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ORIGINAL ARTICLE

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The American slipper limpet *Crepidula fornicata* (L.) in the northern Wadden Sea 70 years after its introduction

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Abstract In 1934 the American slipper limpet *Crepidula fornicata* (L.) was first recorded in the northern Wadden Sea in the Sylt-Rømø basin, presumably imported with Dutch oysters in the preceding years. The present account is the first investigation of the *Crepidula* population since its early spread on the former oyster beds was studied in 1948. A field survey in 2000 revealed the greatest abundance of *Crepidula* in the intertidal/subtidal transition zone on mussel (*Mytilus edulis*) beds. Here, average abundance and biomass was 141 m^{-2} and 30 g organic dry weight per square metre, respectively. On tidal flats with regular and extended periods of emersion as well as in the subtidal with swift currents in the gullies, *Crepidula* abundance was low. The main substrate of attachment was live mussels. Compared with the years following their initial introduction, *Crepidula* is more abundant today and has shifted from the now extinct oyster beds to the epifaunal community of the mussel beds. Their present abundance is considerably lower than at more southern European coasts where the species may dominate the epifauna. Low winter temperatures are suggested to have limited the population expansion in the northern Wadden Sea until now.

Keywords *Crepidula fornicata* · Introduced species · Mollusca · Wadden Sea

Introduction

Unintentionally introduced to Europe in the 1870s, the American slipper limpet *Crepidula fornicata* (L.) can now be found attached to hard substrates along European coasts from the Mediterranean to Norway (Blanchard 1997). In the centre of its European distributional range a population explosion has been observed on the Atlantic coast of France, southern England and the southern Netherlands. This is well documented (reviewed by Blanchard 1997) and sparked a variety of studies on the ecological and economic impacts of *Crepidula*. The ecological impacts of *Crepidula* are manifold, and include the following:

(1) Accumulation of pseudofaeces and of fine sediment through the filtration activity of *Crepidula* and individuals protruding in stacks into the water column. This was reported to cause changes in sediments and near-bottom currents (Ehrhold et al. 1998).
(2) *Crepidula* may lead to modifications in the trophic structure of benthic communities (Chauvaud et al. 2000; Hily 1991).
(3) Changes in macrobenthic community composition which may result in an increase in biodiversity (Barnes et al. 1973; Montaudouin and Sauriau 1999; Montaudouin et al. 1999).
(4) Competition for food with other molluscs was proposed by many authors as a main consequence of high *Crepidula* abundance (Orton 1927; Ankel 1935; Werner 1948; Chipperfield 1951; Korringa 1951; Cole and Hancock 1956; Walne 1956; Marteil 1965; Blanchard 1997) although recent field studies did not support a competitive dominance of *Crepidula* (Montaudouin et al. 1999; Thouzeau et al. 2000). From an economic point of view, high infestations by *Crepidula* on mollusc cultures make expensive cleaning operations necessary (Blanchard 1997).

For the northern part of its distributional range in Europe, data on abundance and possible effects of *Crepidula* are scarce and mostly historical (see Blanchard 1997). This also holds true for the northern Wadden Sea. Here, the species was first recorded on oyster beds in the Sylt-Rømø basin in 1934 (Ankel 1935, 1936), where infected oysters from the Netherlands had been introduced for cultivation in the preceding years. Several investigations

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on this initial introduction were done between 1936 and 1944 (Hagmeier 1941; Werner 1948), when *Crepidula* was found mainly on oyster beds (*Ostrea edulis*) in the subtidal. Based on experiences from the Netherlands and England, a population explosion was also predicted for the northern Wadden Sea (Werner 1948). However, at the beginning of the 1950s the native oyster became extinct in this area (Reise et al. 1989) and since then, no further studies on the spatial distribution and abundance of *Crepidula* have been undertaken.

Hence, this paper will give a detailed account of the current distribution and abundance of *Crepidula* in the Sylt-Rømø basin (northern Wadden Sea) in the northern part of the European distributional range of this species. The results of a survey conducted in 2000 are compared with the spatial distribution of the species in the 1930s and 1940s in order to evaluate the population status 70 years after its introduction. In addition, the abundance and biomass of the present population in the Sylt-Rømø basin are compared with those of more southern populations in Europe.

