a virtual absence of lugworms (Fig. 6A). A more complex pattern is shown by *M. arenaria* spat: although abundances were significantly higher at sites with low densities (<5 ind m^{-2}) of lugworms compared with sites of high densities (>30 ind m^{-2}) (U-test, $P<0.001$), high density patches of spat >500 ind m^{-2} were found at all lugworm densities, and spat >1000 ind m^{-2} were found only at sites with <30 lugworms m^{-2} (Fig. 6B).

Sediment type and epibenthic structure

Categorization of all sampling sites into sand and muddy sand showed that abundances of adults were significantly higher on muddy sand than on sand (U-test, $P<0.001$). However, high density patches of adults (>50 ind m^{-2}) were not restricted to muddy sand (Fig. 7A). There was no significant difference in spat abundance ($p>0.05$) between sand and muddy sand, and the same number of high density patches were found on sand and muddy sand (Fig. 7B).

Only low abundances of *M. arenaria* spat and adults were found at sites with seagrass or projecting *M. arenaria* shells. All sites with seagrass were located in the high or mid intertidal zone. Maximum abundance of spat was 167 ind m^{-2} (mean 15.3 ind m^{-2} of 23 sites). Adults were found at a maximum of 5 ind m^{-2} (mean 1.4 ind m^{-2} of 12 sites). Projecting *M. arenaria* shells were found at all tidal levels except the high intertidal zone. Maximum abundance of spat was 500 ind m^{-2} (mean 176.0 ind m^{-2} of nine sites) and 26 adult *M. arenaria* m^{-2} (mean 5.8 ind m^{-2} of five sites). Because of the low number of sampling sites with epibenthic structures no statistical analysis was performed on these parameters.

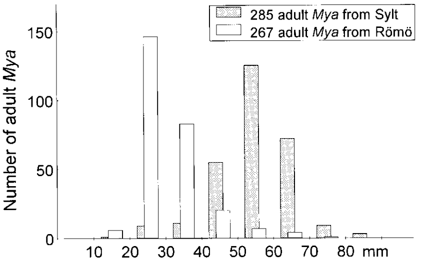


Fig. 8 Length-frequency distribution of adult *M. arenaria* from 75 sampling sites at Sylt (Königshafen Bay and East Sylt combined) and 23 sites at Rømø

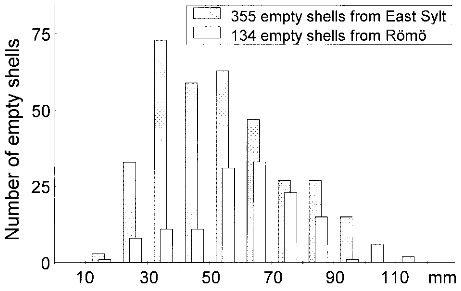


Fig. 9 Length-frequency distribution of empty *M. arenaria* shells (death assemblage) from 43 sampling sites at East Sylt and from 23 sites at Rømø

Distribution of size and age in adults and death assemblage

Shell lengths of living adult clams ranged from 16 to 89 mm with a mean of 44 mm. The length-frequency distribution of 552 individuals showed two peaks, one between 20 and 30 mm and the other between 50 and 60 mm. The two peaks stem from different locations (Fig. 8). *M. arenaria* from the northern part of the Bight (Rømø) with a mean of 32 mm were significantly smaller than *M. arenaria* from the southern part (Königshafen Bay and East Sylt) with a mean of 55 mm (Kolmogorov-Smirnov 2 sample test, $P<0.001$).

A total of 489 empty *M. arenaria* shells were collected from 66 sampling sites (43 at East Sylt and 23 at Rømø). On average, 83 shells m^{-2} were found at East Sylt compared with 58 shells m^{-2} at Rømø. The length-frequency distribution was almost normal, with a peak in the 50–60 mm size class. Average length was 56 mm within a range of 14–111 mm. Empty shells from Rømø were significantly larger (60 mm) than those from East Sylt (Kolmogorov-Smirnov 2-sample test, $P<0.001$) (Fig. 9).

