

Impact of hydrodynamics on development and morphology of intertidal seagrasses in the Wadden Sea

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ABSTRACT: Field surveys and *in situ* experiments were conducted to determine the impact of hydrodynamics (in particular tidal currents) on the development and structure of intertidal seagrass beds. Field observations in the Sylt-Rømø Bight (German Wadden Sea, North Sea) from 1997 to 1999 revealed dense seagrass beds with a high biomass in sheltered areas, whereas at exposed sites seagrass beds occurred only sparsely with a comparatively low biomass. In addition, the shoot length and leaf length were distinctly higher at sheltered sites than in exposed beds. Cross transplantation experiments and enclosure experiments between sheltered and exposed seagrass sites showed that the density as well as the shoot morphology (leaf number per shoot, shoot length, leaf length and leaf width) were drastically reduced after transplantation into an exposed bed, and were even lower than seagrass values of the adjacent exposed seagrasses after 6 wk. In contrast, the seagrass density as well as the length of shoots and leaves increased distinctly after transplantation into a sheltered seagrass bed. By means of an *in situ* 'three-current flume', experimentally modifying current flow at the same site, it was shown that increasing tidal current velocities resulted in decreased densities and length values in seagrass shoots, despite growing under the same habitat conditions. These results suggest that strong hydrodynamics directly affect the development and architecture of *Zostera noltii* beds by reducing seagrass density and shoot morphology, as well as the extent of seagrass beds. Since changes in environmental conditions are ongoing (e.g. higher storm frequency, sea level rise in combination with man-made protective structures, such as dikes and dams), it is suspected that increasing hydrodynamics might contribute to losses in intertidal seagrass beds.

KEY WORDS: Hydrodynamics · Seagrass beds · *Zostera noltii* · Currents · Pattern · Development · Growth · Wadden Sea

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INTRODUCTION

Seagrass beds occur in coastal waters all over the world, and are linked to multiple ecosystem functions characterised by high productivity and biodiversity (e.g. den Hartog 1970, Larkum et al. 1989). Losses of seagrass populations appear to be continuing in many coastal ecosystems, and has been attributed to human-induced disturbances and climatic changes, e.g. enhanced nutrients and deterioration of light availability (Borum 1985, 1996, Burkholder et al. 1992, 1994, Short & Burdick 1996), and/or changes in temperature and salinity (Bulthuis 1987, Kamermans et al. 1999,

van Katwijk et al. 1999). The effect of hydrodynamics, in particular tidal range, current velocities and wave dynamics, is superimposed on most of these factors, and affects various processes in the seagrass system (Fonseca & Kenworthy 1987, Worcester 1995, Short & Neckles 1999). Hydrodynamics can promote the development of seagrass beds, e.g. by mixing the water column, thereby facilitating nutrient uptake and enhancing photosynthesis due to the decreasing thickness of the diffusive boundary layer (Fonseca & Kenworthy 1987, Koch 1994). In addition, lateral and vertical advection is important for pollination and seed dispersal (Thayer et al. 1984, Orth et al. 1994, Verduin 1996,

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Ackerman 1997). On the other hand, seagrasses are able to reduce current flow, and attenuate wave energy, due to their density and the narrow leaf surface (e.g. Fonseca et al. 1982, Gambi et al. 1990, Fonseca & Cahalan 1992, Koch 1996, Koch & Gust 1999, Verduin & Backhaus 2000), thereby reducing erosion and resuspension of the sediment. However, if an increase in hydrodynamics exceeds a certain threshold that surpasses the existing equilibrium between the seagrass bed and the ambient physical conditions (Fonseca et al. 1983, Fonseca & Kenworthy 1987), this might trigger deterioration of seagrasses, due to erosion processes that enhance resuspension of sediments, thereby promoting turbidity, and may in some instances cause the complete loss of a seagrass bed (Scoffin 1970, Patriquin 1975).

