

A. Schanz · P. Polte · H. Asmus

Cascading effects of hydrodynamics on an epiphyte–grazer system in intertidal seagrass beds of the Wadden Sea

Received: 8 October 2001 / Accepted: 18 February 2002 / Published online: 8 May 2002
© Springer-Verlag 2002

Abstract This study examines experimentally how water movement may alter epiphyte–grazer systems in intertidal seagrass beds. Field observations in the Sylt–Rømø Bay (German Wadden Sea, SE North Sea) showed that the biomass of seagrass epiphytes was highest on seagrasses exposed to water movement, whereas at sheltered sites the epiphyte cover was negligible. In contrast, the seagrass shoot density and aboveground biomass was comparably sparse and the abundance of *Hydrobia ulvae* was extremely low at exposed areas, but showed maximum values at sheltered seagrass beds. Cross transplantation experiments and enclosure experiments between sheltered and exposed seagrass beds showed that adhering snails were washed off from seagrasses soon after transplantation into an exposed seagrass bed, and epiphytes started to grow. After 4 weeks the epiphyte biomass was similar to the that of the adjacent exposed seagrass bed. When heavily epiphytised seagrasses were transplanted from exposed into sheltered areas, the epiphytes were completely grazed down by immigrating snails within a week. Experiments carried out by means of an *in situ* “three-current-flume”, modifying the entire current velocity, showed that snail density was significantly negatively correlated with increasing current velocity, whereas epiphyte biomass showed a significant positive correlation with current speed. These results suggest a cascading impact of hydrodynamics on an epiphyte–grazer system in intertidal seagrass beds, by directly affecting the density of grazers and indirectly leading to enhanced epiphyte growth, thereby inhibiting seagrass development. Additionally it shows that cascading effects within the trophic web cannot only be triggered by biotic interdependencies, but can also be caused by physical factors.

Introduction

Epiphyte–grazer systems are characteristic elements of epibenthic communities, such as seaweed stocks and seagrass beds (Gambi et al. 1992; Bologna and Heck 1999). They play an important functional role, because a large part of the energy flow passing the community is dissipated through these systems and is thus transferred to higher trophic levels (Asmus and Asmus 1985, 2000; Klumpp et al. 1992). In some macrophytobenthic communities, especially in seagrass beds, epiphyte grazing tends to surpass or even outweigh the process of direct grazing of the higher plants (Klumpp et al. 1992), which often have developed mechanisms to prevent being grazed upon (Ravn et al. 1994; Vergeer and Develi 1997). Since epiphytes compete with seagrasses for light and nutrients (Sand-Jensen 1977; Shepherd et al. 1989), their regulation by grazers will initiate a cascading effect on the host plants, promoting the growth conditions of seagrasses (e.g. van Montfrans et al. 1982, 1984; Orth and van Montfrans 1984; Howard and Short 1986; Orth 1992; Neckles et al. 1993; Jernakoff and Nielsen 1997; Valentine et al. 1997; Garcia et al. 1999), which is particularly of importance in eutrophicated areas (Williams and Ruckelshaus 1993; Philippart 1995). Despite extensive studies on factors acting directly or indirectly on grazing of epiphytes (Jernakoff et al. 1996), the effect of water movement on these complex animal–plant interactions has rarely been considered until now. Generally the roles of predation and habitat complexity as primary factors influencing abundance and distribution patterns of grazers have been regarded (Orth 1992), whereas the roles of physical factors have rarely been examined. However, previous studies have considered the direct impact of hydrodynamics on seagrasses (Gerard and Mann 1979; Fonseca and Kenworthy 1987; Koch 1994, 1999; Fonseca and Bell 1998; Short and Neckles 1999; Robbins and Bell 2000; van Katwijk and Hermus 2000) and the influences of mechanical factors on seagrass leaf fouling (Patriquin 1973; Fonseca et al. 1982; Jacobs et al. 1983).

A. Schanz (✉) · P. Polte · H. Asmus
Alfred Wegener Institute for Polar and Marine Research,
Wadden Sea Station Sylt, Hafenstrasse 43, 25992 List, Germany
E-mail: aschanz@awi-bremerhaven.de
Tel.: +49-4651-956102
Fax: +49-4651-956200

In the Wadden Sea, the mud snail *Hydrobia ulvae* is the dominant grazer on sheltered tidal flats and intertidal seagrass beds (Asmus and Asmus 1985, 1990; Dekker 1989; Asmus 1994; Reise 1994; Philippart 1995; Schanz et al. 2000). Mud snails are able to drift (Newell 1962; Armonies and Hartke 1995), and therefore a sensitivity of these organisms to hydrodynamics is expected.

Based on field observations comparing a sheltered seagrass bed with low epiphyte coverage and a hydrodynamically exposed *Zostera* bed heavily overgrown with epiphytes, it was hypothesised that the occurrence of epiphytes on seagrass leaves depends on the density of grazers, which in turn is controlled by the hydrodynamic regime.

Field measurements were conducted to support these observations. To demonstrate experimentally how water movement may alter grazing processes in intertidal seagrass beds and may therefore play a fundamental role in seagrass bed development, cross-transplantation experiments with and without enclosures between sheltered and exposed seagrass beds were carried out. To quantify the impact of currents on the abundance of *H. ulvae* and their grazing efficiency, an in situ flume, modifying the entire current velocity, was used.

Sea (North Sea) (Fig. 1). The investigated sites are part of a shallow, nearly closed embayment between the mainland and the two islands Sylt and Rømø (Sylt-Rømø Bight), which are connected to the mainland by causeways. Predominant water circulation patterns are generated by a combination of both wind conditions and tides entering and leaving the bight through one comparatively narrow tidal inlet. Tides are semi-diurnal, with an average amplitude of 1.8 m. Salinity ranges from about 28 to 32 psu. Mean annual water temperature is 9°C, with a seasonal variation from 0°C to 19°C (see also Reise 1985; Bayerl and Higelke 1994; Reise and Lackschewitz 1998; Asmus and Asmus 2000; Asmus et al. 2000).

Seagrass beds of the Sylt-Rømø Bight occupy a relatively high share of the tidal flats (12% or 15.6 km²) (Asmus and Asmus 2000). Except for one small *Zostera marina* stand, they were pure *Zostera noltii* Hornem. stocks on sand and muddy sand during the investigation period. *Z. noltii* beds emerge for 4–6 h per tidal cycle and grow under different hydrodynamic exposure conditions. Two *Z. noltii* beds (Fig. 1) were studied in July, August and September 1999 (the main vegetation period of the seagrass): an exposed *Z. noltii* bed (Fig. 1), where strong initial tidal currents from 0.20 up to 0.33 m s⁻¹ were recorded during calm weather (during 1 h at the beginning of flood) entering the bay in an east–west direction, and which were probably due to the proximity of a deep tidal channel (Table 1); and a second, more extensive, sheltered *Z. noltii* bed (Fig. 1), which was protected by the island from waves, due to prevailing westerly winds. Here tidal currents from 0.06 m s⁻¹ up to maximum values of 0.20 m s⁻¹ were recorded (measured as mentioned above); these currents were about half as strong as those measured at the exposed site (Table 1).

