ABSTRACT: During the past 3 decades, dense mats of green algae (especially *Enteromorpha* spp.) have been recorded regularly from tidal flats worldwide. The development of green algal mats on tidal flats may be initiated by overwintering and regrowth of adult plants or by the formation and release of small propagules, i.e. vegetative fragments, zoospores and zygotes. On soft sediments, macroinvertebrates may constitute prime substrata for germination of algal spores. *Hydrobius* (mud-) snails are widespread along North Atlantic soft sediment shores and were identified previously as important substrata for *Enteromorpha* spp. germlings in 1 of our study areas. To test the generality of this phenomenon, we investigated the presence of *Enteromorpha* spp. germlings attached to *Hydrobius* snails from November 1995 to December 1996 on 6 tidal flats of North Atlantic coasts (Tralebergskile, Sweden; Königshafen Bay, Germany; Mondego Estuary, Portugal; Ria Formosa, Portugal; Cole Harbour, Nova Scotia, Canada; Lowes Cove, Maine, USA). With 1 exception, hydrobiid snails were present in all areas studied, and intensive growth of *Enteromorpha* spp. occurred during summer. Throughout winter 1995/96, hardly any *Enteromorpha* spp. germlings were found on snail shells, but over the following months germlings developed on up to 60% of the hydrobiid snails present. In 2 areas (Königshafen, Germany; Lowes Cove, USA), germling abundance on hydrobiids began to rise before the peak of green algal mat development. In Tralebergskile, Sweden, high mat abundance occurred simultaneous to and after increased germling abundance on *Hydrobia ulvae*. Densities of snails were very low, however, and hydrobiids appeared to be unimportant as substratum. No clear temporal pattern between high germling abundance on snails followed by mat development was found in the other 3 study areas (Ria Formosa, Portugal; Mondego Estuary, Portugal; Cole Harbour, Canada). In Lowes Cove, USA, germlings and juveniles of *Enteromorpha* spp. first grew at the site with high *Hydrobia* abundance and were subsequently drifted to another site where they developed into full mats. We conclude that initiation of green algal mats by germination on *Hydrobia* spp. may be a general phenomenon, but that other modes of development also occur frequently. Pelagic drift of overwintering thalli to new sites, followed by prolific growth, might be of similar or greater importance.

KEY WORDS: Algal blooms · Eutrophication · Epibionts · Tidal flat · *Hydrobia* · *Enteromorpha* · Germination

INTRODUCTION

Over the past 25 yr, excessive growth of ephemeral green macroalgae, i.e. *Cladophora* spp., *Enteromorpha* spp. and *Ulva* spp. has become an increasingly com-

mon phenomenon which represents a problem, particularly in sheltered bays (Soulsby et al. 1985, Vadas & Beal 1987, Fletcher et al. 1990, van den Hartog 1994, Reise & Siebert 1994, Pihl et al. 1996, Thiel & Watling 1996). Eutrophication in estuaries and coastal waters is well documented and may explain the extensive growth of opportunistic macroalgal species which are
able to take advantage of such conditions (Soulsby et al. 1982, Soulsby et al. 1985, Sfriso et al. 1992, Fletcher 1996, Raffaelli et al. 1998). Yet, while eutrophication appears to be an important precondition for the occurrence of green algal mats (Lowthion et al. 1985, Hardy et al. 1993), the particular processes determining the successful development of green macroalgae on smaller temporal and spatial scales remain to be clearly identified. Potentially, green algal mats on intertidal mud and sandflats develop (1) from overwintering adult plants which persist partially embedded in the sediment and start growing in the following spring, or (2) from small reproductive stages released by adults (vegetative fragments, zoospores or gametes/zygotes). Small vegetative propagules, which are detached from the parent plants through various physical and biological forces (Santelices 1990), are able to continue growth in the water column where they eventually entangle and form free-floating aggregates (Schories & Reise 1993). These aggregates are often secondarily anchored (e.g. by nereid polychaetes, Woodin 1977; or lug worms, i.e. Arenicolidae, Reise 1983), and subsequently may develop into dense algal mats. Alternatively, growth of reproductive stages (zoospores or gametes/zygotes) may also lead to a development of large algal mats.

