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Flagging greens: hydrobiid snails as substrata for the development of green algal mats (*Enteromorpha* spp.) on tidal flats of North Atlantic coasts

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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. Hydrobiid (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 hydrobiid snails from November 1995 to December 1996 on 6 tidal flats of North Atlantic coasts (Trälebergskile, 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 Trälebergskile, 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 common 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 1998). Eutrophication in estuaries and coastal waters is well documented and may explain the extensive growth of opportunistic macroalgal species which are

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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 reworked 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 (Schories & Reise 1993, Schories 1995b). Hydrobiid snails are common on tidal flats of North Atlantic coasts. In this study, we investigated their potential role as substrata for the development of green algal mats on 6 different tidal flats of Atlantic coasts of temperate North America and Europe. Emphasis was placed on the following questions: (1) How does the abundance of *Hydrobia* spp. vary over 1 year in any given study area, and can mud snails provide adequate substrata for germination of propagules? (2) Do *Enteromorpha* spp. spores germinate in sufficient quantities on hydrobiid snails in order to provide the basis for subsequent development of green algal mats? (3) Is there a temporal sequence of high numbers of hydrobiids colonized by *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 km^2) in Trälebergskile, Sweden, and Lowes Cove, USA, to moderately large (1 to 10 km^2) in Königshafen Bay, Germany, Mondego Estuary, Portugal and Cole Harbour, Canada, to extensive systems (>10 km^2) 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 Trälebergskile, 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 cm^2 in Ria Formosa, Portugal to 3420 cm^2 in Trälebergskile, Sweden, and was 100 to 200 cm^2 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

	Trälebergskile 58.16° N, 11.26° E	Könighafen Bay 51.05° N, 7.45° E	Mondego estuary 40.12° N, 8.25° E	Ria Formosa 37.01° N, 7.56° E	Cole Harbour 44.39° N, 63.25° W	Lowes Cove 44.15° N, 68.52° W
Size of bay area (km^2)	Approx. 0.8 (inner part of the bay)	3.6	3.5 (south arm of Mondego River near Murraceira Island)	163	Approx. 15	Approx. 1
Sampling site	Sandy-silt sediment organic content 1.2–1.6 %	Mud and sand flat	a) *Zostera noltii* meadow: mud flat b) Mud flat c) Sandy mud flat	Muddy sand flat	Mud flat	Mud flat (clayey silt)
***Hydrobia* species**	*H. ulvae*	*H. ulvae*	*H. ulvae*	*H. ulvae* *H. neglecta* *H. ventrosa*	*H. totteni*	*H. totteni*
Water temp. (°C)						
Min.	0–5 winter	0	5	12	0	0
Max.	14–20 summer	18	30	26	22	18
Avg.		9	–	18.5	11	–
Salinity						
Min.	0	26	5	15	11	29
Max.	30	32	28	36	21	33
Avg.	–	30	–	36	–	–
Benthic communities dominated by following endo-/ epibenthic organisms (in alphabetical order)	*Carcinus maenas* *Corophium voltator*, *Crangon crangon*, *Hediste diversicolor*, *Heteromastus filiformis*, *Mytilus edulis*, *Palemon* spp., *Phyllodocidae*; *Pomatoscistus* spp.,	*Arenicola marina* *Cerastoderma edule*, *Hydrobia ulvae*,	*Carcinus maenas*, *Cerastoderma edule*, *Echinogammarus marinus*, *Hediste diversicolor*, *Scrobicularia plana*	*Carcinus maenas*, *Cerithium vulgatum*, *Hamninea navicula*, *Hediste diversicolor*, *Nassarius pfeifferi*, *Uca tangeri*	*Clymenella* spp., *Gemma gemma*, *Hediste* spp., *Hydrobia totteni*, *Lunatia heros*,	Capitellid & spionid polychaetes, *Hediste succinea*, *Macoma balthica*, *Mya arenaria*, oligochaetes
Sample area (cm^2)	342–3420	100–400	70.88	50	100	176
Number of replicates	6 (with up to 10 subsamples of 342 cm^2)	4	6	5	5	6
Preservation of sample	4 % formalin	4 % formalin	4 % formalin	4 % formalin	5 % formalin	4 % formalin, later transferred to 70 % -EtOH, living snails collected from trays before preservation
Sampling procedure of green algae	Estimates of percentage cover, by eye	Random samples of a fixed 50 × 50 m area, calculated by biomass was multiplying dry wt with coverage of algal species within the entire area	Random, algae present in each sample of snails	Random	Collection of seaweeds from surface and dry wt determination- (3d, 60°C)	Dry wt of algae from same 6 replicates from which snails were collected

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 hydrobiid 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 override 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 29219 ± 19833 ind. m^{-2}, and as high as 35520 ± 14544 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, hydrobiid 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 hydrobiid 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 29219 ± 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, hydrobiids 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, hydrobiid abundances fluctuated between 450 ± 960 ind. m^{-2} (February 1996) and 5500 ± 2600 ind. m^{-2} (November 1995). The percentage of hydrobiids 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.