Materials and methods

Study sites

The studies were performed at two intertidal seagrass beds near the island of Sylt, which is situated in the German part of the Wadden

Seagrass density and biomass

To compare both seagrass sites, shoot density and aboveground biomass of *Z. noltii* were estimated in summer 1999. Shoot density was determined monthly in six replicate test areas using a frame (25×25 cm). Aboveground biomass of *Z. noltii* was calculated by taking box cores of 100 cm² ($n=6$). Seagrass plants were clipped at

Fig. 1. Location of the study area in the Wadden Sea near the island of Sylt, North Sea, Germany. Distribution of intertidal seagrass beds (shading) in the Sylt-Rømø Bay. Arrows indicate the investigated hydrodynamically exposed (*E*) and sheltered (*S*) seagrass sites (*D*: Germany; *DK*: Denmark; *NL*: The Netherlands)

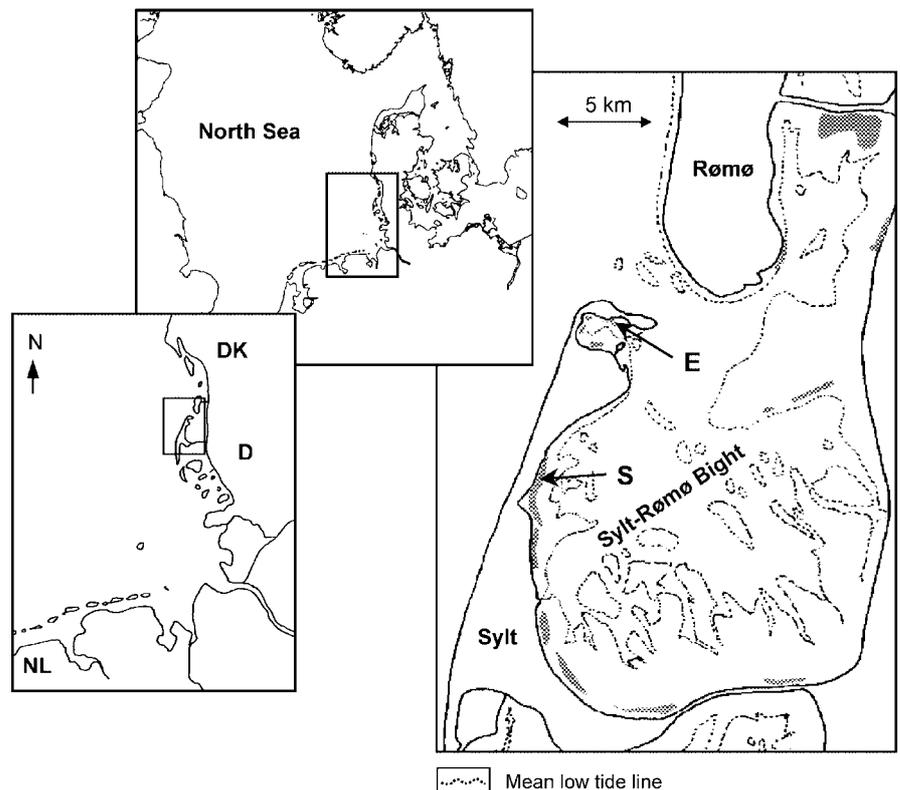


Table 1. Tidal current velocities (m s^{-1}) of the hydrodynamically different seagrass beds and within the differently treated lanes of the *in situ* “three-current-flume” (mean \pm SE, pooled data from April to September 1999)

Seagrass sites		Flume treatments		
Exposed	Sheltered	Increased	Mean	Reduced
0.26 (0.01)	0.10 (0.01)	0.13 (0.02)	0.08 (0)	0.04 (0.01)

the sediment surface and washed to remove sediment, adherent fauna and algae. If necessary, larger amounts of epiphytes were carefully scraped off with a scalpel. To estimate ash-free dry weight (AFDW), seagrass plants were separately dried at 80°C and ashed at about 500°C for 24 h.

Epiphyte biomass and algal composition

To measure the biomass of epiphytes, seagrasses were collected by carefully digging out the plants from below the substratum level. Of six random samples, 12 leaves were investigated once in September at each seagrass site. Epiphytes were carefully scraped off the leaves with a sharp scalpel onto a flexible plastic sheet rinsed with filtered seawater. This suspension of epiphytes was collected and filtrated by vacuum onto precombusted and preweighted Whatman GF/C glass microfibre filters. Epiphyte dry weight (DW) was determined after drying at 60°C (2–5 days), and AFDW was determined after combustion at 500°C (12 h). All measurements were related to macrophyte leaf area (cm^2). The composition of epiphytic algae was additionally estimated on 12 seagrass leaves. Epiphytic algae were identified to genus or species level, when possible, using an epifluorescence microscope.

Abundance of *Hydrobia ulvae*

To estimate the abundance of the dominant grazer *H. ulvae*, 12 replicate core samples (5.4 cm diameter and 5 cm depth) at each study site were taken monthly. Samples were passed through a 500 μm sieve, and specimens were collected and counted.

Transplantation experiments

To test whether the grazing impact of *H. ulvae* led to epiphytic removal and how this was influenced by currents, cross transplantation experiments were carried out in September 1999. Small sections of the seagrass bed, including epiphytes and associated snails, were taken from each site by carefully pushing a plastic tube (11.8 cm diameter, high 20 cm) into the sediment without disturbing the leaves of the plants (Fig. 2). Seagrass cores were transported and kept separately in their plastic tubes with a thin layer of seawater at a temperature of about 15°C . Six seagrass cores from one location were exchanged with six seagrass cores from the other site. In addition, six control areas of about 110 cm^2 were selected within the donor seagrass beds. Previous control transplantations revealed no transplantation effects on seagrass epiphytes or on mud snail abundance at the donor sites.

The abundance of *H. ulvae* was monitored after 2 days, when snails were observed migrating from or to the transplanted sections; thereafter, recordings took place at irregular intervals for 1 week (third, fourth and seventh day) until the number of *H. ulvae* remained constant. Six replicate core samples were taken from both the transplanted sections and the control areas on each sampling date. Concurrently, biomass of epiphytic growth on seagrass leaves was recorded, as changes in epiphyte cover were visible (following the method described above).



Fig. 2. Freshly transplanted seagrass section from the exposed into the sheltered bed, heavily covered by epiphytes

Enclosure experiments

To prevent flushing of grazers at the exposed seagrass bed, enclosure experiments were carried out at the end of August 1999. A total of 1,500 individuals of *H. ulvae*, corresponding to mean snail abundance at the sheltered site ($161,000\text{ ind. m}^{-2}$), were transferred into six closed cages, six open cages (both PVC frames, 11.8 cm in diameter, 1 mm mesh size) and uncaged areas at the exposed seagrass bed. The open cages had one lateral opening (7 cm width, 10 cm height), which was placed directly above the sediment (each cage opening pointed towards a different direction). After an experimental period of 1 week, grazer abundance and biomass of epiphytes on seagrass leaves were estimated (see above).

To compare the long-term differences of the cross transplantations and the enclosure experiments, abundance of grazers and epiphyte biomass were recorded again after 4 weeks.

Flume experiments

By using an *in situ* “three-current-flume”, the impact of current velocity on the presence of *H. ulvae* and the effect of mud snails on seagrass epiphyte removal was quantified experimentally (Fig. 3). The flume system (modified after Judge et al. 1992) was made of a heavy steel construction with flexible walls of strong textile awning. The whole flume construction was 7 m long, 12 m wide and 1 m high and consisted of nine lanes. It was placed into the sheltered *Z. noltii* bed parallel to the main flow direction (allowing a bi-directional intertidal current) at the beginning of April 1999. By modifying the channel openings, this system was able to either: (1) accelerate (broad opening of lane), (2) canalise, i.e. nearly unaltered (parallel walls with the same width along its total length) or (3) decelerate (central widening of lane) the tidal current in the mid-section of the flume relative to ambient current velocities outside the flume (Fig. 3). Each flow treatment consisted of three replicate lanes. Mean current velocity of each treatment was measured in the central section, approximately 10 cm above sediment surface, by using an induction current meter (Marsh McBirney) during calm weather. From April to October 1999 current speeds were monitored 12 times during the beginning of both flood and ebb tides, for half an hour every 2–3 min. Ambient current (control) was measured at marked seagrass sections outside the flume.

Abundances of *H. ulvae* within the differently treated lanes of the flume were monitored four times in September 1999, whilst the biomass of epiphytes on seagrass leaves was recorded once at the end of September 1999.