Methods

Study site

The study was conducted in the Sylt-Rømø basin (54°50′–55°10′ N and 08°20′–08°40′ E) in the northern Wadden Sea (see Fig. 1). This area of 407 km^2 is enclosed by the islands of Sylt and Rømø to the west, the mainland to the east and causeways to the islands in the north and south. The basin is connected with the North Sea by a 2.8 km-wide tidal inlet. Tidal flats comprise 33% of the area. Sand is the prevailing sediment type (72%) in the intertidal, followed by muddy sand (25%) and mud (3%). The dominant biota in the intertidal zone are *Arenicola* flats (66%) and *Zostera* meadows (12%). Mussel beds (*Mytilus edulis*) cover approximately 2.7% of the intertidal area (Nehls 2000). In the subtidal, macrobenthic biomass is generally lower than in the intertidal (one-fifth of intertidal). Tides are semidiurnal with a mean range of 1.8 m. Salinity ranges from 30 to 32 psu. For further information on the area see Gätje and Reise (1998).

Distribution and abundance

The distribution and abundance of *Crepidula* was determined in three habitat types:

(1) Eight mussel beds (Fig. 1) were surveyed for *Crepidula* between mid-August and mid-September 2000. All samples were taken in the intertidal/subtidal transition zone, which can be accessed by foot at spring low tides or easterly offshore wind. It extends from –0.9 m mean tidal level (MTL) (= mean low water level) down to about –1.5 m MTL. Average abundance of *Crepidula* for each mussel bed was calculated from 36–76 counts of *Crepidula* within randomly tossed frames of 0.25 m^2. To prevent overlooking of small individuals, only specimens larger than 7 mm shell length were considered. On one mussel bed (Diedrichsenbank in Fig. 1) the spatial distribution of *Crepidula* was studied in detail in a stratified random design of the 0.25 m^2 replicates: on 16 September the intertidal/subtidal transition zone, the intertidal with mussels covered and not covered with fucoid algae (*Fucus vesiculosus*), and tide pools were surveyed.

(2) On tidal flats without mussel beds the abundance of *Crepidula* was estimated along nine transects (Fig. 1) between mid-August and mid-September 2000. Each transect was walked perpendicular to the coastline from mean high water level into the intertidal/subtidal transition zone. Every 50 to 200 m – depending on the total distance from shore to low water – a frame of 1 m^2 was thrown randomly four times and all individuals of *Crepidula* >7 mm shell length within the frame were counted. Transects were divided into four intervals: upper intertidal: above +0.6 m of mean tidal level (MTL); mid-intertidal: +0.6 to –0.6 m MTL; lower intertidal: –0.6 to –0.9 m MTL; intertidal/subtidal transition zone: –0.9 to –1.5 m MTL. Mean abundance was calculated from intervals pooled across transects.

(3) In the subtidal (below –1.5 m MTL) *Crepidula* was sampled from a research vessel with a dredge of 1 m width and a mesh size of 1 cm. The dredge was towed over the bottom for approximately 500 m. In August 2000 an area with subtidal mussel beds ("Königshafen") (five dredge hauls between 3 and 6 m below MTL) and a bottom devoid of mussel beds ("Lister Ley") at a former oyster ground (five dredge hauls between 3 and 16 m below MTL) were sampled (Fig. 1). Additionally, six hauls were taken close to the latter site in December (Fig. 1).