Stable substrata that remain at the illuminated sediment surface are essential for small propagules to germinate. Thus, although mud particles and sand grains are frequently colonised by propagules settling from the water column (Schories 1995a, Schories et al. 1997a), they represent unsuitable substrata because sediment layers are often re-worked and surface particles are re-located to deeper (i.e. darker) layers. Macroinvertebrates, in contrast, may provide stable substrata to support the growth of epibiotic macroalgae in an otherwise highly dynamic soft sediment environment (Schories et al. 1997b, Albrecht 1998 and references therein). Mud snails Hydrobia ulvae, which only grow to a few mm in size, can serve as biogenic substrata for Enteromorpha spp. germlings followed by the development of green algal mats. (4) Are the observed processes generic, or does the significance of hydrobiids as substrata for green algal mat development vary among study areas along North Atlantic coasts?

**MATERIALS AND METHODS**

**Study areas.** The 6 study areas are located between 37° and 59°N on the European and North American Atlantic coasts. All investigation sites are situated within sheltered bays with moderate tidal currents and low or no wave exposure. The size of the respective bay system varies from small (<1 km²) in Trälebskile, Sweden, and Lowes Cove, USA, to moderately large (1 to 10 km²) in Königshafen Bay, Germany, Mondego Estuary, Portugal and Cole Harbour, Canada, to extensive systems (>10 km²) in Ria Formosa, Portugal. Average and extreme water temperatures, salinities, sediment characteristics and the main macrobenthic organisms differ considerably between study areas (Table 1). Except for the most southerly investigation areas in Portugal, all other tidal flats studied underwent ice cover for several months in the winter of 1995/96. Within 2 of the study areas—Mondego Estuary, Portugal, and Lowes Cove, USA—sampling took place at 3 sites. In Mondego Estuary, the 3 sites were characterised as (1) sandy mud flat, (2) mud flat and (3) a seagrass meadow of Zostera noltii. In Lowes Cove, USA, the 3 sites were selected at different tidal elevations (low, mid and high intertidal zone).

**Hydrobia spp. sampling.** From November 1995 to December 1996, hydrobiid snails (for species see Table 1) were sampled monthly at specific sites within each study area. Sediment samples (n = 4 to 6) were collected randomly from the sites known to support green algal mats. Sample areas were adapted site-specifically to provide minimum abundances of 50 to 100 hydrobiids per sample, but remained constant throughout the study period for each site. Exceptions apply to Trälebskile, Sweden, where sample area had to be adjusted repeatedly to suddenly increasing Hydrobia ulvae densities and to Königshafen Bay, Germany, where sample area was reduced in June 1996 to match very high H. ulvae abundance (see Table 1). Thus, sample area ranged from 50 cm² in Ria Formosa, Portugal to 3420 cm² in Trälebskile, Sweden, and was 100 to 200 cm² in most cases (Table 1). Sediment samples were taken to at least 1 cm depth in order to collect all living snails. Samples were sieved (1 mm mesh size) and preserved in 4% formalin or 70% ethanol. Although some contributors sorted living snails prior to sample preservation, generally the proportion of living snails was identified in retrospect.
### Table 1. Characteristics of sampling areas and details of sampling execution among 6 investigation areas on both sides of the North Atlantic Ocean