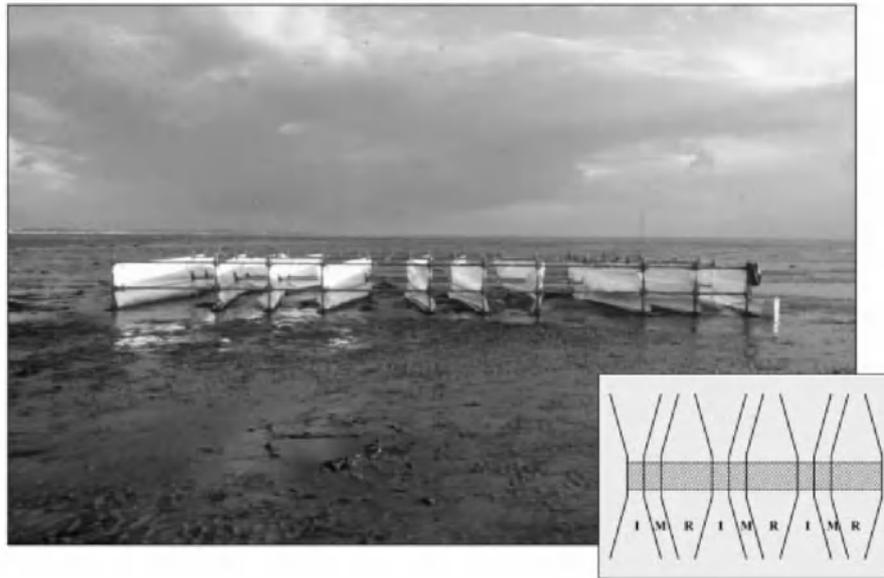


Fig. 3. Front view of the *in situ* “three-current-flume”, placed in a sheltered seagrass bed and aligned with the prevailing flow direction in a bi-directional intertidal current regime. The flume system (7 m length×12 m width×1 m high) was made of a heavy steel construction with flexible walls of textile awning and consisted of nine lanes. Schematic representation of the flume: by modifying the channel openings the system either increased (*I*), did not notably alter (*M*) or reduced (*R*) the tidal currents in the central section of the flume (*hatched area*) relative to ambient current velocities outside the flume. Each flow treatment consisted of three replicates. The density of *Hydrobia ulvae* and the biomass of seagrass epiphytes were recorded in the central working section of the flume, as well as in the control areas outside the system

Statistical analysis

Results are presented as arithmetic or geometric means (\pm SE). Standard errors of logarithmically transformed variables were calculated according to Mood et al. (1974). All experiments were analysed by means of analysis of variance (ANOVA), followed by a Tukey’s honest-significant-differences (HSD) multiple comparison test (Sokal and Rohlf 1995). First the data were tested for homoscedasticity of variances by using Cochran’s test. When necessary, the data were log transformed to fulfil the assumptions of ANOVA. Data series that contained zeros were transformed by using log ($x+1$). Effects were considered to be statistically significant, if the *P*-value was < 0.05 .

To explore the relationship between the density of grazers and the biomass of seagrass epiphytes within the different experimental treatments, the Pearson correlation test was used. All statistical analyses were conducted using the STATISTICA programme (StatSoft, Tulsa, Oklahoma).

Results

Comparison of seagrass stands

Zostera noltii occurred at both localities during the investigation period, but the mean aboveground biomass of the sheltered seagrass bed was twice as high and the density of the shoots was almost threefold higher compared to the exposed area (Tables 2, 3; pooled data of July, August and September).

The mud snail *Hydrobia ulvae* was the dominant epibenthic grazer at both study sites. It was extremely rare in the exposed seagrass bed (Table 2; pooled data of July, August and September) and fluctuated monthly between 0 and 291 ind. m^{-2} (± 291). *H. ulvae* was significantly more abundant at the sheltered site (Tables 2, 3; pooled data of July, August and September) and varied monthly between average numbers of 77,794 ind. m^{-2} ($\pm 8,703$) and a maximum density of 160,946 ind. m^{-2} ($\pm 24,654$).

Exposed seagrasses were heavily overgrown by epiphytes during the whole vegetation period, while, at

Table 2. Characteristics of the hydrodynamically different seagrass beds (mean \pm SE, pooled data of July, August, September 1999, $n=6$) (AFDW ash-free dry weight)

	Exposed	Sheltered
Aboveground biomass (g AFDW m^{-2})	58.82 (± 5.8)	117.42 (± 11.8)
Shoot density ^a m^{-2}	2,816 (± 1)	8,817 (± 1)
Epiphyte biomass (mg AFDW cm^{-2} leaf)	2.43 (± 0.21)	0.11 (± 0.01)
Grazer abundance m^{-2}	27 (± 27)	151,508 ($\pm 18,956$)

^aGeometric mean (\pm SE) calculated after Mood et al. (1974)

Table 3. *F*-values and significance levels (*P*) of ANOVA for differences between the hydrodynamically exposed and sheltered seagrass beds, describing the conditions during the investigation period from July, August and September in 1999 (pooled data)

Parameter	<i>df</i>	<i>F</i>	<i>P</i>
Aboveground biomass	1	20.597	< 0.001
Shoot density ^a	1	45.699	< 0.001
Epiphyte biomass	1	121.174	< 0.001
Grazer abundance	1	63.861	< 0.001

^aLogarithmic transformation

the sheltered site, seagrass leaves were macroscopically clean (Tables 2, 3). Mean epiphytic biomass of the exposed seagrass bed was 22 times higher than that of the sheltered site, where the extremely low epiphytic biomass reached only 5% of the value at the exposed site (Table 2). Composition of the epiphytic algae on seagrass leaves differed markedly between both areas with respect to the taxonomic groups (Table 4). Epifluorescence microscopical observations showed that epiphytes of exposed seagrasses consisted primarily of filamentous Rhodophyta and Chlorophyta, diatoms and cyanobacteria, while sheltered leaves were covered by diatoms and inorganic as well as organic debris (Table 4). Exposed epiphytes had higher ash contents, forming 40–65% of DW, whereas the average percentage of ash of sheltered epiphytes was only 10% of DW.

Transplantation experiments

After transplantation of heavily epiphytised seagrasses from the exposed into the sheltered bed, the abundance of the mud snail *H. ulvae* strongly increased (Fig. 4A; Table 5). After 2 days, the abundance of *H. ulvae* within transplanted sections was already almost as high as the mean density of the surrounding sheltered seagrass bed (105,584 ind. m⁻², ±33,002). During the following days, no further change of abundance was recorded (ANOVA, $F=0.12$, $df=2$, $P=0.887$) (Fig. 4A).

Accordingly, epiphytic biomass of exposed seagrasses drastically decreased after transplantation into the sheltered area (Table 5). The initial high biomass of epiphytes within the transplants was completely grazed down to 5% by *H. ulvae* within 1 week (Tukey's test, $P<0.001$) (Fig. 4B). No significant difference existed between algal biomass of the transplants and the surrounding sheltered seagrasses after 1 week (ANOVA, $F=4.450$, $df=1$, $P=0.061$) (Fig. 4B).

In contrast, after transplanting small sections of sheltered, "macroscopically clean" leaves with associated snails into an area with strong currents, mean abundance of *H. ulvae* strongly decreased to about 95% of initial snail number within 2 days (Fig. 5A; Table 5). After 3 days, *H. ulvae* was almost absent, and no significant difference in abundance of mud snails compared to the ambient seagrass bed was recorded (Tukey's test, $P=0.355$) (Fig. 5A).

Epiphytes started growing significantly after transplantation of sheltered seagrasses into an exposed seagrass bed (Table 5). After 4 weeks, a 20-fold increase of the initial epiphytic biomass was accumulated (Tukey's test, $P<0.001$) (Fig. 5B). There was no significant difference in epiphytic biomass between transplants and ambient seagrasses (ANOVA, $F=0.519$, $df=1$, $P=0.488$).

Enclosure experiments

The enclosures prevented the flushing of *H. ulvae* from sites of the exposed seagrass bed (Fig. 6A; Table 5). The final number of *H. ulvae* was significantly higher within closed cages than in open cages (Tukey's test, $P<0.05$) or in uncaged seagrass sections (Tukey's test, $P<0.01$). No significant difference was found between open cages and uncaged areas (Tukey's test, $P=0.369$) (Fig. 6A).

The enclosed grazers significantly reduced the epiphytic biomass at the exposed seagrass site within 10 days by >98% (Fig. 6B; Table 5), compared to the epiphytic biomass in open cages (Tukey's test, $P<0.001$) and uncaged treatments (Tukey's test, $P<0.001$). In contrast, the algal overgrowth in open cages and in untreated seagrass sections remained almost unaltered during the experimental period (Tukey's test, $P=0.597$) (Fig. 6B).