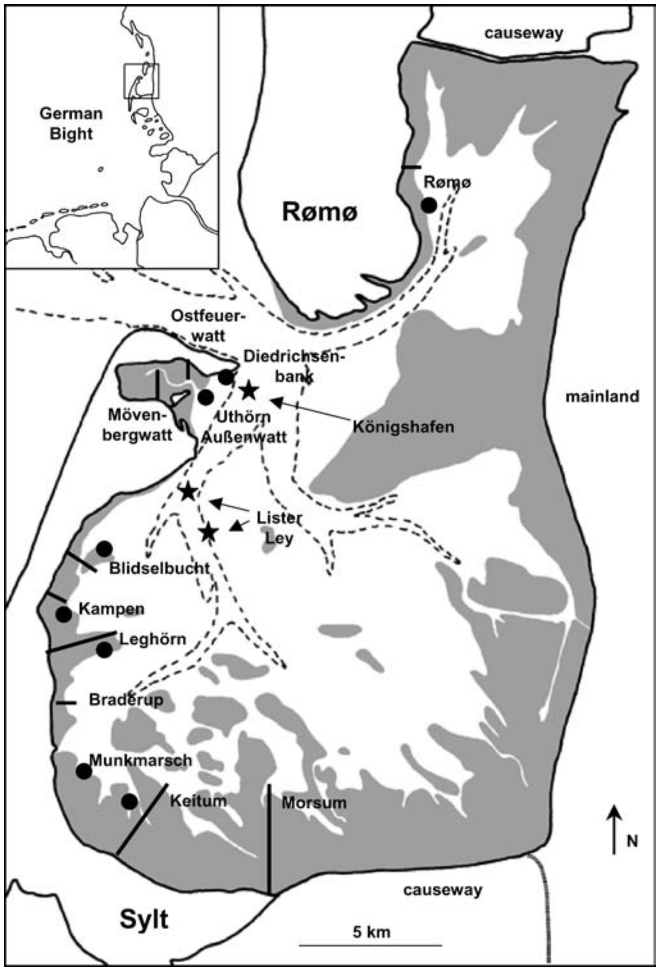

Fig. 1 Sampling sites in the Sylt-Rømø basin. Mussel beds are indicated by a *filled circle*, transects by a *straight line* and subtidal sites by an *asterisk*. *Shaded areas* indicate the intertidal zone

Biomass and substrates

Biomass of *Crepidula* was determined on eight mussel beds. Within 7 to 20 random replicates of 0.25 m^2 – also used for determining abundance – all individuals of *Crepidula* were separated from their substrates, subsequently dried at 75°C for 3 days and then burned at 500°C for 24 h to determine ash-free dry weight (AFDW).

The substrates to which *Crepidula* was attached were recorded for all three habitats. For mussel beds, the samples for determining biomass were used, and the substrate of each individual was noted. On the transects, the substrate of each *Crepidula* was recorded. For the subtidal, one of the hauls at the Königshafen and all of the hauls on the bottom devoid of mussel beds were used to record the substrate of each individual.

Statistics

For the statistical treatment of the data, parametric tests (ANOVA) were used. Post hoc calculations were done with the "Tukey's honest significant difference (HSD) test" for balanced and the "Spjotvoll/Stoline test" for unbalanced data sets (StatSoft, Tulsa). All data sets were tested for homogeneity of variance with the Bartlett χ^2 test and log-transformed if variances were heterogeneous. Calculations were done with the software STATISTICA (StatSoft). Graphs show arithmetic means and standard deviations. Levels of significance are indicated by asterisks (*P<0.05; **P<0.01; ***P<0.001).

Results

Distribution and abundance

Average abundance of *Crepidula* on the eight mussel beds in the intertidal/subtidal transition zone was 140.8±132.4 m^{-2}, with lowest abundances at Rømø (1.4 m^{-2}) and highest abundances at Munkmarsch (482 m^{-2}) (Fig. 2). At the latter locality, the maximum density in this study (1,760 m^{-2}) was found. Concerning the spatial distribution of *Crepidula* within four habitats on the mussel bed Diedrichsenbank, there was a significant difference in the distribution of individuals (ANOVA; F=427.6; df=3; P<0.001). Abundance was significantly higher in the intertidal/subtidal transition zone (74 m^{-2}) and in tide pools (51 m^{-2}) than in the intertidal with and without *Fucus* cover (0.1 m^{-2}) (Tukey's HSD test; P<0.001) (Fig. 3). The intertidal/subtidal transition zone and the tide pools were devoid of fucoid algae.

On tidal flats, mean abundance of *Crepidula* was 3.3±3.2 m^{-2}. The highest abundances were encountered from Blidselbucht to Keitum (Fig. 4). Compared with the other areas, hard substrate (single or clumps of mussels, shells etc.) was more common. There was a significant difference in abundance of *Crepidula* at different tidal levels (ANOVA; F=46.86; df=3; P<0.001). This difference was caused by a significantly higher abundance in the intertidal/subtidal transition zone (21 m^{-2}) than in the upper, mid and low intertidal (<3 m^{-2}) (Tukey's HSD test; P<0.001) (Fig. 5).

In the subtidal, mean abundance of *Crepidula* in the area with a natural subtidal mussel bed (Königshafen) was 518.2±355.2 per haul (n=5) compared with 3.7±4.5 per haul (August; n=5) and 4.3±2.3 per haul (December; n=6) on bottoms devoid of mussel beds (Lister Ley).