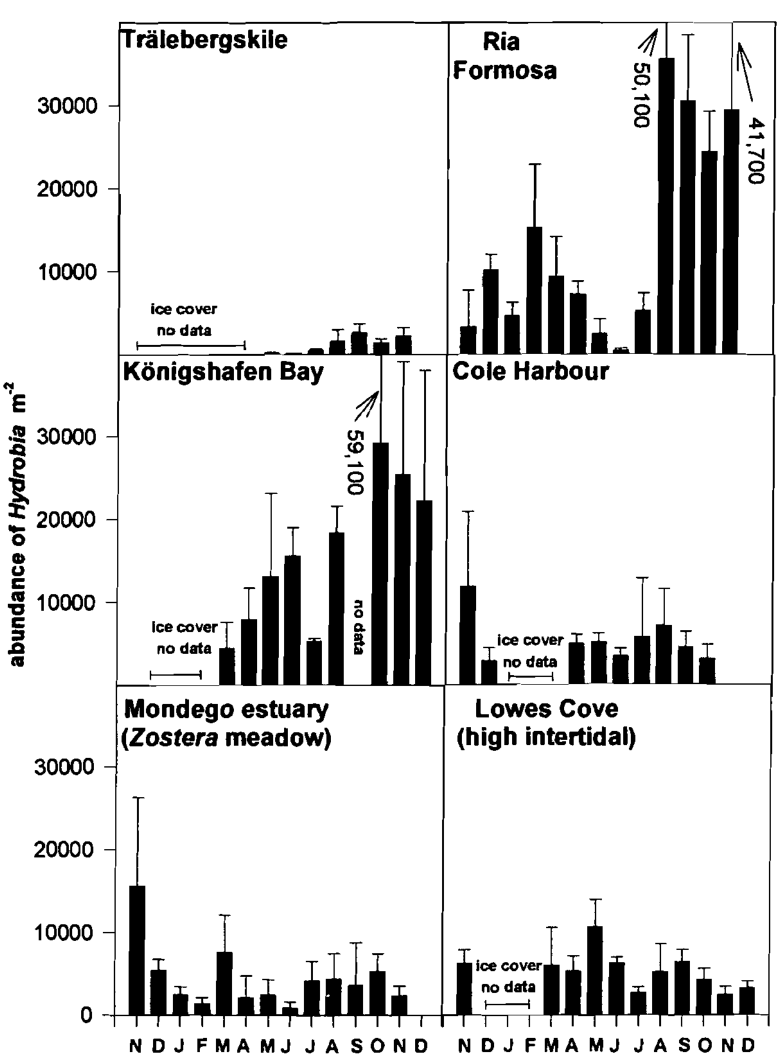

Fig. 1. Abundance of hydrobiid snails (mean + 1 SD) during the investigation period from November 1995 to December 1996. For Mondego Estuary, Portugal, and Lowes Cove, USA, only 1 of the 3 study sites with highest snail densities is presented; at each study site 4 to 6 replicate samples were taken each month

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

During the study period, abundances of *Hydrobia totteni* varied from 12000 ± 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 10621 ± 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