<table>
<thead>
<tr>
<th>Trålebergskile</th>
<th>Königshafen Bay</th>
<th>Mondego estuary</th>
<th>Ria Formosa</th>
<th>Cole Harbour</th>
<th>Lowes Cove</th>
</tr>
</thead>
<tbody>
<tr>
<td>58.16°N, 11.26°E</td>
<td>51.05°N, 7.45°E</td>
<td>40.12°N, 8.25°E</td>
<td>37.01°N, 7.56°E</td>
<td>44.39°N, 63.25°W</td>
<td>44.15°N, 68.52°W</td>
</tr>
<tr>
<td><strong>Size of bay area (km²)</strong></td>
<td>Approx. 0.8 (inner part of the bay)</td>
<td>3.6</td>
<td>3.5 (south arm of Mondego River near Murraceira Island)</td>
<td>163</td>
<td>Approx. 15</td>
</tr>
<tr>
<td><strong>Sampling site</strong></td>
<td>Sandy-silt sediment organic content 1.2–1.6%</td>
<td>Mud and sand flat</td>
<td>a) Zostera noltii meadow: mud flat b) Mud flat c) Sandy mud flat</td>
<td>Mud flat</td>
<td>Mud flat</td>
</tr>
<tr>
<td><strong>Hydrobia species</strong></td>
<td>H. ulvae</td>
<td>H. ulvae</td>
<td>H. ulvae</td>
<td>H. ulvae</td>
<td>H. totteni</td>
</tr>
<tr>
<td><strong>Water temp. (°C)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Min.</td>
<td>0–5 winter</td>
<td>0</td>
<td>5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Max.</td>
<td>14–20 summer</td>
<td>18</td>
<td>30</td>
<td>26</td>
<td>22</td>
</tr>
<tr>
<td>Avg.</td>
<td>9</td>
<td>–</td>
<td>18.5</td>
<td>11</td>
<td>–</td>
</tr>
<tr>
<td><strong>Salinity</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Min.</td>
<td>0</td>
<td>26</td>
<td>5</td>
<td>15</td>
<td>11</td>
</tr>
<tr>
<td>Max.</td>
<td>30</td>
<td>32</td>
<td>28</td>
<td>36</td>
<td>21</td>
</tr>
<tr>
<td>Avg.</td>
<td>–</td>
<td>–</td>
<td>39</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><strong>Sample area (cm²)</strong></td>
<td>342–3420</td>
<td>100–400</td>
<td>70.88</td>
<td>50</td>
<td>100</td>
</tr>
<tr>
<td><strong>Number of replicates</strong></td>
<td>6 (with up to 10 subsamples of 342 cm²)</td>
<td>4</td>
<td>6</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td><strong>Preservation of sample</strong></td>
<td>4% formalin</td>
<td>4% formalin</td>
<td>4% formalin</td>
<td>4% formalin</td>
<td>5% formalin</td>
</tr>
<tr>
<td><strong>Sampling procedure of green algae</strong></td>
<td>Estimates of percentage cover, by eye</td>
<td>Random samples of a fixed 50 x 50 m area, calculated by biomass was multiplying dry wt with coverage of algal species within the entire area</td>
<td>Random, algae present in each sample of snails</td>
<td>Random</td>
<td>Collection of seaweeds from surface and dry wt determination (3d, 60°C)</td>
</tr>
</tbody>
</table>
through cracking of snail shells. Only living snails were considered, because they remain at the sediment surface while empty shells are commonly present at deeper sediment layers where they are of no value for Enteromorpha spp. germination. Preserved samples were dyed with Lugol's solution (2 g potassium iodide and thereafter 1 g iodine dissolved in 100 ml distilled water) which made Enteromorpha spp. germlings more conspicuous on hydrobid shells and thus facilitated identification. The percentage of mud snails per sample carrying Enteromorpha spp. germlings (>200 µm in length) was thus determined. However, no distinction was made with respect to the degree of germling colonization on individual snail shells.

**Biomass and surface cover of green algae.** Development of algal mats and abundance of adult greens on the sediment surface was monitored monthly in the respective sampling areas. Wherever possible, samples corresponding to Hydrobia spp. were taken on the surface (Table 1) and algal dry wt determined subsequently (24 h, 70°C). Otherwise, percent surface cover of adult green algae was estimated. Although green algal mats are often dominated by 1 genus or even 1 species, they do consist of species aggregations. For example, in Königshafen Bay at least 13 species of Enteromorpha spp. were identified, most of which occurred in algal mats (Schories et al. 1997b). Although these species differ with respect to their ecophysiological requirements (Koeman & van den Hoek 1982, 1984, Lotze et al. 1999), they were not distinguished in this study since, with respect to large scale mat development factors such as light, temperature and nutrient regimes are believed to overcome the differences between species (Fitzgerald 1978, Schories 1995b, Raffaelli et al. 1998). In this study, we focused on Enteromorpha because species from this genus usually dominate in algal mats worldwide.