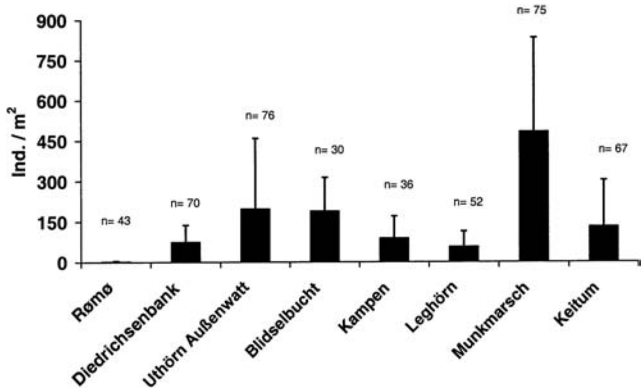

Fig. 2 Mean (+SD) abundance of *Crepidula fornicata* m^{-2} on eight mussel beds in the intertidal/subtidal transition zone in the Sylt-Rømø basin in September 2000. *n* number of subsamples per mussel bed

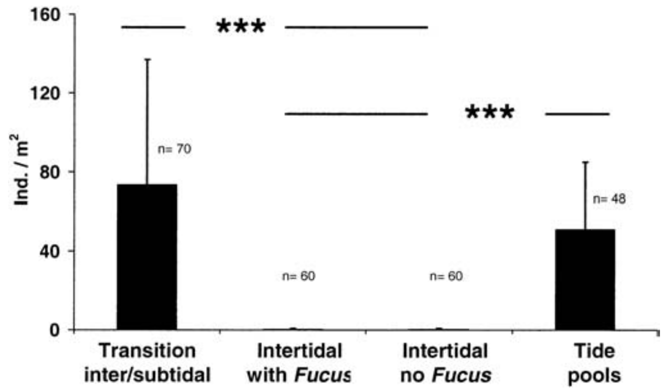

Fig. 3 Mean (+SD) abundance of *C. fornicata* m^{-2} in four different habitats on the mussel bed 'Diedrichsenbank'. Abundance was significantly higher (P<0.001) in the intertidal/subtidal transition zone and tide pools than in the intertidal with and without cover of *Fucus vesiculosus*. *n* number of subsamples in each habitat

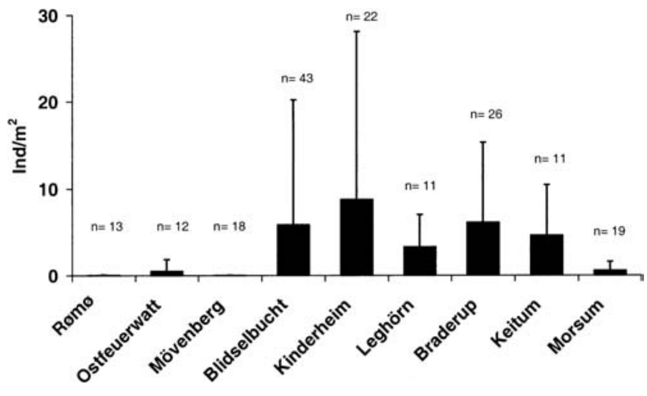

Fig. 4 Mean (+SD) abundance of *C. fornicata* m^{-2} on nine transects in the Sylt-Rømø basin in September 2000. *n* number of stations on each transect

Table 1 Percentages of substrates utilized for attachment by *Crepidula fornicata* living on mussel beds in the transition zone intertidal/subtidal, on tidal flats and on subtidal bottoms with and without mussel beds. Primary substrate: substrate for attachment of solitary specimens or lowest individuals in a stack. Secondary substrate: live *Crepidula* used as substrate for attachment by individuals living in a stack