In the Wadden Sea seagrasses are regularly exposed to strong water movement. Long-term observations showed that hydrodynamics incrementally increased during the last century, due to the construction of dikes and dams, increased fishery, as well as a rise in the sea level (Reise 1989, de Jonge & de Jong 1992). As a consequence, historical changes in seagrass habitats, as well as the lack of re-establishment of former extensive meadows, might have been triggered by increasing

water volume in the tidal channels due to erosion processes (Harlin et al. 1982, de Jonge & de Jong 1992, Asmus & Asmus 1998). Recent transplantation and restoration experiments in the Dutch Wadden Sea gave evidence that zonation patterns of *Zostera marina* in the lower and upper tidal areas might be affected by higher water movement, such as wave dynamics (de Jonge et al. 2000, van Katwijk & Hermus 2000).

Based on field observations comparing a dense, sheltered seagrass bed and a comparatively sparse seagrass stand exposed to stronger tidal currents and waves, it was hypothesised that higher hydrodynamics may directly alter seagrass bed architecture and may lead to a restricted distribution of *Zostera noltii* in the Wadden Sea. To demonstrate experimentally whether a difference in water movement influences the growth of *Z. noltii* and how this may impact seagrass bed structure and plant morphology, cross transplantation experiments with and without enclosures between sheltered and exposed seagrass beds were carried out. To quantify the direct impact of modified tidal current velocities on seagrass architecture and development under the same habitat conditions, an *in situ* 'three-current flume' modifying the entire range of current velocities was used.