Different experimental treatments of seagrass epiphytes at both sites confirmed that biomass of algal

Table 4. Main taxa of epiphytic algae identified on *Zostera noltii* leaves at the exposed and sheltered seagrass beds during the investigation period in summer 1999

	Exposed	Sheltered
	<i>Berkeleya</i> sp.	<i>Cocconeis scutellum</i> Ehrenberg
	<i>Navicula</i> sp.	<i>Navicula</i> sp.
	<i>Licmophora</i> sp.	<i>Licmophora</i> sp.
	<i>Synedra</i> sp.	
	<i>Cylindrotheca closterium</i> Ehrenberg	
	<i>Pleurosigma</i> sp.	
Diatoms	<i>Gyrosigma</i> sp.	
	<i>Grammatophora</i> sp.	
	<i>Achnanthes</i> sp.	
	<i>Nitzschia</i> sp.	
	<i>Biddulphia</i> sp.	
	<i>Tropidoneis</i> sp.	
	<i>Acrochaetium</i> sp.	
Rhodophyta	<i>Esydrodrichia</i> sp.	
Chlorophyta	<i>Enteromorpha</i> sp.	
	<i>Litosiphon</i> sp.	
Phaeophyta	<i>Ectocarpus</i> sp.	
Cyanobacteria	<i>Merismopedia glauca</i> Ehrenberg	

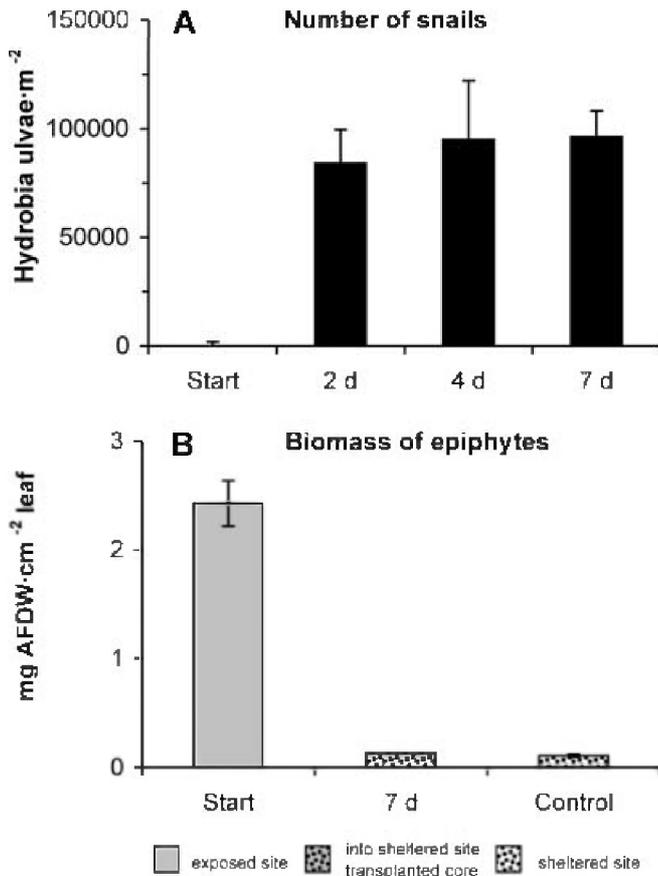


Fig. 4A, B. Transplantations of exposed seagrass sections covered with epiphytes into the sheltered seagrass bed. **A** Abundance of *Hydrobia ulvae* (mean \pm SE) significantly increased within 2 days after transplantation. **B** Initial biomass of epiphytes (mean \pm SE) significantly decreased within 7 days after transplantation and reached ambient biomass of sheltered seagrass epiphytes

overgrowth is negatively correlated with abundance of grazers (Pearson's correlation, $r = -0.870$) (Fig. 7). Biomass was strikingly higher at the exposed seagrass bed (pooled data of exposed sections and those transplanted into the exposed site), due to the absence of *H. ulvae*, in all treatments except for the enclosure experiment with artificially increased snail numbers (ANOVA, $F = 153.482$, $df = 3$, $P < 0.0001$) (Fig. 7). There was no significant difference between epiphyte biomass of exposed seagrasses and seagrass cores transplanted from the sheltered into the exposed area (ANOVA, $F = 0.519$, $df = 1$, $P = 0.488$). In treatments with high abundance of

grazers, algal biomass was comparatively low, but differed significantly between enclosures at the exposed site compared to untreated sheltered seagrasses and sections transplanted from the exposed into the sheltered site (ANOVA, $F = 20.92$, $df = 2$, $P = 0.0001$) (Fig. 7). No further significant difference in epiphytic overgrowth was recorded among sheltered seagrass treatments (Tukey's test, $P = 0.102$).

“Three-current-flume” experiment

With the in situ “three-current-flume” experiment, the tidal current velocity of the ambient seagrass bed was either increased or reduced by about 50%, whilst flow reduction of the third-lane type resulted in nearly the same speed as the mean ambient current velocity of 0.09 m s^{-1} (± 0.01) outside the flume (ANOVA, $F = 15.70$, $df = 2$, $P < 0.001$; pooled data of September) (Table 1).

The density of *H. ulvae* distinctly decreased with increasing average velocities within the different lanes of the in situ “three-current-flume” (Fig. 8A; Table 5; pooled data of September) (Tukey's test, $P < 0.01$ between lanes of highest and lowest currents). From lanes with lowest currents to the lanes of mean flow rates, the abundance of snails decreased by almost 60%, and was further reduced by 40% between lanes of mean and highest current velocities. At lanes with the fastest currents (maximum value = 0.18 m s^{-1}), only 10% of *H. ulvae* individuals m^{-2} compared to the surrounding seagrass bed outside the flume was observed.

Biomass of seagrass epiphytes increased from lanes of low to high current velocity by a factor of almost 3 (Fig. 8B; Table 5; Tukey's test, $P < 0.01$). From reduced to mean current flow, epiphytes increased by about 43% (Tukey's test, $P = 0.137$), and between mean and increased current velocities, an increase of epiphytic biomass of 36% was recorded (Tukey's test, $P < 0.05$). At the highest current flow, algal biomass exceeded that of the ambient, untreated seagrass epiphytes outside the flume by a factor of 1.4 (Tukey's test, $P < 0.05$).

Discussion

The field experiments of this study emphasised a distinct impact of hydrodynamics on the epiphyte-grazer system

Table 5. *F*-values and significance levels (*P*) of ANOVA for effects of transplantations, enclosure experiments and *in situ* flume experiments on the abundance of the mud snail *Hydrobia ulvae* and the biomass of seagrass epiphytes

	Grazer density (ind. m^{-2})			Epiphyte biomass (g AFDW cm^{-2} leaf)		
	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>
Transplantations						
Exposed into sheltered	3	962.37	< 0.0001	1	328.04	< 0.0001
Sheltered into exposed	2	8.32	< 0.01	1	93.93	< 0.0001
Enclosures	1	8.60	< 0.01	2	85.33	< 0.0001
Three-current-flume	2	6.97	< 0.01	2	16.29	< 0.01

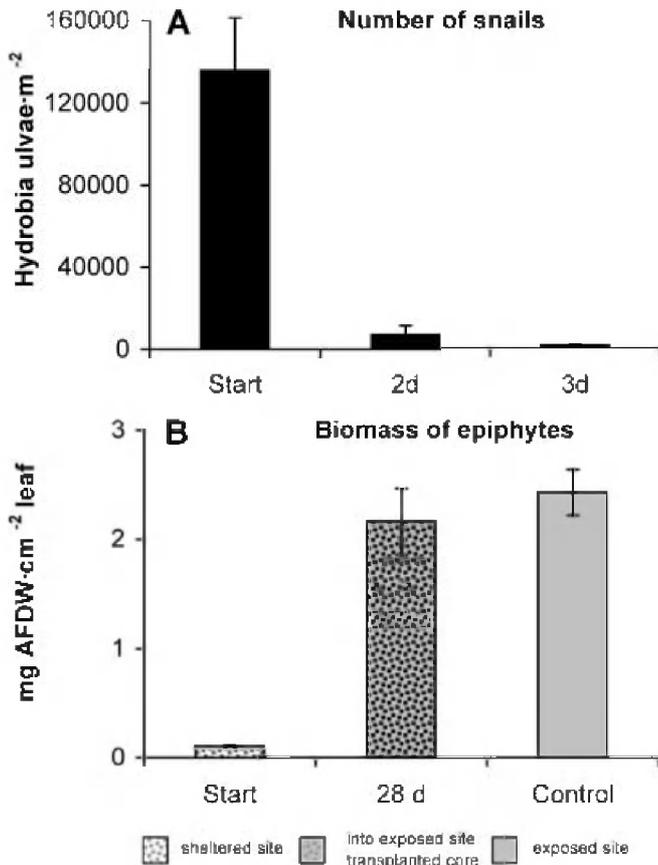


Fig. 5A, B. Transplantations of sheltered seagrasses, devoid of epiphytes, with associated snails into a seagrass bed with strong currents. **A** Abundance of *Hydrobia ulvae* (mean \pm SE) drastically decreased within 2 days. **B** After 4 weeks, nearly the same epiphytic biomass (mean \pm SE) of the ambient exposed seagrass bed was recorded