Substrate type	Mussel beds	Tidal flats	Subtidal with mussel beds	Subtidal without mussel beds
On primary substrate	46.3	42.3	47.3	56.3
On secondary substrate	53.7	57.7	52.7	43.7
Primary substrates				
Mytilus edulis – alive	57.7	50.4	47.8	–
Mytilus edulis – shell	20.7	16.1	8.4	–
Crepidula fornicata – shell	14.9	15.8	3.7	–
pebble	2.3	0.5	22.0	–
Mya arenaria – shell	1.5	12.7	1.6	–
Cerstoderma edule – shell	1.1	2.8	9.6	–
Littorina littorea – alive	0.5	0.1	–	–
Ensis directus – shell	0.4	0.4	5.0	–
Buccinum undatum – shell	0.3	–	–	14.3
Cerastoderma edule – alive	0.1	0.3	–	–
Petricola pholadiformis – shell	0.1	–	–	–
Ostrea edulis – shell	0.1	0.2	0.9	–
Crassostrea gigas – alive	0.1	0.5	–	–
Macoma balthica – shell	0.0	–	–	–
Buccinum undatum – alive	0.0	–	0.9	2.0
Littorina littorea – shell	0.0	–	–	–
Pagurus bernhardus in *Buccinum*	–	–	–	69.4
Carcinus maenas	–	–	–	14.3
n (primary substrate)	2,472	1,344	322	49

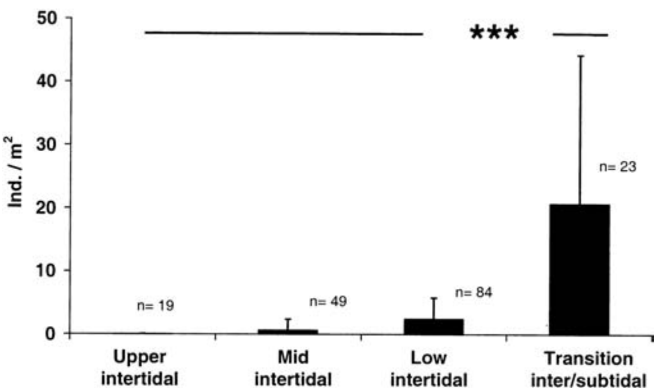

Fig. 5 Mean (+SD) abundance of *C. fornicata* m^{-2} at four tidal levels on tidal flats without mussel beds. Abundance was significantly higher ($P<0.001$) in the intertidal/subtidal transition zone than at all other tidal levels. *n* = number of stations within each tidal level

Biomass and substrates

Mean biomass (AFDW) of *Crepidula* on all eight mussel beds in the intertidal/subtidal transition zone was 29.6±34.1 g m^{-2} (equivalent to 519 g fresh weight) with the lowest values at Rømø (0.48±0.41 g m^{-2}) and the highest values at Munkmarsch (118.2±96.1 g/m^2), where the maximum value was found (322.1 g m^{-2} AFDW equivalent to 5.6 kg m^{-2} fresh weight) in one subsample.

The main substrate of attachment used by solitary *Crepidula* or individuals at the base of stacks (primary substrate) on mussel beds, tidal flats and in the subtidal with mussel beds were living mussels (*Mytilus edulis*) (Table 1). Individuals and stacks of *Crepidula* were mostly orientated with their front towards the siphonal end of the mussels. On subtidal bottoms devoid of mussel beds, shells of whelks (*Buccinum undatum*) inhabited by hermit crabs (*Pagurus bernhardus*) were mainly used as substrate (Table 1). Half of all individuals were found attached to other *Crepidula* (secondary substrate) (Table 1).

Discussion

Comparison of stocks 1936–1944 and 2000

In the years following its introduction to the Sylt-Rømø basin, *Crepidula* was found almost exclusively in the subtidal on oyster beds (Werner 1948; some data were pre-published by Hagmeier 1941). Originally introduced to an oyster bed at the entrance of the Königshafen at the north of Sylt ("Ellenbogenbank"), the species spread further south in the following years. Until 1944 *Crepidula* was recorded on five oyster beds (Werner 1948) (Fig. 6). Apart from on oyster beds only a few specimens were found at a beach in the north of the Königshafen (Werner 1948). Unfortunately, no exact data on the abundance of the species exists, as neither author gave any area measurements for their data. Hagmeier (1941) used an abundance scale from 0 ("absent") to 6 ("mass occurrence") and gave a 5 ("many pieces regularly present") for *Crepidula* on the "Ellenbogenbank" and a 2 ("sporadic occurrence") for the other four oyster beds. Werner (1948) gave absolute numbers of *Crepidula* on single oyster beds but neither the numbers of dredge hauls nor a number per area relationship is mentioned. However, in most cases the number of individuals found on an oyster bed was lower than ten. Only a few higher figures are mentioned (maximum 131 individuals on "Ellenbogenbank" on 26 October 1939). It can be presumed that in most cases several dredge hauls were taken at an oyster