The length-frequency distribution of live adult *M. arenaria* strongly suggests that the tidal flats at Rømø and Sylt were dominated by different cohorts. In order to age the cohort from Rømø, length-frequency distributions of *M. arenaria* sampled from Tagholm in 1995 1996 and 1997 were compared (Fig. 10). In 1995 the clams showed a peak in the 25 to 30-mm size class. A year later the majority attained 30 to 45-mm. In 1997 a peak was visible in the 35–50 mm size class. Considering that *M. arenaria*

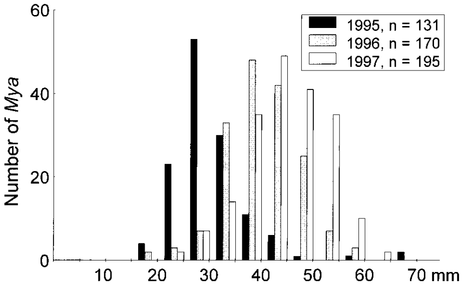


Fig. 10 Length-frequency distribution of *M. arenaria* sampled at Tagholm, Rømø, in June 1995, August 1996, and July 1997

grows fastest in its first years (Brousseau 1978) it is suggested that the *M. arenaria* from Tagholm were 2 years old in 1995 (originating in 1993). The clams from Sylt were larger than the 4-year-olds in 1997, and probably 8–10 years old, originating from the mid-1980s.

Temporal variability of spat

In 1995 spat abundance remained rather constant throughout summer and declined in October. Of the six sites sampled for spat about fortnightly between July and September 1995, two sites were each established at mid intertidal level, at upper low intertidal level and close to the low tide mark (Table 2). The sites in the upper low intertidal zone showed the highest mean abundances of *M. arenaria* spat (around 1000 ind m^{-2}). These two sites were also characterized by high abundances of adults (112 and 170 ind m^{-2}, respectively). Abundance of spat was relatively low at the other sites, especially in the mid intertidal zone. Between July and September a decreasing trend in abundance was only visible at site Sylt II. Here, the abundance of spat differed significantly between the sampling dates (H-test, $P<0.01$). The other five sites showed no significant difference in spat abundance during July and September ($P>0.2$). Later in October, abundance also declined at the sites Rømø II and Rømø III. The temporal variability between July and October at both Rømø and Sylt never changed the order of abundance at the sites. Abundance was always highest in the upper low intertidal zone followed by the sites close to the low tide mark and those at mid intertidal level.

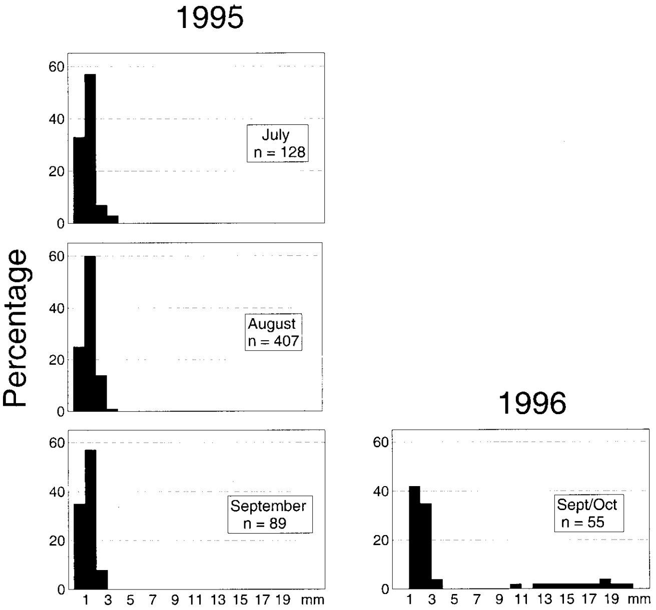


Fig. 11 Length-frequency distribution of *M. arenaria* spat in 1995 and 1996

In 1995 spat remained small throughout summer, with a maximum size of 4 mm (Fig. 11). Average size hardly changed between July (1.4 mm), August (1.5 mm) and September (1.3 mm). In all length-frequency distributions there was a marked decline in abundance in the size range 2–3 mm. In 1996 the majority of *M. arenaria* spat were also <3 mm. However, in this year 18% of spat attained sizes between 10 and 21 mm by September.