in intertidal seagrass beds of the Wadden Sea. In previous studies, both biotic and abiotic factors, in particular predation, habitat complexity, nutrient enrichment, water depth and temperature, have been shown to control the animal–plant interactions of seagrass communities (e.g. Mazzella et al. 1992; Orth 1992; Neckles et al. 1993; Williams and Ruckelshaus 1993; Jernakoff et al. 1996). The response of the epiphyte–grazer system to hydrodynamics has been left nearly unconsidered in the past, except for an early study by Lubchenco and Menge (1978). Most studies focussed on the hydrodynamic impact on particular compartments of the seagrass community, such as the seagrasses themselves.

In contrast to studies revealing that strong water movement (e.g. waves and currents) has a positive impact on seagrass viability by removing epiphytic algae from their hosts (e.g. Cambridge 1979; Reise and Siebert 1994; Strand and Weisner 1996; Kendrick and Burt 1997), this study recorded a high biomass of epiphytes at the exposed seagrass bed, whereas at the sheltered seagrass site epiphytic biomass was found to be extremely low. Removal of epiphytes due to water dynamics generally depends on the degree of wave exposure, as well as

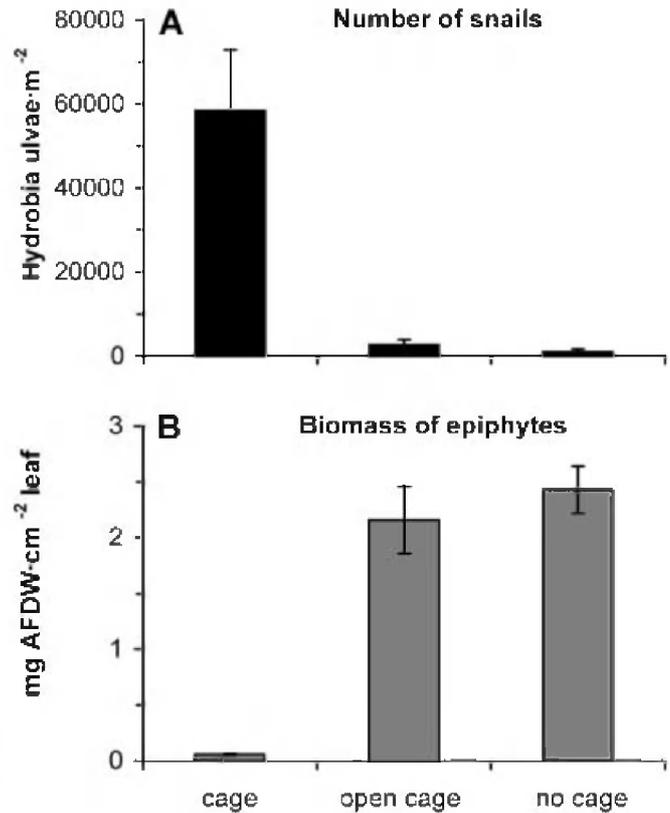


Fig. 6A, B. Enclosure experiments (cage, open cage and no cage with added mud snails) in exposed seagrasses covered with epiphytes. **A** Abundance of *Hydrobia ulvae* (mean \pm SE) after 1 week. Cages significantly prevented the washing away of mud snails. **B** Biomass of epiphytes (mean \pm SE). Enclosed *H. ulvae* significantly reduced algal overgrowth on seagrass leaves within 1 week

on the stature of algae (Cambridge 1979; Kendrick 1991). In this study, the thick layer of epiphytes on seagrasses growing at high tidal current velocities was caused by the low density of the grazer *Hydrobia ulvae*, which in turn was a result of the hydrodynamic regime. Even in an artificially sheltered situation (in open cages), the epiphyte cover was high without a significant density of snails. The open cages, on the one hand, enabled the mud snails to escape but, on the other hand, slightly reduced water movement at the exposed site (particularly tidal currents and wind waves) as a result of the mesh walls of the cages.

H. ulvae is one of the most abundant epibenthic faunal species grazing on the tidal flats of the Wadden Sea (Hauser and Michaelis 1975; Asmus and Asmus 1985, 1990; Dekker 1989). Although the mud snail feeds on microphytobenthos, bacteria and detritus (e.g. Newell 1965; Fenchel 1975; Cadée 1980; Jensen and Siegmund 1980; Asmus 1982, 1994; Asmus and Asmus 1990), high abundances of *H. ulvae* can substantially reduce seagrass epiphytes in sheltered *Zostera noltii* beds (e.g. Asmus et al. 1980; McLusky and Elliot 1981; Asmus 1984; Phillipart 1995; Asmus and Asmus 2000). This is supported by the observation that at sheltered seagrass sites,

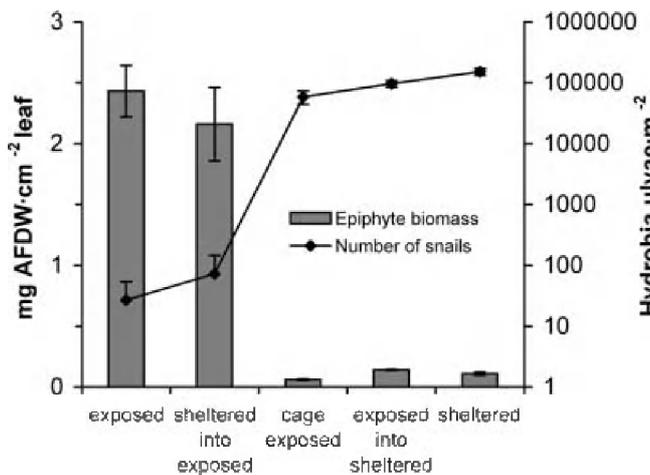


Fig. 7. Epiphyte biomass (mean \pm SE) and abundance of *Hydrobia ulvae* (mean \pm SE) 4 weeks after cross transplantations into exposed and sheltered seagrass beds, enclosures at the exposed site and untreated sites. Algal biomass was negatively correlated to grazer abundance

epiphytic biomass was minimal during the whole vegetation period. Substantial reduction of epiphytes by epifaunal grazers has been confirmed by studies from widely separated geographical areas (e.g. Richardson 1980; Orth and van Montfrans 1984; van Montfrans et al. 1984; Nelson 1995; Jernakoff et al. 1996). At the seagrass sites of the Sylt-Rømø Bay, other epifaunal grazers such as the periwinkle *Littorina littorea* and the isopod *Idothea balthica* were also affected by enhanced water dynamics (Schanz et al. 2000). However, since these species were found in comparably low abundances (Reise and Lackschewitz 1998; Polte 2000; Schanz et al. 2000), their grazing efficiency on seagrass epiphytes is probably negligible in this area.

Epiphyte removal by grazers has commonly been tested using cages and containers to exclude grazers and to compare the epiphytic biomass on grazed and ungrazed plants in the field (e.g. Robertson and Mann 1982; Klumpp et al. 1992; Phillipart 1995; Jernakoff and Nielsen 1997). In this study, cross transplantations of seagrass cores demonstrated the strong impact of water dynamics on grazing capacity, by affecting the abundance of *H. ulvae*, and were proven to be a suitable method for establishing a small part of a seagrass community under different hydrodynamic conditions, without appreciable disturbances or losses of the entire community. In addition, the still intact roots and rhizomes brace the plants firmly and prevent the shoots from being flushed away due to wave action and fast tidal-current velocities (Phillips 1990; Davis and Short 1997).