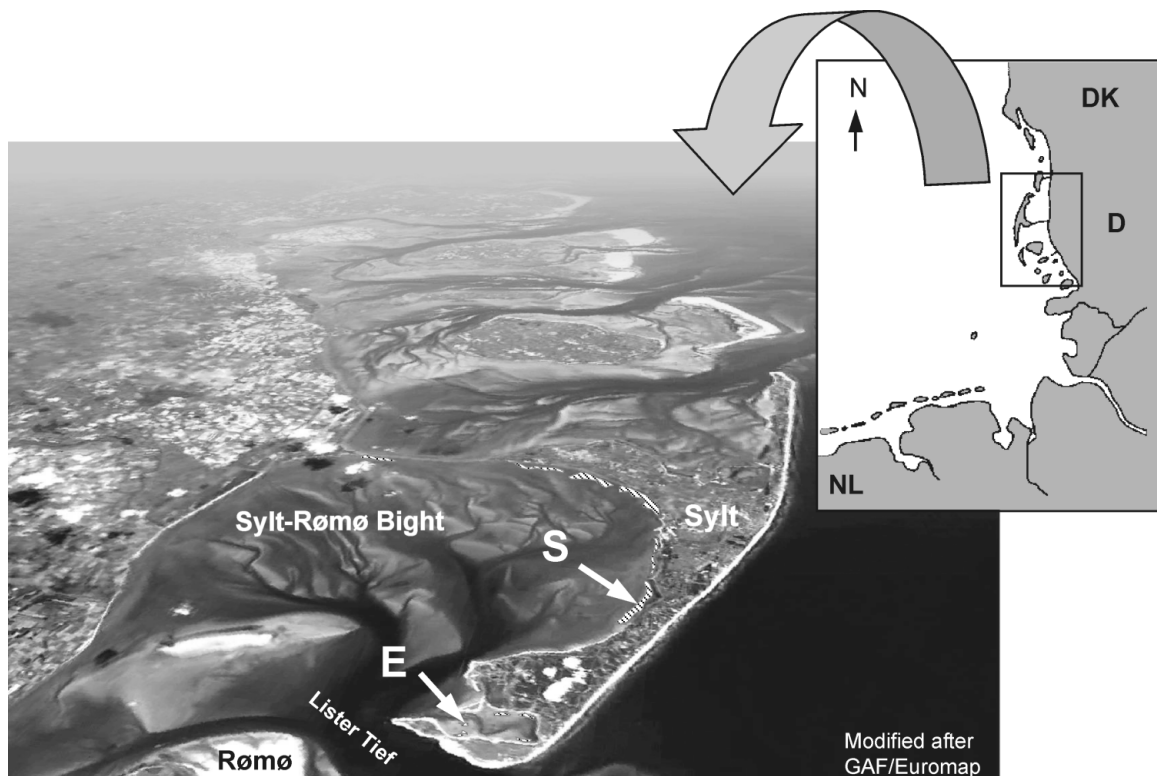


Fig. 1. Location of the study area in the Wadden Sea near the island of Sylt, North Sea, Germany. Distribution of intertidal *Zostera noltii* beds (hatching) along the eastern coast of Sylt. Arrows indicate the investigated hydrodynamically exposed (E) and sheltered (S) seagrass sites in the Sylt-Rømø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

MATERIALS AND METHODS

Study site. The study was conducted within 2 intertidal *Zostera noltii* beds near the island of Sylt, which is situated in the German part of the North Sea (Fig. 1). The investigated seagrass sites are part of a shallow tidal basin (Sylt-Rømø Bight), where only one connection to the North Sea exists (Fig. 1). Tides are semi-diurnal, with a mean tidal range of about 2 m, and salinity varies seasonally between 25 and 32‰.

In the Sylt-Rømø Bight, 12% of the tidal flats is covered by seagrass beds, dominated by *Zostera noltii*. *Z. noltii* beds grow under different degrees of hydrodynamic exposure, and are emerged for 4 to 6 h per tidal cycle. Although the exposure of seagrass beds to water dynamics primarily consists of both tidal currents and wind-induced waves, this study primarily considered the effect of currents as the most stable component of water movement for investigations of long-term processes and their effect on seagrass bed development. Wind-induced waves are highly variable, and can only be considered a short-term effect, due to the lack of historical data. Two *Z. noltii* beds were studied from 1997 to 1999 during their main vegetation periods (Fig. 1): an exposed, sparse *Z. noltii* bed growing on very coarse sand (poorly sorted) close to a deep tidal channel, where initial tidal currents from 0.20 up to 0.33 m s⁻¹ were recorded in the centre of the seagrass bed during calm weather (during the first hour of the flood tide from April to September 1999) (Fig. 1, Table 1); and a second, sheltered and more extensive *Z. noltii* bed on coarse sand (well to poorly sorted), which was located deeper in the bight, and therefore was protected by the island from prevailing westerly winds and stronger currents, due to deep tidal gullies. Here initial tidal current velocities of 0.04 up to 0.20 m s⁻¹ were recorded in the centre of the seagrass bed and averaged only half the values measured at the exposed area (Table 1). Mean water depth at both seagrass sites varied from 0.7 to 1 m at high tide. The seagrasses in the exposed seagrass site were covered by epiphytes as a consequence of stronger currents, promoting fouling on seagrass leaves by reducing the density of grazers (Schanz et al. 2002).

Seagrass stands. To compare both seagrass sites, extent, biomass and plant morphology of *Zostera noltii* were estimated at times with highest seagrass density in August and September from 1997 to 1999. Density of *Z. noltii* was recorded in 1997 and 1999.

The extents of seagrass stands were recorded twice in summer 1999, by pacing off the edges of the seagrass beds and determining the position every 3 s using a Global Positioning System (GPS).

Aboveground and belowground biomass was estimated monthly by taking box cores of 100 cm² (n = 6). Seagrass cores were washed to remove sedi-

ment, adherent fauna and algae; shoots were separated from roots and rhizomes. When necessary, the seagrass leaves were cleaned of epiphytes using a scalpel. Ash-free dry weight (AFDW) was calculated as the difference in dry weight (DW) (2 to 5 d at 60°C) and ashed weight (combusted 12 h at 500°C). Shoot density was determined in summer in 6 replicate test areas using a frame (625 cm²), except for 1998. To compare plant morphology, 20 to 25 seagrass shoots were sampled monthly at both sites. The number of leaves per shoot was counted, and the length of shoots, as well as the length and width of leaves, was measured.