**RESULTS**

The study sites differed considerably with respect to abundance of Hydrobia spp. present (Fig. 1). While in Trälebergskile, Sweden, abundances never exceeded 3000 ind. m⁻², maximum abundances in Königshafen Bay, Germany were 29 219 ± 19833 ind. m⁻², and as high as 35 520 ± 14 544 ind. m⁻² in Ria Formosa, Portugal. The strongest seasonality of snail abundance occurred in Königshafen Bay, Germany (high recruitment to population over the summer). In the Mondego Estuary, Portugal, Cole Harbour, Canada, and Lowes Cove, USA, hydrobid populations remained at intermediate levels (~5000 ind. m⁻²) throughout the year.

**Trälebergskile, Sweden (Figs. 1 & 2a)**

Abundance of Hydrobia ulvae was lower in this area than at most others and ranged from 214 ± 55 ind. m⁻² in May 1996 to 2690 ± 1080 ind. m⁻² in September 1996. Highest snail abundances coincided with nearly half of the hydrobid population carrying Enteromorpha spp. germlings (44 ± 17%). In May 1996, snails were negligible as germling substrata (<1%), and no adult green algae were encountered at the site. Nevertheless, green algal cover peaked at 70% in June after which algal mats gradually disappeared again before the end of August.

**Königshafen Bay, Germany (Figs. 1 & 2b)**

Hydrobia ulvae reached high abundance in this area; we recorded maximum densities of 29 219 ± 13630 ind. m⁻² in October 1996, and even minimum densities did not drop below 4475 ± 3130 ind. m⁻² (March 1996). Just before and immediately after the strong ice winter that year (November 1995 and March 1996, respectively), no Enteromorpha spp. germlings were found growing on Hydrobia spp. shells. In the remaining spring, summer and fall periods, hydrobids carrying green algal germlings did not exceed 10% of the total snail population, except in June 1996 (29 ± 13%). Enteromorpha cover was 20 to 30% from June to August 1996. The highest phytomass recorded in 1996 was 416 g dry wt m⁻² in July, and this occurred subsequent to the highest percentage of the Hydrobia spp. population carrying Enteromorpha spp. germlings within our study period.

**Mondego Estuary, Portugal (Figs. 1 & 2c)**

In this sampling area, snail abundances appeared site specific (3 sites sampled): From November 1995 to February 1996, no Hydrobia spp. occurred at the sandy mud flat, and abundances remained low throughout the year (maximum density 1200 ± 1400 ind. m⁻² in September 1996). Within the mud flat, hydrobid abundances fluctuated between 450 ± 960 ind. m⁻² (February 1996) and 5500 ± 2600 ind. m⁻² (November 1995). The percentage of hydrobids carrying green algal germlings on the mud flat ranged from 3 ± 3% (November/December 1995) to 40 ± 20% (September 1996). Similarly, in the seagrass bed, the maximum percentages of snails carrying Enteromorpha spp. germlings were recorded in August 1996 (50 ± 21%) and September 1996 (46 ± 12%). Biomass of Enteromorpha spp. was low on the sandy mud flat throughout the sampling period, and never exceeded 25 g dry wt.
m⁻² (August 1996). At both other sites, adult algal biomass was higher than 25 g dry wt m⁻² between March and May 1996 and peaked at 200 g dry wt m⁻² on the mud flat.