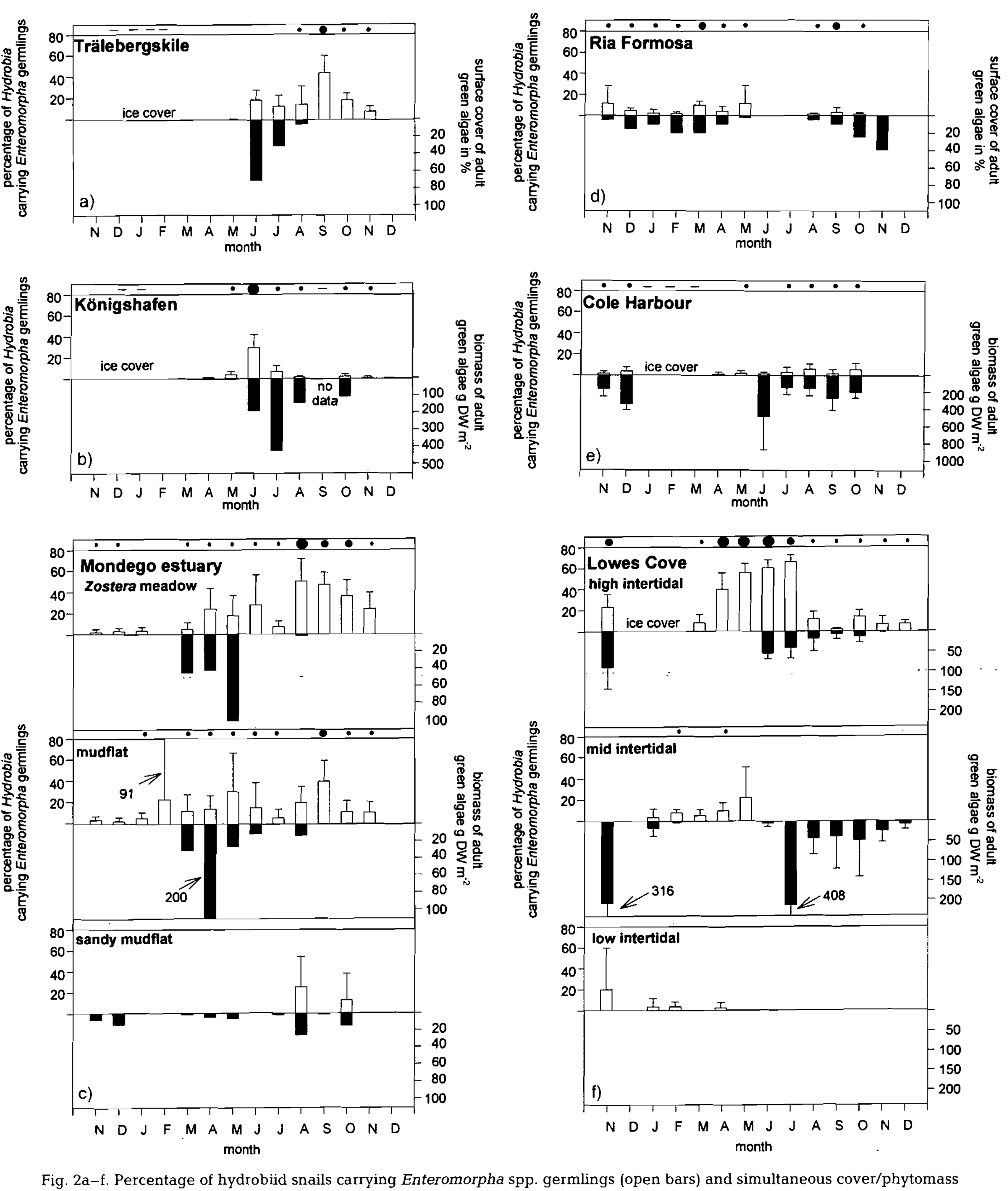

Fig. 2a–f. Percentage of hydrobiid snails carrying *Enteromorpha* spp. germlings (open bars) and simultaneous cover/phytomass of adult green algae on tidal flats (solid bars) in 6 sampling areas (a–f) throughout investigation period (November 1995 to December 1996). Error bars = means + 1 SD. Hydrobiid 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

	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Trälebergskile, Sweden	–	–	–	–	–	–	0	41	80	435	**1072**	251	151	–
Königshafen Bay, Germany	–	–	–	–	0	75	306	**4250**	350	206	–	513	225	13
Mondego Estuary, Portugal														
Zostera noltii bed	282	141	71	0	235	329	635	165	329	**2281**	1458	1905	470	–
Mud flat	71	94	118	24	282	400	188	118	188	988	**1646**	658	188	–
Sandy mud flat	0	0	0	0	0	0	0	0	0	**47**	0	24	0	–
Ria Formosa, Portugal	200	467	100	280	1040	240	**1867**	0	0	480	1000	280	40	–
Cole Harbour, Canada	217	100	–	–		50	100	50	**400**	360	100	180	–	–
Lowes Cove, USA														
High intertidal zone	1492	–	–	–	444	2059	**6062**	3787	1775	482	113	510	198	227
Mid intertidal zone	0	–	9	142	5	**321**	66	0	0	0	0	0	0	0
Low intertidal zone	28	–	19	**28**	0	9	0	0	0	0	0	0	0	0

intertidal area with 213 ± 199 g dry wt m^{-2} (July 1996).

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 20 000 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 Trälebergskile, 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 1995b) and was re-confirmed for most investigation areas in this study (see next section).

Enteromorpha spp. germlings on *Hydrobia* spp.

In all investigation areas, hydrobiid snails carried germlings 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 Trälebergskile, Sweden, *Enteromorpha* spp. germlings 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 germlings are likely to have been released from parent material of the same year. In Mondego Estuary, Portugal, 2 germling peaks (in spring and autumn) indicate that unfavourable environmental conditions may have suppressed germling abundance during the summer. High temperatures lead to stress and bleaching or sporulation of *Enteromorpha* spp. germlings (Schories 1995b) and may have caused the observed summer decline of germlings 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* germlings 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. germlings under such conditions (Schories 1995b). This situation seems to have applied in Trälebergskile 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 germlings 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. germlings 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. germlings followed by dense aggregations of adult green algae at the same site indicates that mat development was initiated by germlings (Königshafen Bay, Germany, and Lowes Cove, mid/high intertidal zone, USA). In Mondego Estuary, Ria Formosa in Portugal, and in Trälebergskile, Sweden, highest germling 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. germlings 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 & Gudder 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 (Königshafen 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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