After transplantation of exposed, heavily epiphytised seagrasses into the sheltered seagrass bed, mud snails from surrounding seagrasses immediately started immigrating into the freshly transplanted sites, ridding the leaves of epiphytes within a week. Active movement of mud snails to sites with a high food supply was also observed for *Hydrobia truncata* and *Ilyanassa obsoleta*

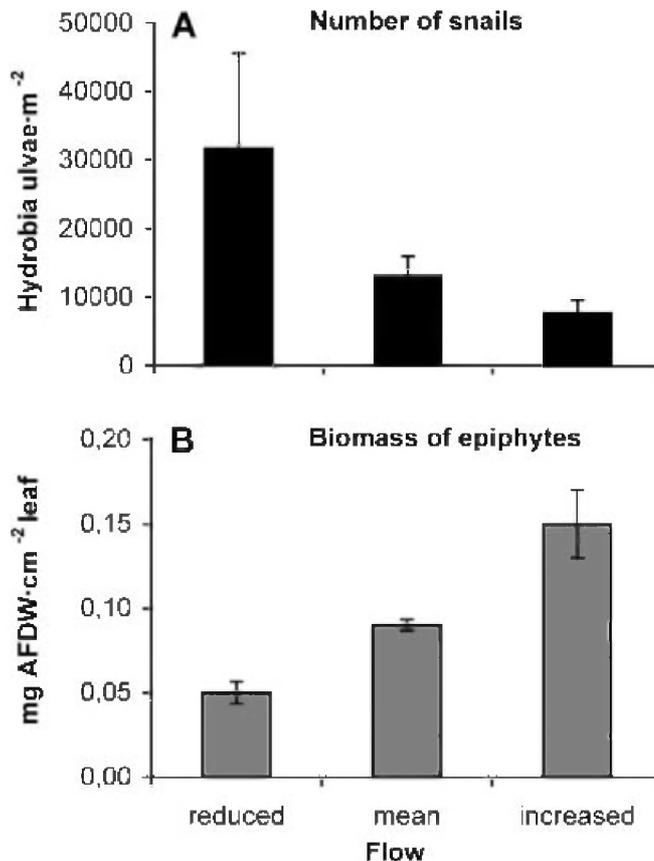


Fig. 8A, B. Effects of reduced-, mean- and increased flow treatments in the “three-current-flume” experiment. **A** Abundance of mud snails (mean \pm SE) drastically decreased with increasing current velocities. **B** Concurrently, epiphyte biomass (mean \pm SE) significantly increased with higher current speeds

Say, causing an increase of snail density in those areas (Forbes and Lopez 1986; Levinton et al. 1995). In contrast, after transplanting visually “clean” seagrasses and associated snails from sheltered sites into an area with strong water dynamics, these snails were completely washed away from the new site by high tidal current velocities during the following tides. Consequently, epiphytes immediately started overgrowing seagrasses. *H. ulvae* is able to drift on the water surface and is transported by strong water motion over great distances (Armonies and Hartke 1995).

As cages prevented the washing away of artificially added *H. ulvae* from the exposed seagrass site, these snails were able to substantially remove epiphytic growth from the plants. After 4 weeks, epiphytic biomass on exposed seagrasses with enclosed *H. ulvae* was even lower than that in the sheltered seagrass bed with comparable numbers of *H. ulvae*, probably due to the high number of grazers restricted by the cages in their ability to move to alternative feeding grounds, thus enhancing grazing pressure on enclosed epiphytes.

Although growth of epiphytes is known to be primarily determined by nutrients, light and temperature levels (Jernakoff and Nielsen 1997), the results indicate

that significant biomasses of epiphytes on intertidal *Z. noltii* only developed when the grazer *H. ulvae* was absent or rare. Nutrient concentrations, such as phosphate and silicate, generally showed the same values at both seagrass sites and within the open North Sea during high tide in summer 1999 (Gutthann 1999; Martens and van Beusekom, personal communication), whereas nitrate concentrations near zero in summer generally lead to extremely low nitrate fluxes (Asmus et al. 2000). Hence, the limitation of growth of epiphytes on sheltered seagrasses, due to reduced nutrient concentrations in water column, is not to be expected. Likewise, the effect of shade on epiphytes at sheltered sites, due to the high shoot density, may be excluded, since no difference in algal biomass was recorded between uncaged and caged seagrass sections (in which shade may have been caused artificially by the gauze).

However, field observations showed that both the number of epiphyte taxa as well as the ash content were distinctly higher at the exposed seagrass bed, whereas at the sheltered area only a few diatoms, representing the first stages of succession, were recorded (Sieburth and Thomas 1973). Since grazing processes modified the epiphyte composition (e.g. Odum 1980; Mazzella and Russo 1989), these results additionally indicate the high grazing pressure on sheltered epiphytes (Asmus 1983). Previous studies documented that hydrodynamics can also directly affect species composition of epiphytes (e.g. Harlin et al. 1985; Kendrick et al. 1988; Borowitzka and Lethbridge 1989; Mazzella et al. 1989; Kendrick and Burt 1997), whilst Pinckney and Micheli (1998) did not find an effect on total epiphytic biomass in habitats exposed to high wave energy.

The experiments with the "three-current-flume" showed a distinctly negative correlation between the density of grazers and the maximum current speed of the near bottom water, thus demonstrating a substantial linkage between hydrodynamics and the epiphyte-grazer system in intertidal seagrass beds.

Although the impact of hydrodynamics on the study sites and during the experiments consisted of both tidal currents and wave exposure, this study predominantly focussed on the impact of currents, as the most stable component for calculations compared to the high variability of wind-induced waves, and is therefore considered to well represent the overall water movement during the experimental period. Comparing both the current regime of the investigated sites, as well as the flow velocities recorded during the flume experiments, it is suggested that *H. ulvae* might be excluded, when current velocities exceed a threshold value between 0.18 and 0.33 m s⁻¹. The less than average densities of *H. ulvae* recorded in intertidal seagrass beds of the Dutch, as compared to the German, Wadden Sea (Hauser and Michaelis 1975; Beukema 1976; Asmus and Asmus 1985; Reise 1991; Phillipart 1995; Schanz et al. 2000) may reflect possible higher maximum orbital velocities of up to 0.35 m s⁻¹ at Balgzand and 0.42 m s⁻¹ at Wierschuur, calculated by van Katwijk and Hermus (2000).

Epiphyte removal by grazers has been found to enhance productivity and biomass of seagrasses (Hootsman and Vermaat 1985; Howard and Short 1986; Phillipart 1995; Nelson and Waaland 1997). In addition, epiphyte grazing could reduce the risk of leaf loss due to heavy epiphyte loads that reduce the flexibility of the leaves and increase drag, leading to severance of plant parts (Jernakoff et al. 1996; Verduin and Backhaus 2000). Therefore, the lower seagrass biomass and density at the exposed seagrass site is at least partly due to the dense epiphyte layer, resulting from the absence of grazers, which themselves were directly influenced by high hydrodynamics. This cascading impact will intensify the influence of eutrophication on seagrass systems in areas with higher hydrodynamic forces and should be considered in future studies focussing on seagrass bed decline due to eutrophication. In addition, it shows that cascading effects within the trophic web are not only triggered by biotic interdependencies but also caused by physical factors.

In conclusion, hydrodynamic forces may act as a top-down regulator in intertidal seagrass communities on different system levels.

Acknowledgements We would like to thank B. Ipsen for supplying useful ideas for the construction of the in situ flume. In addition, we thank several students and colleagues of the Wadden Sea Station Sylt for dragging tons of the heavy steel construction of this flume onto the tidal flats. Without their help this would have been a hopeless project. We are grateful to R. Asmus for critically reading the manuscript and B. Goeck (University of Port Elizabeth, South Africa) for carefully correcting the English. Two anonymous reviewers are thanked for their useful comments on the manuscript. I am grateful to A.W.D. Larkum, who encouraged me to prepare this study for publication in Marine Biology. This article is part of the doctoral study of A. Schanz in the Faculty of Biology, University of Bremen.