**Ria Formosa, Portugal (Figs. 1 & 2d)**

Abundance of *Hydrobia* spp. varied strongly with season from 440 ± 260 ind. m⁻² (June 1996) to 35 520 ± 14 544 ind. m⁻² in August 1996). This reflects a major recruitment event of hydrobiids in the area. The percentage of snails carrying green algal germlings was always lower than 10%, except in November 1995 and May 1996, when about 11% of snails harboured *Enteromorpha* spp. germlings on their shells. Surface cover of adult greens was low during the summer months (<5% in May and completely absent in June and July 1996). In contrast, surface cover of adult greens reached 25% in October and 40% in November of 1996.

**Cole Harbour, Nova Scotia, Canada (Figs. 1 & 2e)**

During the study period, abundances of *Hydrobia totteni* varied from 12 000 ± 9015 ind. m⁻² (November 1995) to 3200 ± 1759 ind. m⁻² (October 1996). In November 1995, high densities of green algae covered the sediment surface (333 ± 67 g dry wt m⁻²). These algae disappeared during the winter when large parts of the tidal flats in Cole Harbour were ice-covered. No adult green algae were found in the spring months but in early summer (June 1996), green algal mats suddenly reappeared on the flats (479 ± 385 g dry wt m⁻²). In late summer and fall, biomass of adult greens fluctuated between 148 ± 77 g dry wt m⁻² (July 1996) and 236 ± 140 g dry wt m⁻² (September 1996).

**Lowes Cove, Maine, USA (Figs. 1 & 2f)**

In Lowes Cove, 3 sites (high, mid and low intertidal zones) were sampled for snails *Hydrobia totteni* and green algae. Clearly, *H. totteni* was most abundant in the high intertidal zone (with a minimum density of 2400 ± 1000 ind. m⁻² (November 1996) and a maximum density of 10 621 ± 3300 ind. m⁻² in May 1996). In the mid intertidal zone, snails only occurred from January to May 1996 (110 ± 95 ind. m⁻² and 2700 ± 1000 ind. m⁻² density range). In the low intertidal zone, snail abundances never exceeded 710 ± 730 ind. m⁻² (January 1996). Corresponding to highest snail abundances, the percentage of hydrobiids carrying *Enteromorpha* spp. germlings was also highest in the upper intertidal zone. Between March 1996 and July 1996, this percentage increased steadily from 8 ± 7 to 65 ± 7%. In the mid intertidal zone, where snail abundance was significantly lower, 23 ± 29% of all snails carried germlings in May 1996. Contrary to our expectations, the biomass of adult *Enteromorpha* spp. was not highest in the high intertidal zone but rather in the mid
Fig. 2a–f. Percentage of hydrobiid snails carrying Enteromorpha spp. germlings (open bars) and simultaneous cover/phytomass of adult green algae on tidal flats (solid bars) in 6 sampling areas (a–f) throughout investigation period (November 1995 to December 1996). Error bars = means ± 1 SD. Hydrobiid abundance with colonizing Enteromorpha spp. indicated by top dark circles: (•) 100–1000 ind. m⁻², (●) 1000–2000 ind. m⁻², (○) >2000 ind. m⁻². No dot indicates that snail abundances were <100 ind. m⁻², (--) no samples were taken. At each study site 4 to 6 replicate samples were taken each month.
Table 2. Abundances of hydrobiid snails carrying Enteromorpha spp. germlings during the investigation period from November 1995 to December 1996; at each study site 4 to 6 replicate samples were taken each month; bold = highest abundance observed at each study site.