Discussion

Sampling intervals and recruitment

A large-scale (20-km) mapping approach was taken to investigate the distribution pattern of *M. arenaria*. A potential drawback of a survey on this scale was the time needed to cover such long distances. As a result, completion of the sampling program took 5 weeks for adult *M. arenaria* and 8 weeks for spat in 1995. According to Brousseau (1978), the survivorship curve of *M. arenaria* is L-shaped. Mortality is extremely high in both larval and juvenile stages and levels off close to the age of first

Table 2 Abundance (m^{-2}) of *M. arenaria* spat (mean of 9–10 sediment cores of 20 cm^2)±standard error at the six permanent sites at Rømø and East Sylt between July and October 1995

Perm. site	Tidal level	Sediment	11–12 July	27–28 July	10–12 Aug	29–30 Aug	11–12 Sept	11–12 Oct
Rømø I	Mid	Muddy sand	50±50	0	0	0	50±50	–
Rømø II	Upper low	Muddy sand	1650±505	450±240	750±270	800±185	1050±230	150±75
Rømø III	Lower low	Muddy sand	300±110	56±50	300±135	200±155	350±150	56±50
Sylt I	Mid	Muddy sand	50±50	100±65	0	50±50	50±50	–
Sylt II	Upper low	Sand	900±235	2150±350	750±260	800±215	400±180	400±100
Sylt III	Lower low	Sand	150±75	150±105	100±100	–	100±65	50±50

reproduction. Based on these findings, we assume that no bias occurred on adult abundances. In contrast, we expected a steep decline of spat abundances in the course of the summer. However, at most of the regularly sampled sites abundances of spat did not decrease during the 8-week sampling period (July – September), contradicting results from other studies (e.g. Smidt 1951; Jensen and Jensen 1985; Möller 1986; Günther 1992). Therefore, we assume that the 8-week sampling period adequately depicted spat distribution in summer 1995.

The spatial variability of *M. arenaria* in the Sylt-Rømø Bight was characterized by a highly patchy distribution for both spat and adults. A patchy distribution of adults was reported from many areas (the Wadden Sea: e.g. Kühl 1955; east coast North America: e.g. Brousseau 1978). The patchy recruitment pattern of *M. arenaria* is confirmed by Reise (1987) who found a CV of 2.02 in July/August 1979 in the North Frisian Wadden Sea.

No adult-larval interactions

It was hypothesized that assemblages of filter feeders will have a negative impact on larval settlement because when the water is filtered the larvae will be destroyed (Woodin 1976). This hypothesis is not confirmed by the results of this study because there was a positive, although not significant, correlation between abundances of adults and spat of *M. arenaria*. In fact recruitment was relatively high at sites with high abundances of adults. Although it cannot be ruled out that recruitment would have been even higher at these sites if adults had been absent, the large-scale distribution pattern of spat was clearly not shaped by negative effects of adults. Similar results were also found in other studies in the Wadden Sea (Kühl 1955; Günther 1992) and in North America (Brousseau and Baglivo 1988). In contrast, studies along the Swedish west coast showed a significant negative impact of suspension feeders on the recruitment of total bivalve spat (André and Rosenberg 1991) and *M. arenaria* (Möller 1986). One must notice that recruitment in the shallow waters of the Swedish investigation areas is usually at least one order of magnitude higher than in the Wadden Sea. It seems possible that very high settlement rates are necessary to be able to detect any negative effects of filter feeders.

Effects of tidal level and of juvenile dispersal

Abundances of *M. arenaria* spat and adults were low in the high intertidal zone. Spat occurred abundantly at all other tidal levels, with a general increase toward the subtidal, which confirms Reise (1987) who found the same spatial pattern on a 100-km scale. This pattern is in line with the hypothesis of larvae settling passively like inanimate particles (Hannan 1984). In the case of passive sedimentation, larval abundance decreases in a landward direction because of the lower water volume in the higher intertidal. Alternatively, larvae may have also settled at higher elevations but subsequently disappeared due to mortality or dispersal. However, there was no indication of dispersal in a landward or seaward direction contributing significantly to the distribution pattern of the *M. arenaria* population on a larger scale in the relatively sheltered Sylt-Rømø Bight. At the permanent sites, changes in abundance were irrespective of tidal level and relatively stable between July and September. In addition, settlement of *M. arenaria* did not take place at higher intertidal sites in previous studies in the Wadden Sea (Günther 1992; Armonies 1996). Minimal transport is also suggested by the similar distribution pattern of spat and adults. Dispersal of juvenile *M. arenaria* may be an important factor on more exposed flats (Matthiessson 1960) as part of bedload sediment transport (Emerson and Grant 1991). In the Sylt-Rømø Bight, stormy weather caused passive displacement with subsequent bedload transport of *M. arenaria* spat onto more exposed sandy flats, while this effect was less important in muddy sediment (Armonies 1998).