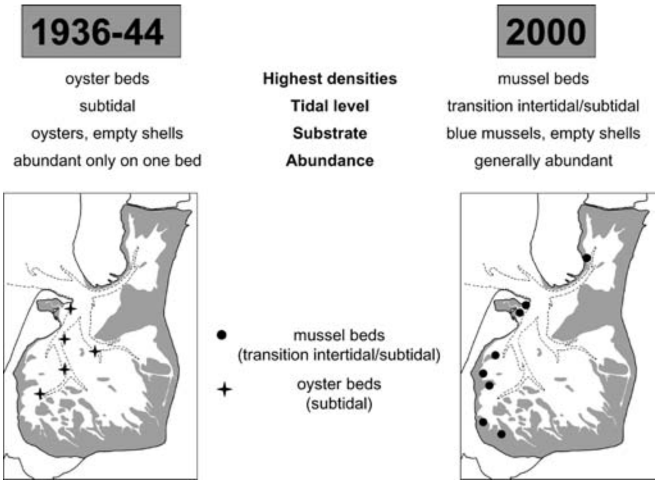

Fig. 6 Comparison of *Crepidula* stocks shortly after its introduction to the basin (1936–1944) (Hagmeier 1941; Werner 1948) and in 2000 (this study). *Maps* show habitats with highest densities

bed. As the given figures are sums of all hauls on a bed, the abundance of *Crepidula* seems to have been relatively low between 1936 and 1944. For substrates of *Crepidula* quantitative data are also lacking. However, Werner (1948) stated that *Crepidula* was found on oysters and on whelk shells (*Buccinum undatum*) inhabited by hermit crabs (*Pagurus bernhardus*) and sometimes on other shells. Only one live mussel (*Mytilus edulis*) was mentioned as a substrate for *Crepidula*.

Between 1944 and 2000, *Crepidula* was constantly present in the area as indicated by its appearance in species lists from sporadic macrobenthos surveys (Buhs and Reise 1997; K. Reise, unpublished data) and continuous observations of researchers at the local institute (K. Reise, personal observation; M. Söhl, personal communication). However, detailed quantitative data on the spatial distribution and abundance do not exist for this period.

Today *Crepidula* is no longer confined to local areas but is found over the entire study area (Fig. 6 and also Figs. 2 and 4) in all surveyed habitats. The population of *Crepidula* no longer lives on oyster beds in the subtidal but instead on mussel beds and tidal flats in the transition zone between the intertidal and subtidal (Figs. 3 and 5). In dredge hauls taken on some former oyster beds, no *Crepidula* were found on the oyster shells.

The concentration of the population in the Sylt-Rømø basin within the intertidal/subtidal transition zone is apparently linked to the occurrence of most mussel beds at this depth level. Although mussel beds have been recorded at greater depths as well (Riesen and Reise 1982; Buhs and Reise 1997), these beds may be less permanent. They are under high exploitation pressure by the mussel fishery and are mostly replaced by extensive bottom cultures in this area (Seaman and Ruth 1997). These mussel culture plots are in a depth range between 2 and 6 m below mean tide level and have not been sampled. Culture plots are stocked with seed mussels and are harvested 2–3 years later, occasionally relayed intermittently. It is assumed that cultured mussels are too short-lived to provide a suitable substrate for *Crepidula*.

Most of the subtidal zone consists of tidal channels with swift currents (>0.5 m s $^{-1}$) and consequently of a rather unstable sandy bottom (Lackschewitz and Reise 1998) with limited opportunities for *Crepidula* to find a suitable substrate for attachment. This may also explain the present finding that the population centre of *Crepidula* is found in the intertidal/subtidal transition zone rather than on subtidal bottoms as recorded elsewhere (e.g. Walne 1956; Loomis and van Nieuwenhuyze 1985; Quiniou and Blanchard 1987). The low abundance of *Crepidula* at higher tidal levels (Figs. 3 and 5) cannot be explained by low resistance to emersion, as *Crepidula* is able to withstand even longer periods of emersion without a negative oxygen balance (Newell and Kofoed 1977). Selective settlement of larvae (D.W. Thieltges, unpublished data) might be responsible for the low abundance. The estimates from dredge hauls are at best tentative, given the limitations of this sampling gear (Eleftheriou and Holme 1984). However, the paucity of *Crepidula* on substrates other than live mussels excludes the possibility of a 'missed' high-density area on subtidal sandy bottoms. The high frequency of *Buccinum* shells inhabited by hermit crabs does not affect this conclusion, given the low abundance of *Pagurus bernhardus* in these shells (Wilmes 1996).