<table>
<thead>
<tr>
<th>Location</th>
<th>Nov</th>
<th>Dec</th>
<th>Jan</th>
<th>Feb</th>
<th>Mar</th>
<th>Apr</th>
<th>May</th>
<th>Jun</th>
<th>Jul</th>
<th>Aug</th>
<th>Sep</th>
<th>Oct</th>
<th>Nov</th>
<th>Dec</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trälebergskile, Sweden</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0</td>
<td></td>
<td>41</td>
<td>80</td>
<td>435</td>
<td>1072</td>
<td>251</td>
<td>151</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Königshafen Bay, Germany</td>
<td></td>
<td>75</td>
<td>306</td>
<td>4250</td>
<td>350</td>
<td>206</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>513</td>
<td>225</td>
<td>13</td>
<td></td>
</tr>
<tr>
<td>Mondego Estuary, Portugal</td>
<td>282</td>
<td>141</td>
<td>71</td>
<td>0</td>
<td>235</td>
<td>329</td>
<td>635</td>
<td>165</td>
<td>329</td>
<td>2281</td>
<td>1458</td>
<td>1905</td>
<td>470</td>
<td></td>
</tr>
<tr>
<td>Zostera noltii bed</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mud flat</td>
<td>71</td>
<td>94</td>
<td>118</td>
<td>24</td>
<td>282</td>
<td>400</td>
<td>188</td>
<td>118</td>
<td>188</td>
<td>988</td>
<td>1646</td>
<td>658</td>
<td>188</td>
<td></td>
</tr>
<tr>
<td>Sandy mud flat</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>47</td>
<td>0</td>
<td>24</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ria Formosa, Portugal</td>
<td>200</td>
<td>467</td>
<td>100</td>
<td>280</td>
<td>1040</td>
<td>240</td>
<td>1867</td>
<td>0</td>
<td>0</td>
<td>480</td>
<td>1000</td>
<td>280</td>
<td>40</td>
<td></td>
</tr>
<tr>
<td>Cole Harbour, Canada</td>
<td>217</td>
<td>100</td>
<td></td>
<td></td>
<td>50</td>
<td>100</td>
<td>50</td>
<td>400</td>
<td>360</td>
<td>100</td>
<td>180</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>High intertidal zone</td>
<td>1492</td>
<td>28</td>
<td>19</td>
<td>28</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mid intertidal zone</td>
<td>0</td>
<td>9</td>
<td>142</td>
<td>5</td>
<td>321</td>
<td>66</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Low intertidal zone</td>
<td>28</td>
<td>19</td>
<td>28</td>
<td></td>
<td></td>
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<td></td>
<td></td>
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</tr>
</tbody>
</table>

The maximum number of snails carrying Enteromorpha spp. germlings varied considerably among the study areas (Table 2). In some areas and at some sampling sites (Cole Harbour; Mondego Estuary — sandy mud flat; Lowes Cove — mid and low intertidal), there were never more than 1000 ind. m\(^{-2}\) carrying germlings. Maximum numbers of snails with germlings were intermediate (1000 to 2000 ind. m\(^{-2}\)) in Trälebergskile, Mondego Estuary mud flat and Ria Formosa. At Mondego Estuary (Zostera meadow) the maximum number of snails with germlings found during the study was 2281 ind. m\(^{-2}\). Only in Königshafen Bay and in Lowes Cove (high intertidal zone), did maximum numbers of germling-carrying snails exceed 4000 ind. m\(^{-2}\). At both these sites, the maximum biomass of Enteromorpha spp. was reported following maximum abundance of Hydrobia spp. with Enteromorpha spp. germlings.

**DISCUSSION**

In most temperate regions, green algal mats are highly seasonal in that they disintegrate or are removed in late autumn and are absent during winter months. Thus, mat development is re-initiated in spring and early summer of the following year. Little attention has been directed towards development of mats from germination of small reproductive stages. Only recently, it was shown that surface-dwelling mobile macrofauna such as hydrobiid snails serve as germination substrata for large numbers of algal propagules (Schories & Reise 1993, Schories 1995b). Enteromorpha spp. spores and gametes/zygotes settle on Hydrobia ulvae and develop either directly into juveniles or overwinter on the snail substratum prior to germination the following spring (Schories 1995b). In the latter case, newly germinated Enteromorpha spp. propagules grow into juveniles which — once beyond a certain length — are dislodged from the sediment surface where they entangle into aggregates and ultimately form mats. Since hydrobiid snails, however small and inconspicuous, often contribute significantly to tidal flat macrofauna in the northern hemisphere (Smidt 1951, Hunter & Hunter 1962, Reise 1987), we investigated the hypothesis that they may play a major role as substrata for the development of green algal mats from germinating propagules.