Effect of *A. marina*

Numbers of *M. arenaria* recruits showed a negative relationship with lugworm densities in the Dutch Wadden Sea (Flach 1992). However, in this study *A. marina* densities of up to 30 ind m^{-2} did not prevent high abundances of *M. arenaria* recruits from occupying the same habitat. It remains unclear whether the lack of high abundances of spat at *A. marina* densities exceeding 30 ind m^{-2} reflected a negative interaction between the two species because large numbers of *A. marina* were found primarily in higher tidal regions where *M. arenaria* spat abundance was generally low. However, all sampling sites with adult *M. arenaria* of more than 50 ind m^{-2} were characterized by very low densities of *A. marina*. Incompatibility of *A. marina* and *M. arenaria* beds was also reported by Linke (1939) and Kühl (1951). Perhaps *A. marina* does not prevent recruitment of *M. arenaria*, but establishment of adult beds is impeded by direct and indirect effects of the lugworm that act on a larger time scale.

Effect of sediment type and epibenthic structure

Five sites with adult abundances >50 ind m^{-2} were located on muddy sand whereas only one site was situated on sand. It cannot be concluded from this that larvae prefer muddy sediments because in 1995 recruitment was independent of sediment type. The region with the highest abundance of spat (Blidselbucht) even consisted entirely of sandy substrates. Furthermore, the conspicuous patchiness of spat does not coincide with a similar patchiness of sediment composition. The independence of *M. arenaria* with regard to sediment type is confirmed by Smidt (1951), but is contradicted by several other studies (e.g. Emerson et al. 1988). In conclusion, sediment type cannot explain the distribution pattern of *M. arenaria* in the Sylt-Rømø Bight.

Blundon and Kennedy’s (1982) suggestion of seagrass acting as a refuge for *M. arenaria* spat cannot be confirmed because *M. arenaria* was virtually absent in seagrass. Thus, there is no indication of *M. arenaria* larvae being attracted to seagrass, as found, for example, in *Mercenaria mercenaria* (Peterson 1986). However, since all sites with seagrass were located in the mid and high intertidal zone, larvae simply may not have reached these habitats.

Sites with projecting *M. arenaria* shells could have shown higher recruitment if larvae were attracted to the remains of their conspecifics. An area that was once suitable for predecessors might have been favoured by substrate-testing larvae. The cause of low recruitment at these sites might be the generally high level of erosion. Without erosion these shells would not have become exposed in the first place.

Mortality and distribution of cohorts

The 4-mm maximum length of *M. arenaria* spat found in 1995 is in marked contrast to the maximum of 21 mm found in 1996. In 1995, predators had probably consumed most 0-group *M. arenaria* once they reached a size of 2–3 mm. Consequently, no growth was apparent between July and September 1995. The decline in numbers of spat >2 mm coincides with the size of the diet of epibenthic predators. While *Crangon crangon* cannot prey on bivalves larger than 2 to 3 mm, flounders preyed on *M. arenaria* in the size range 2–12 mm (Pihl 1982). Plaice and flounder may consume more than 2000 bivalves (*M. arenaria* and *Cerastoderma edule*) per m^2 per year according to data given by de Vlas (1979). A study in the Danish Wadden Sea suggests that *Carcinus maenas* played a key role in the elimination of 0-group *M. arenaria* in 1982 (Jensen and Jensen 1985). In the Sylt-Rømø Bight settlement of *C. maenas* was delayed in summer 1996 after the hard winter of 1995/1996 (Strasser, in preparation). These results corroborate the hypothesis that survival is enhanced when spat manage to grow beyond a critical size that protects them from being captured by these main predators (Reise 1985; Möller 1986). As this size was not reached by *M. arenaria* spat in 1995, no new beds will become established in the subsequent years. An alternative explanation for the lack of larger spat in 1995 would be dispersal into the subtidal. However, as already mentioned, there was no indication of spat dispersal in 1995. We suggest that recruitment failure in most years due to predation is the reason why the Sylt-Rømø Bight is colonized mainly by a few cohorts originating in 1993 and the mid 1980s.