Transplantation of seagrass sections. To test whether hydrodynamics influence seagrass bed development and plant morphology, cross transplantation experiments of seagrasses were carried out at the end of July 1999. Four seagrass sods, comprising 1 replicate test area (2000 cm²), were taken from each site by carefully pushing a box corer (22 × 21.6 cm, 20 cm high) into the sediment without disturbing the leaves of the plants. Seagrass sods were kept in boxes and transported to the laboratory, where they were kept covered by a thin layer of seawater at a temperature of 15°C for 1 d. Six replicate seagrass sections from each donor seagrass bed were exchanged with 6 seagrass sections from the other site. In addition, 4 replicate control areas were transplanted within each donor site. To prevent initial transplantation losses at the exposed seagrass site due to erosion processes, probably caused by higher current speeds, the freshly transplanted seagrass sections were covered by a 5 mm PVC gauze (2000 cm²), anchored by iron pegs, during

Table 1. Characteristics of the hydrodynamically different seagrass beds (mean ± 1 SE, pooled data of August and September from 1997 to 1999)

	Exposed	Sheltered
Sediments		
Median grain size (mm) ^a	1.03 (±0.05)	0.81 (±0.01)
Sorting coefficient [φ (phi)] ^b	0.99 (±0.06)	1.24 (±0.19)
Currents (m s⁻¹)		
	0.26 (±0.01)	0.08 (±0.01)
Seagrass		
Shoot density m ⁻²	1.987 (±202)	4.869 (±558)
Aboveground biomass (g AFDW m ⁻²)	30.65 (±2.76)	49.64 (±5.82)
Belowground biomass (g AFDW m ⁻²)	28.10 (±2.06)	47.92 (±5.14)
Plant morphology		
Leaf number per shoot	3.00 (±0.08)	3.00 (±0.06)
Shoot length (cm)	10.72 (±0.35)	16.18 (±0.49)
Leaf length (cm)	7.02 (±0.21)	10.46 (±0.30)
Leaf width (cm)	0.09 (±0)	0.09 (±0)
^a Wentworth grade classification		
^b Scale in Gray (1981)		

the first day. Previous control transplantations within the donor sites revealed no transplantation effects on seagrass density and morphology.

The density and morphology of *Zostera noltii* shoots were monitored within the transplanted seagrass sections and in both control areas after 6 wk. To analyse the shoot morphology, 10 seagrass shoots were randomly sampled at each replicate seagrass section, and the number of leaves per shoot was counted. Furthermore, the length of shoots and the length and width of the associated leaves were determined as mentioned above.

Enclosure experiments. To test the influence of reduced tidal current velocities at the exposed seagrass site, enclosure experiments were carried out at the end of August 1999. Cages (PVC frames, 11.8 cm in diameter, 10 cm height, 1 mm mesh size) were placed on exposed seagrasses, as well as on sheltered seagrass sections freshly transplanted into the exposed area. After an experimental period of 4 wk, leaf length and leaf width of seagrasses were measured within the enclosures, as well as within the donor sites.

Flume experiment. By using an *in situ* 'three-current flume' (Schanz et al. 2002), the direct impact of modified current velocities on seagrass bed architecture was quantified experimentally under the same habitat conditions. The flume consisted of a heavy steel frame with flexible walls of textile awning (7 m long, 12 m wide, 1 m high) forming 9 lanes. At the beginning of April 1999 the flume was placed into the *Zostera noltii* bed with a moderate ambient current regime and aligned with the prevailing flow direction, allowing for a bi-directional current regime. By modifying the channel openings the system either increased ($0.13 \pm 0.02 \text{ m s}^{-1}$), not notably altered ($0.08 \pm 0 \text{ m s}^{-1}$) or reduced ($0.04 \pm 0.01 \text{ m s}^{-1}$) mean tidal currents in the mid-section of the flume relative to ambient mean current velocities outside the flume (0.10 ± 0.01) (Schanz et al. 2002). Each flow treatment consisted of 3 replicates. Mean current velocities were recorded in the central section of the different lanes, about 10 cm above the sediment surface by using an induction current meter (Marsh MCBirney). Mean current velocities were monitored 12 times during the beginning of both flood and ebb tide for half an hour about every 3 min, from April to October 1999, during calm weather.