**Hydrobiid snails on tidal flats**

Overall abundances of Hydrobia spp. varied considerably among study areas. Within areas, strong seasonal variation in mud snail density became apparent in some cases (Fig. 1). Populations of hydrobiids are subject to recruitment and mortality events, as well as to mobility through pelagic drift (Armonies 1994). Maximum annual abundances were at least 2600 ind. m\(^{-2}\) and exceeded 20000 ind. m\(^{-2}\) in 3 study areas (Cole Harbour, Canada; Königshafen Bay, Germany; Ria Formosa, Portugal). Our results underestimate the total population densities, because with a mesh size of 1 mm\(^{2}\) for sample processing, many juvenile hydrobiids were lost. Mud snail abundances exceeding 100 000 ind. m\(^{-2}\) appear to be common on tidal flats across North Atlantic shores (Smidt 1951, Hunter & Hunter 1962, Reise 1987, Lillebø et al. in press) and densities may be as high as 1 000 000 ind. m\(^{-2}\) (Schories 1995b). Thus, mud snails often comprise a significant...
component of the macroinvertebrate fauna of tidal flats. However, in some of our investigation areas (Lowes Cove, low intertidal zone, USA; Mondego Estuary, eutrophicated sandflat, Portugal, and Trålebergskile, Sweden) snail populations appeared comparatively minor and insignificant (Fig. 1). Hydrobiid snails graze on microphytobenthos (e.g. epipsammic diatoms) within the top layers of the sediment. Hence, hydrobiids are frequently exposed to colonizing algal spores from the water column. Furthermore, hydrobiids serve as ideal substrata for algal propagules, because they guarantee sufficient light levels for germination through their surface affinities. In addition, conspecific grazing of shell surfaces—as described for littorinid gastropods (Wahl & Soennichsen 1992) — may be suppressed to protect externally deposited egg cases of mating partners within a population. The potential suitability of hydrobiids as substrata for Enteromorpha spp. germlings has been demonstrated previously for Königshafen Bay, Germany (Schories & Reise 1993, Schories & Soennichsen 1992) and was reconfirmed for most investigation areas in this study (see next section).

Enteromorpha spp. germlings on Hydrobia spp.

In all investigation areas, hydrobiid snails carried gromlings of Enteromorpha spp. on their shells (Fig. 2a–f). In 2 of the 6 study areas, Enteromorpha spp. germlings were most abundant on hydrobiids during spring and summer (Königshafen Bay, Germany and Lowes Cove, USA, high intertidal zone). A strong seasonality of green algal germling abundance on temperate tidal flats was documented by Kim et al. (1991), Flavier & Zingmark (1993) and Schories & Reise (1993). We propose that at least in some of the investigation areas, green algal propagules overwintered in the absence of adult thalli. Physiologically, the reproductive stages of Enteromorpha linza can tolerate strong temperature variations, including freezing, and are able to survive 10 mo of complete darkness (Kylin 1947). Similarly, E. intestinalis germinate after 18 mo in darkness (Arasaki 1953), and germinated juveniles of Enteromorpha spp. survive 8 mo of darkness at 5°C (Schories 1995a). In Mondego Estuary, Portugal and in Trålebergskile, Sweden, Enteromorpha spp. gromlings on snails became gradually more abundant towards autumn. Because dense mats of mature green algae were already present on most tidal flats at this time, these gromlings are likely to have been released from parent material of the same year. In Mondego Estuary, Portugal, 2 gromling peaks (in spring and autumn) indicate that unfavourable environmental conditions may have suppressed gromling abundance during the summer. High temperatures lead to stress and bleaching or sporulation of Enteromorpha spp. gromlings (Schories 1995b) and may have caused the observed summer decline of gromlings in 1 of the warmer areas of this study. Generally, juvenile stages of Enteromorpha spp. are more sensitive to temperature stress than adults (Woodhead & Moss 1975, Soe-Htun et al. 1986). The proportion of hydrobiids carrying Enteromorpha gromlings was highly variable among investigation areas and did not obviously correlate either with Hydrobia spp. abundances or with the surface cover of adult algal mats (Figs. 1 & 2a–f). When algal mats and hydrobiids are abundant simultaneously during spring/summer months within the same area, propagules that are continually released from adults (a process which is only inhibited under temperature extremes, particularly in the winter) are likely to use hydrobiids as attachment and germination substrata (Schories 1995b). Thus, a high proportion of the Hydrobia spp. population would be expected to carry Enteromorpha spp. gromlings under such conditions (Schories 1995b). This situation seems to have applied in Trålebergskile and Lowes Cove (high intertidal zone). In contrast, a high exchange rate to and from the population of mud snails within a sampling area may be the reason for low proportional growth of gromlings on snail shells in the presence of an adult algal mat. Hydrobiid populations are highly dynamic and subject to pelagic drift (Armonies 1994), a process which could have operated in Königshafen Bay, Ria Formosa, and Cole Harbour (Fig. 2b,d,e), where the proportion of hydrobiids carrying Enteromorpha spp. gromlings was low, although (1) overall snail abundances were high and (2) algal mats were present simultaneously at the respective sites.