Highest densities of *Crepidula* are reached on present mussel beds (Fig. 2). With a mean abundance of 141 m^{-2} on mussel beds, the abundance of *Crepidula* in the area can be considered to be much higher today than in the 1940s – even though area-related data are lacking from those years. Although in 2000 the highest abundances occurred on mussel beds, the total number of individuals might be roughly the same on tidal flats (2.5×10^8 individuals) as on mussel beds (2.9×10^8 individuals) – calculated on the basis of data on the areas of mussel beds and tidal flats given by Nehls (2000). However, abundance on tidal flats underlies high fluctuations. Due to storm events, single mussels or clumps of mussels can get washed away from mussel beds onto the tidal flats, disappearing again at some later tides (personal observations). The abundance of possibly attached *Crepidula* varies accordingly.

Comparison with other European populations

Abundance and biomass of *Crepidula* as well as the extent of areas with a high density of *Crepidula* can be very high along the coastline further south of our study area. In Lake Grevelingen (Netherlands), *Crepidula* comprises 50% of the macrobenthic biomass on extensive areas of the sea bottom (Nienhuis 1992). In the south of England, *Crepidula* is also the dominant macrobenthic species at some coasts reaching densities over 1,000 m^{-2} (Walne 1956; Connor et al. 1997). The highest abundances, biomasses and area extensions are reported from France. Abundances over 1,000 individuals m^{-2} are commonly observed and *Crepidula* can locally reach up to 9,000 m^{-2} (Hily 1989; Blanchard 1995; Ehrhold et al. 1998; Blanchard and Ehrhold 1999; Montaudouin and Sauriau 1999; Chauvaud et al. 2000; Thouzeau et al. 2000). Accordingly, *Crepidula* comprises the majority of macrobenthic biomass with up to 18,000 g fresh weight m^{-2} (Deslous-Paoli 1985; Hily 1989; Blanchard and Ehrhold 1999; Chauvaud et al. 2000; Montaudouin and Sauriau 1999; Montaudouin et al. 1999), and covers extensive areas (up to 61%) of the subtidal surface, locally forming literally carpets of shells (Blanchard 1995; citations in Montaudouin et al. 2001).

In the Sylt-Rømø basin, high abundance and biomass were only attained locally on mussel beds (i.e. Munkmarsch; Fig. 2) but were still considerably lower than the values quoted above. In addition the areal extension of higher abundance of *Crepidula* can be considered to be relatively low, with mussel beds covering only 2.7% of the intertidal and intertidal/subtidal transition zone. Low winter temperatures are possibly the main limiting factor for a population expansion in the Sylt-Rømø basin leading to lower abundances than further south in Europe. Losses following strong winters and a low freezing tolerance were reported from various places (Korringa 1942; Werner 1948; Cole and Hancock 1956; Walne 1956; Crisp 1964; Deslous-Paoli 1985; Minchin et al. 1995). For our study area a strong decline of the local *Crepidula* population after the severe winter of 1978/1979 is known (Buhs and Reise 1997) and recent observations and experiments emphasise the strong influence of winter severity on the population size (D.W. Thieltges et al., unpublished results).

Conclusion

In the present-day Sylt-Rømø basin, *Crepidula* can be considered a well established introduced species which has become a significant part of the epifauna of mussel beds in the intertidal/subtidal transition zone. Its abundance seems to have increased strongly compared to the situation in the first years following the introduction. Hence, a proposed decline of *Crepidula* caused by habitat loss (oyster beds) (Nehring 2000) cannot be confirmed for the northern Wadden Sea. Concerning remarks on the abundance of *Crepidula* in German waters in Blanchard (1997) it can be deduced that at least in the northern Wadden Sea the species is relatively abundant. However, compared with more southern European populations, a population explosion as expected by Werner (1948) is not apparent. Thus, potential ecological and economic consequences may be currently less serious than further south in Europe. Milder winters caused by global warming might result in a strong increase in the population in the future.

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