Density of seagrasses and seagrass shoot morphology (number of leaves per shoot, shoot length, and the length and width of seagrass leaves) within the different lanes of the flume were recorded once in August and September 1999. As a control, seagrass development outside the flume was determined simultaneously (as mentioned above).

In addition, the grain-size distribution was analysed

once at the end of the experiment by taking core samples (each ~60 g) in each of the lanes ($n = 9$ per flow treatment) and using the standard dry sieving method (mesh series: 2 to 0.063 mm).

Statistical analysis. All results were presented either as arithmetic or geometric means (\pm SE). If variables were log-normally distributed, data were log-transformed prior to analysis, and back-transformed means were used as a central measure. Corresponding standard errors were calculated according to Mood et al. (1974). Differences between sites and experimental effects were analysed by means of analysis of variance (ANOVA), followed by Tukey's honest-significant-differences (HSD) multiple-comparison test. Data were previously tested for homoscedasticity of variances by using Cochran's test to fulfil the assumptions of ANOVA. Differences were considered to be statistically significant if p-values were < 0.05 . All statistical tests were carried out using the STATISTICA programme (StatSoft).

RESULTS

Comparison of seagrass stands

Zostera noltii stands occurred at both locations during the study period, but the extent of the sheltered seagrass bed ($546\,013 \text{ m}^2$) exceeded that of the exposed stand ($12\,525 \text{ m}^2$) by > 40 -fold.

The mean density of seagrass shoots at the sheltered site was slightly higher than that at the exposed site in 1997, but reached almost the 3-fold value in 1999 (Fig. 2, Tables 1 & 2; pooled data of August and September each year). The mean biomass of sheltered seagrasses increased slightly in 1997, but exceeded the exposed seagrass biomass by almost 65% in 1998, and was twice as high in 1999 (Fig. 2, Tables 1 & 2; pooled data of August and September each year). Although the aboveground biomass, as well as the belowground biomass, of sheltered seagrasses was almost twice as high compared to the biomass in the exposed area (Tables 1 & 2; pooled data of August and September each year), there was no difference in the leaf/rhizome ratio between seagrass stands during the study period (ANOVA, $F = 0.223$, $df = 1$, $p = 0.646$).

The mean length of shoots and the length of leaves were distinctly higher at the sheltered seagrass site than at the exposed area during the whole study (Fig. 2, Tables 1 & 2; pooled data of August and September each year). The width of sheltered seagrass leaves was slightly greater than the width of exposed seagrass leaves in 1997, whereas in 1999 the width of exposed leaves slightly exceeded that of the sheltered seagrasses (Table 2; pooled data of August and Sep-

tember each year). No difference in leaf width between both seagrass sites was observed in 1998 (Table 2).

The number of seagrass leaves per shoot did not differ among exposed and sheltered seagrasses from 1997 to 1999 (Tables 1 & 2; pooled data of August and September each year).

Transplanted seagrasses

All seagrass sods were established successfully, and no losses of seagrass shoots were observed at either site 1 d after transplantation. After transplantation of sheltered seagrasses into the exposed stand, some seagrass plants temporarily changed their colour from green to red-brown. After 6 wk, the initial high number of transplanted, sheltered seagrass shoots was reduced by 77%, and had diminished to the same density as the surrounding exposed seagrass bed (Tukey's test, $p = 0.72$) (Fig. 3A, Table 3). The initial number of leaves per shoot decreased by 25% after transplantation (Fig. 4A, Table 3). The length of shoots was reduced by 70%, and the length of leaves by 71% of the initial length values (Fig. 4A, Table 3). Even the width of transplanted leaves decreased by 30% of the initial value within 6 wk. After 6 wk these plant morphological characteristics showed an even stronger reduction within the transplants than these same parameters showed in the ambient, exposed seagrasses (leaf number per shoot: Tukey's test, $p < 0.001$; leaf length: Tukey's test, $p < 0.0001$; leaf width: Tukey's test, $p < 0.0001$) (Fig. 4A).