Development of green algal mats

Mat development of adult green algae took place in all sampling areas during the investigation period (Fig. 2a–f). A temporal sequence of large Hydrobia spp. abundances carrying Enteromorpha spp. gromlings followed by dense aggregations of adult green algae at the same site indicates that mat development was initiated by gromlings (Königshafen Bay, Germany, and Lowes Cove, mid/high intertidal zone, USA). In Mondego Estuary, Ria Formosa in Portugal, and in Trålebergskile, Sweden, highest gromling percentages were found when mats of adult greens were already present. In Cole Harbour, Canada, the percentage of hydrobiids serving as substratum for Enteromorpha spp. gromlings remained low throughout the year, despite medium overall abundances of snails. Our interpretation is that at these 4 study areas,
overwintering of adult fragments as described for the genus *Cladophora* (Dodds & Gunder 1992) and secondary drift import of adults (Kramer et al. 1990, Geertz-Hansen et al. 1993, Thybo-Cristensen et al. 1993, A.S.C. pers. obs., this study) were more important for the establishment of large algal mats than germination of propagules. For Ria Formosa, Portugal, we suggest that large algal aggregations re-developed from algal thalli having remained elsewhere within the larger investigation area. In this case, periods without coverage of adult greens were very short and revealed no distinct temporal correlation with germling growth on hydrobiids. At 2 sites in Mondego Estuary, Portugal (*Zostera noltii* meadow and less eutrophicated sand flat), the percentage of hydrobiids carrying Enteromorpha spp. germlings appeared to increase after highest abundances of adult greens were found in the spring. This sequence suggests that adult mats of green algae are initiated by a mechanism other than germination on Hydrobia spp. The importance of drift of adult algal thalli to secondary colonization sites became apparent through a comparison of algal development in the mid and high intertidal zones of Lowes Cove, USA: In late July 1996—during the major growing season of adult greens—dense algal mats suddenly appeared in the nearby mid intertidal zone where few algae (and no hydrobiids) had been found on previous sampling occasions. Hence, germination of propagules seemed to have initiated algal growth in the upper eulittoral zone at first, but subsequently secondary drift of adults to other sites caused the development of algal mats.

It was conspicuous that a temporal sequence of high numbers of snails with germlings followed by relatively high biomass of Enteromorpha spp. on the tidal flats was found in only 2 sampling areas (Königsfahnen Bay, Germany and Lowes Cove mid/high intertidal zone, USA). The total number of Hydrobia spp. carrying Enteromorpha spp. germlings was also considerably higher at these 2 sites than at all other sampling sites. This implies that the total number of successfully developing algal recruits affects the population dynamics of Enteromorpha spp. on tidal flats.

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