References

- Armonies W, Hartke D (1995) Floating of mud snail *Hydrobia ulvae* in tidal waters of the Wadden Sea, and its implications in distribution patterns. *Helgol Meeresunters* 49:529–538
- Asmus H (1982) Field measurements on the respiration and secondary production of a benthic community in the northern Wadden Sea. *Neth J Sea Res* 16:403–413
- Asmus R (1983) Benthische und pelagische Primärproduktion und Nährsalzbilanz – Eine Freilanduntersuchung im Watt der Nordsee. PhD thesis, University of Kiel, Kiel, Germany
- Asmus H (1984) Freilanduntersuchungen zur Sekundärproduktion und Respiration benthischer Gemeinschaften im Wattenmeer der Nordsee. *Ber Inst Meereskd Kiel* 122:1–171
- Asmus H (1994) Benthic grazers and suspension feeders: which one assumes the energetic dominance in Königshafen? *Helgol Meeresunters* 48:217–231
- Asmus H, Asmus R (1985) The importance of grazing food chain for energy flow and production in three intertidal sand bottom communities of the northern Wadden Sea. *Helgol Meeresunters* 39:273–301
- Asmus H, Asmus R (1990) Trophic relationships in tidal flat areas: to what extent are tidal flats dependent on imported food? *Neth J Sea Res* 27:93–99
- Asmus H, Asmus R (2000) Material exchange and food web of seagrass beds in the Sylt-Rømø Bight: how significant are community changes at the ecosystem level? *Helgol Mar Res* 54:137–150

- Asmus H, Theede H, Neuhoﬀ H, Schramm W (1980) The role of epibenthic macrofauna in the oxygen budget of *Zostera* communities from the Baltic Sea. *Ophelia* 1:99–111
- Asmus RM, Sprung M, Asmus H (2000) Nutrient fluxes in intertidal communities of a South European lagoon (Ria Formosa) – similarities and differences with a northern Wadden Sea bay (Sylt–Rømø Bay). *Hydrobiologia* 436:217–235
- Bayerl KA, Higelke B (1994) The development of northern Sylt during the last Holocene. *Helgol Meeresunters* 48:145–162
- Beukema JJ (1976) Biomass and species richness of the macrobenthic animals living on the tidal flats of the Dutch Wadden Sea. *Neth J Sea Res* 10:236–261
- Bologna PAX, Heck KL Jr (1999) Macrofaunal associations with seagrass epiphytes: relative importance of trophic and structural characteristics. *J Exp Mar Biol Ecol* 242:21–39
- Borowitzka MA, Lethbridge RC (1989) Seagrass epiphytes. In: Larkum AWD, McComb AJ, Shepherd SA (eds) *Biology of seagrasses: a treatise on the biology of seagrasses with special reference to the Australian region*. Elsevier, Amsterdam, pp 565–609
- Cadée GC (1980) Reappraisal of the production and import of organic carbon in the western Wadden Sea. *Neth J Sea Res* 14:305–322
- Cambridge ML (1979) Cockburn Sound environmental study: technical report on seagrasses. Report no. 7, Department of Conservation and Environment, University of Western Australia, Nedlands
- Davis RC, Short FT (1997) Restoring eelgrass, *Zostera marina* L., habitat using a new transplanting technique: the horizontal rhizome method. *Aquat Bot* 59:1–15
- Dekker R (1989) The macrozoobenthos of the subtidal western Dutch Wadden Sea. I. Biomass and species richness. *Neth J Sea Res* 23:57–68
- Fenchel T (1975) Factors determining the distribution patterns of mud snails (Hydrobiidae). *Oecologia* 20:1–17
- Fonseca MS, Bell SS (1998) Influence of physical setting on seagrass landscapes near Beaufort, North Carolina, USA. *Mar Ecol Prog Ser* 171:109–121
- Fonseca MS, Kenworthy J (1987) Effects of currents on photosynthesis and distribution of seagrasses. *Aquat Bot* 27:59–78
- Fonseca MS, Fisher JS, Ziemann JC, Thayer GW (1982) Influence of the seagrass, *Zostera marina* L., on current flow. *Estuar Coast Shelf Sci* 15:35–364
- Forbes VE, Lopez GR (1986) Changes in feeding and crawling rate of *Hydrobia truncata* (Prosobranchia: Hydrobiidae) in response to sedimentary chlorophyll a and recently egested sediment. *Mar Ecol Prog Ser* 33:287–294
- Gambi MC, Lorenti M, Russo GF, Scipione MB (1992) Depth and seasonal distribution of some groups of the vagile fauna of the *Posidonia oceanica* leaf stratum: structural and trophic analyses. *Mar Ecol* 13:17–39
- Garcia E, Littler MM, Littler DS (1999) An experimental test of the capacity of wood web interactions (fish–epiphytes–seagrasses) to offset the negative consequences of eutrophication on seagrass communities. *Estuar Coast Shelf Sci* 48:757–766
- Gerard V, Mann KH (1979) Growth and production of *Laminaria longicurvis* populations exposed to different intensities of water movement. *J Phycol* 15:33–41
- Gutthann F (1999) Bodennahe Stoffflüsse in der Gezeitenzone des Sylter Wattenmeeres. Diplomarbeit, University of Kiel, Germany
- Harlin MM, Woelkerling WJ, Walker DI (1985) The effects of hypersalinity gradient on epiphytic Corallinaceae (Rhodophyta) in Shark Bay, Western Australia. *Phycologia* 24:389–402
- Hauser B, Michaelis H (1975) Die Makrofauna der Watten, Strände, Riffe und Wracks um den Hohen Knechtsand in der Wesermündung. *Jahresber Forschstelle Norderney* 26:85–119
- Hootsman MJM, Vermaat JE (1985) The effect of periphyton grazing by three epifaunal species on the growth of *Zostera marina* L. under experimental conditions. *Aquat Bot* 22:83–88
- Howard RK, Short FT (1986) Seagrass growth and survivorship under the influence of epiphyte grazers. *Aquat Bot* 24:287–302
- Jacobs RPWM, Hermelink PM, van Geel G (1983) Epiphytic algae on eelgrass at Roscoff, France. *Aquat Bot* 15:157–173
- Jensen KT, Siegismund HR (1980) The importance of diatoms and bacteria in the diet of *Hydrobia*-species. *Ophelia* 1:193–199
- Jernakoff P, Nielsen J (1997) The relative importance of amphipod and gastropod grazers in *Posidonia sinuosa* meadows. *Aquat Bot* 56:183–202
- Jernakoff P, Brearley A, Nielsen J (1996) Factors affecting grazer–epiphyte interactions in temperate seagrass meadows. *Oceanogr Mar Biol Annu Rev* 34:109–162
- Judge L, Coen LD, Heck KL Jr (1992) The effect of long-term alteration of in situ currents on the growth of *Mecynaria mercenaria* in the northern Gulf of Mexico. *Limnol Oceanogr* 37:1550–1559
- Kendrick GA (1991) Recruitment of coralline crusts and filamentous turf algae in the Galapagos archipelago: effect of simulated scour, erosion and accretion. *J Exp Mar Biol Ecol* 147:47–63
- Kendrick GA, Burt JS (1997) Seasonal changes in epiphytic macroalgal assemblages between offshore exposed and inshore protected *Posidonia sinuosa* Cambridge et Kuo seagrass meadow, Western Australia. *Bot Mar* 40:77–85
- Kendrick GA, Walker DI, McComb AJ (1988) Changes in distribution of macro-algal epiphytes on stems of the seagrass *Amphibolis antarctica* along a salinity gradient in Shark Bay, Western Australia. *Phycologia* 27:201–208
- Klumpp DW, Salita-Espinosa JT, Fortes MD (1992) The role of epiphytic periphyton and macroinvertebrate grazers in the trophic flux of a tropical seagrass community. *Aquat Bot* 43:327–349
- Koch EW (1994) Hydrodynamics, diffusion-boundary layers and photosynthesis of the seagrass *Thalassia testudinum* and *Cymodocea nodosa*. *Mar Biol* 118:767–776
- Koch EW (1999) Preliminary evidence on the interdependent effect of currents and porewater geochemistry on *Thalassia testudinum* seedlings. *Aquat Bot* 63:95–102
- Levinton JS, Martínez DE, McCartney MM, Judge ML (1995) The effect of water flow on movement, burrowing and distributions of the gastropod *Ilyanassa obsoleta* in a tidal creek. *Mar Biol* 122:417–424
- Lubchenco J, Menge BA (1978) Community development and persistence in a low rocky intertidal zone. *Ecol Monogr* 59:67–94
- Mazzella L, Russo GF (1989) Grazing effect of two *Gibbula* species (Mollusca, Archaeogastropoda) on the epiphytic community of *Posidonia oceanica* leaves. *Aquat Bot* 35:357–373
- Mazzella L, Scipione MB, Buia MC (1989) Spatio-temporal distribution of algal and animal communities in a *Posidonia oceanica* meadow. *Mar Ecol* 10:107–129
- Mazzella L, Buia M, Gambi MC, Loretti M, Russo GF, Scipione MB, Zupo V (1992) Plant–animal trophic relationships in the *Posidonia oceanica* ecosystem of the Mediterranean Sea. In: John DM, et al (eds) *Plant–animal interactions in the marine benthos*. Syst Assoc Spec Vol 46:165–187
- McLusky DS, Elliot M (1981) The feeding and survival strategies of estuarine molluscs. In: Jones NV, Wolf WJ (eds) *Feeding and survival strategies of estuarine organisms*. Plenum, New York, pp 109–121
- Mood AM, Graybill FA, Boes DC (1974) *Introductions of the theory of statistics*. McGraw-Hill, Kogakusha
- Neckles HA, Wetzel RL, Orth RJ (1993) Relative effects of nutrient enrichment and grazing on epiphyte–macrophyte (*Zostera marina* L.) dynamics. *Oecologia* 93:285–295
- Nelson TA (1995) Interactions and dynamics of eelgrass (*Zostera marina* L.), epiphytes, and grazers in subtidal meadows of Puget Sound. PhD dissertation, University of Washington, Seattle
- Nelson TA, Waaland JR (1997) Seasonality of eelgrass, epiphyte and grazer biomass and productivity in subtidal eelgrass meadows subjected to moderate tidal amplitude. *Aquat Bot* 56:51–74
- Newell R (1962) Behavioural aspects of the ecology of *Peringia* (= *Hydrobia*) *ulvae* (Pennant) (Gastropoda, Prosobranchia). *Proc Zool Soc Lond* 138:49–75