However, why is the 1993 cohort found mainly in the northern part of the Bight, while clams from the 1980s are predominantly found in the southern part? One (pre-settlement) explanation is that there is a difference between Rømø (north) and Sylt (south) with regard to larval supply. For *M. arenaria* the majority of larvae are in the plankton at the end of May and the beginning of June (Günther 1992). Stable wind conditions during this period could result in higher larval transport to certain areas of the semi-enclosed Bight. In these areas chances of high recruitment are enhanced if post-settlement mortality is not higher than elsewhere. The similar length-frequency distributions of adult *M. arenaria* in Königshafen Bay and at East Sylt compared with a very different distribution at Rømø support this hypothesis of wind/current dependency, because net larval transport to the south supplies both Königshafen Bay and East Sylt with larvae. Predominant transport of bivalve larvae depending on wind direction was reported by Möller (1986). For the Sylt-Rømø Bight Kopacz (1994) suggested a relation between wind conditions and abundance of gelatinous plankton. Winds from the southwest resulted in higher abundances in the Rømø Deep than in the Lister Ley, which lies south of Rømø, whereas northeastern winds had the opposite effect.

An alternative (post-settlement) explanation for the different cohorts in Rømø and Sylt requires the assumption that the strong year class(es) in the mid 1980s survived at Sylt but were eliminated at Rømø. The reverse must have happened to the 1993 year class: *M. arenaria* was eliminated at Sylt but survived at Rømø. Considering the geographic neighbourhood of Sylt and Rømø, physical disturbance as a factor of differential mortality is not a likely explanation. It is likewise unreasonable to assume that dispersal differed regionally. If predation caused the pattern, the abundance of predators must have been very different at the two locations in the same years and vice versa in other years. Given the high mobility of the predators in question, we regard this as rather unlikely, too. We therefore conclude that differential wind-driven larval supply in some years with subsequent low predation pressure on the benthic juveniles is the most plausible explanation for the observed adult cohorts.

Death assemblages

The length-frequency distribution of the death assemblages provides information about the size of *M. arenaria* when they died of causes other than predation or displacement (washout). Interpretations of the death assemblages must take into account that the size-frequency distribution may be altered by so-called taphonomic processes such as dissolution, breakage and displacement by bioturbation (Powell et al. 1982) as well as by size selective predation by birds (Cadée 1989). With regard to *M. arenaria*, birds preferably prey on individuals <45 mm (Zwarts and Wanink 1989).

The length-frequency distributions of the death assemblages at Rømø and Sylt (Fig. 9) have in common the virtual absence of the smallest shells (<20 mm). The lack of small shells is in accordance with the length-frequency distributions of death assemblages of *M. arenaria* collected in the Dutch Wadden Sea (Cadée 1992). The shells <20 mm were probably rare because their thin shells are more subject to taphonomic processes such as breakage than larger shells. In addition, these size classes undergo heavy predation by crabs and birds; but this cause of mortality is not recorded in the death assemblages. Predation pressure usually ceases when the clams reach a size of 50 mm because at that point they are able to reach a depth refuge from avian predators (Zwarts and Wanink 1984). Provided predation is the main cause of mortality, one would expect the size classes between 50 mm and the average size reached at natural death to dominate in the death assemblages. This expected size distribution corresponds exactly to the length-frequency distribution of shells at Rømø. In contrast, the length-frequency distribution of shells from East Sylt showed a peak in the size class 30–40 mm (Fig. 9), implying that non-predatory mortality played an important role, too. At some sites at East Sylt, high abundances of shells <50 mm were found, but live *M. arenaria* were missing. This suggests that some unknown factor killed *M. arenaria* at these sites. Potential causes of mortality may be disturbance, competition or disease. Parasitism appears to have no impact on the population structure of *M. arenaria* in the Wadden Sea because the parasites inherent to populations in North America have not followed the invasion of *M. arenaria* to Europe yet (Lauckner, personal communication).

Conclusions

Mapping juvenile and adult subpopulations over a wide area, combined with some local information on temporal change, provides a rich source of information on population ecology. Although the precision of detailed local analysis cannot be achieved, the strength of the mapping approach is, when one considers the general picture it presents, that it enables one to separate the rare from the more common phenomena. We therefore believe that the following conclusions are foolproof with regard to errors which may arise when upscaling a rather localized study.

Basically, the population of *M. arenaria* in the Wadden Sea is centred in the mid and lower tidal zone. This pattern originates from larval settlement. Survival to adulthood is to some extent influenced by sediment properties and the presence of bioturbating lugworms. However, the striking patchiness and dominance of single year classes in the population is the outcome of contingency of events during early lifetime: wind direction during peak larval supply in those years when subsequent predation pressure on the benthic juveniles happens to be low. Larvae neither seem to aggregate at sites with high adult abundances nor do these generally prevent successful recruitment. Once the first year has been survived, *M. arenaria* cohorts may achieve an age of several years. However, occasional mass mortalities may happen at any time, and their causes have still to be revealed.

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