- Newell R (1965) The role of detritus in the nutrition of two marine detritus feeders, the prosobranch *Hydrobia ulvae* and the bivalve *Macoma balthica*. Proc Zool Soc Lond 144:25–45
- Odum EP (1980) Grundlagen der Ökologie, vol 1. Thieme, Stuttgart
- Orth RJ (1992) A perspective on animal–plant interactions in seagrasses: physical and biological determinants influencing plant and animal abundance. In: John DM, et al (eds) Plant–animal interactions in the marine benthos. Syst Assoc Spec Vol 46:147–164
- Orth RJ, van Montfrans J (1984) Epiphyte–seagrass relationships with an emphasis on the role of micrograzing: a review. Aquat Bot 18:43–69
- Patriquin DG (1973) Estimation of growth rate, production and age of the marine angiosperm *Thalassia testudinum* König. Caribb J Sci 13:111–123
- Philippart CJM (1995) Effect of periphyton grazing by *Hydrobia ulvae* on the growth of *Zostera noltii* on a tidal flat in a Dutch Wadden Sea. Mar Biol 122:431–437
- Phillips RC (1990) Transplant methods. In: Phillips RC, McRoy CP (eds) Seagrass research methods. UNESCO, Paris, pp 51–54
- Pinckney JL, Micheli F (1998) Microalgae on seagrass mimics: does epiphyte community structure differ from live seagrasses? J Exp Mar Biol Ecol 221:59–70
- Polte P (2000) Einfluß hydrodynamischer Exposition auf die Präferenz mobiler Epifauna für eulitorale Seegrashabitats im Sylter Wattenmeer. Diplomarbeit, University of Oldenburg, Oldenburg, Germany
- Ravn H, Pedersen MF, Borum J, Andary C, Andary U (1994) Seasonal variation and distribution of two phenolic compounds, rosmarinic acid and caffeic acid, in leaves and roots–rhizomes of eelgrass (*Zostera marina* L.). Ophelia 40:51–61
- Reise K (1985) Tidal flat ecology. Springer, Berlin Heidelberg New York
- Reise K (1991) Macrofauna in mud and sand of tropical and temperate tidal flats. In: Elliott M, Ducroty JP (eds) Proc ECSA19 Symp. Estuaries and coasts: spatial and temporal inter-comparisons. Olsen and Olsen, Fredensborg, Denmark, pp 211–216
- Reise K (1994) Changing life under the tides of the Wadden Sea during the 20th century. Ophelia 6[Suppl]:117–125
- Reise K, Lackschewitz D (1998) Benthos des Wattenmeeres zwischen Sylt und Rømø. In: Gätje C, Reise K (eds) Ökosystem Wattenmeer, Austausch- Transport- und Stoffumwandlungsprozesse. Springer, Berlin Heidelberg New York, pp 55–64
- Reise K, Siebert I (1994) Mass occurrence of green algae in the German Wadden Sea. Ger J Hydrogr[Suppl 1]:171–180
- Richardson FD (1980) Ecology of *Ruppia maritima* L. in New Hampshire (U.S.A.) tidal marshes. Rhodora 82:403–439
- Robertson AI, Mann KH (1982) Population dynamics and life history adaptations of *Littorina neglecta* Bean in an eelgrass meadow (*Zostera marina* L.) in Nova Scotia. J Exp Mar Biol Ecol 63:151–171
- Robbins BD, Bell SS (2000) Dynamics of a subtidal seagrass landscape: seasonal and annual changes in relation to water depth. Ecology 81:1193–1205
- Sand-Jensen K (1977) Effects of epiphytes on eelgrass photosynthesis. Aquat Bot 3:55–63
- Schanz A, Polte P, Asmus H, Asmus R (2000) Currents and turbulence as a top-down regulator in intertidal seagrass communities. Biol Mar Mediterr 7:278–281
- Shepherd SA, McComb AJ, Bulthuis DA, Neverauskas V, Steffensen DA, West R (1989) Decline of seagrasses. In: Larkum AWD, McComb AJ, Shepherd SA (eds) Biology of seagrasses. Elsevier, Amsterdam, pp 346–393
- Short FT, Neckles HA (1999) The effect of global climate change on seagrasses. Aquat Bot 63:169–196
- Sieburth JM, Thomas CD (1973) Fouling on eelgrass (*Zostera marina* L.). J Phycol 9:46–50
- Sokal RR, Rohlf FJ (1995) Biometry, 3rd edn. Freeman, New York
- Strand JA, Weisner SEB (1996) Wave exposure related growth of epiphyton: implications for the distribution of submerged macrophytes in eutrophic lakes. Hydrobiologia 325:113–119
- Valentine JF, Heck KL, Busby J Jr, Webb D (1997) Experimental evidence that herbivory increases shoot density and productivity in a subtropical turtlegrass (*Thalassia testudinum*) meadow. Oecologia 112:193–200
- van Katwijk MM, Hermus DCR (2000) Effects of water dynamics on *Zostera marina*: transplantation experiments in the intertidal Dutch Wadden Sea. Mar Ecol Prog Ser 208:107–118
- van Montfrans J, Orth RJ, Vay SA (1982) Preliminary studies of grazing by *Bittium varium* on eelgrass periphyton. Aquat Bot 14:75–89
- van Montfrans J, Wetzel RL, Orth RJ (1984) Epiphyte–grazer relationships in seagrass meadows: consequences for seagrass growth and production. Estuaries 7:289–309
- Verduin JJ, Backhaus JO (2000) Dynamics of plant–flow interactions for the seagrass *Amphibolis antarctica*: field observations and model simulations. Estuar Coast Shelf Sci 50:185–204
- Vergeer LHT, Develi A (1997) Phenolic acids in healthy and infected leaves of *Zostera marina* and their growth limiting properties towards *Labyrinthula zosterae*. Aquat Bot 58:65–72
- Williams SL, Ruckelshaus MH (1993) Effects of nitrogen availability and herbivory on eelgrass (*Zostera marina*) and epiphytes. Ecology 74:904–918