After transplantation of seagrass sections from exposed into the sheltered seagrass stand the initial shoot number increased nearly 2-fold and reached almost the same value of the surrounding sheltered seagrasses within 6 wk (Fig. 3B, Table 3). The initial shoot length increased by 29%, and the length of leaves increased by almost 40% within the trans-

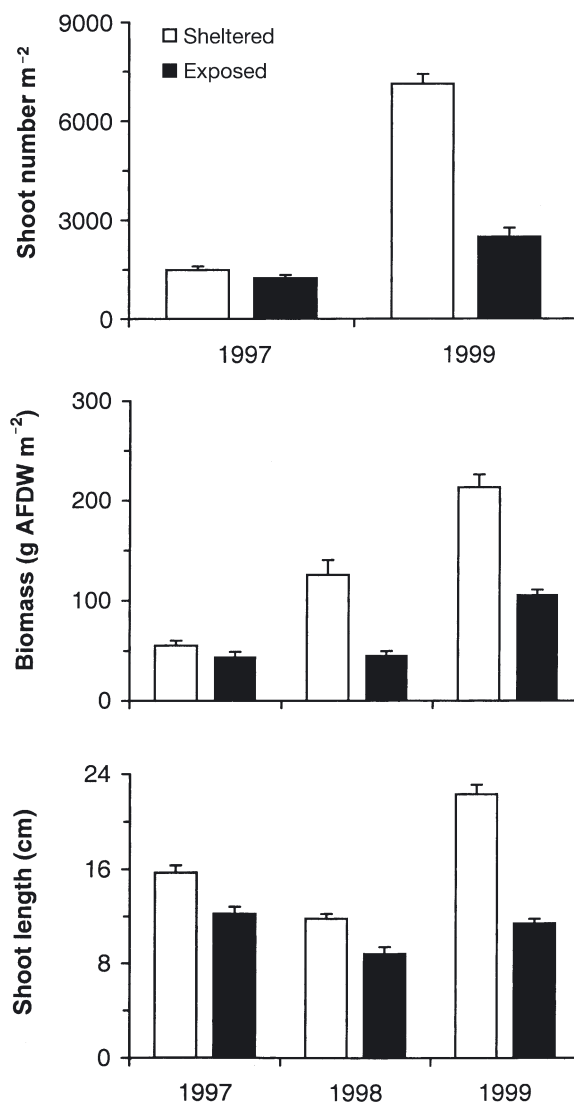


Fig. 2. Comparison of the hydrodynamically exposed and sheltered *Zostera noltii* stands from 1997 to 1999. Density ($n = 18$), biomass ($n = 12$) and shoot length ($n = 50$) (means \pm SE) of sheltered seagrasses were distinctly higher than in exposed seagrass bed

Table 2. *F*-values and significance levels (*p*) of ANOVA for differences between the seagrass beds with different hydrodynamic exposure describing the conditions during the investigation period in August and September from 1997 to 1999 (pooled data). -: data missing

Parameter	1997				1998				1999			
	df	MS	<i>F</i>	<i>p</i>	df	MS	<i>F</i>	<i>p</i>	df	MS	<i>F</i>	<i>p</i>
Biomass	1	98.30	2.76	ns	1	5.30	39.13	<0.0001 ^a	1	2.80	84.62	<0.0001 ^a
Shoot density	1	393 300.53	0.56	ns	-	-	-	-	1	11.48	79.14	<0.0001
Leaf number per shoot	1	0.02	0.27	ns	1	0.35	2.42	ns ^a	1	0.05	0.10	ns ^a
Shoot length	1	312.23	17.71	<0.0001	1	229.52	18.53	<0.0001	1	8.34	154.44	<0.0001 ^a
Leaf length	1	14.32	20.74	<0.0001 ^a	1	193.61	17.09	<0.0001	1	30.64	94.97	<0.0001 ^a
Leaf width	1	0.00	8.59	<0.01 ^a	1	0.00	0.13	ns	1	0.00	5.28	<0.05 ^a

^aLogarithmic transformation

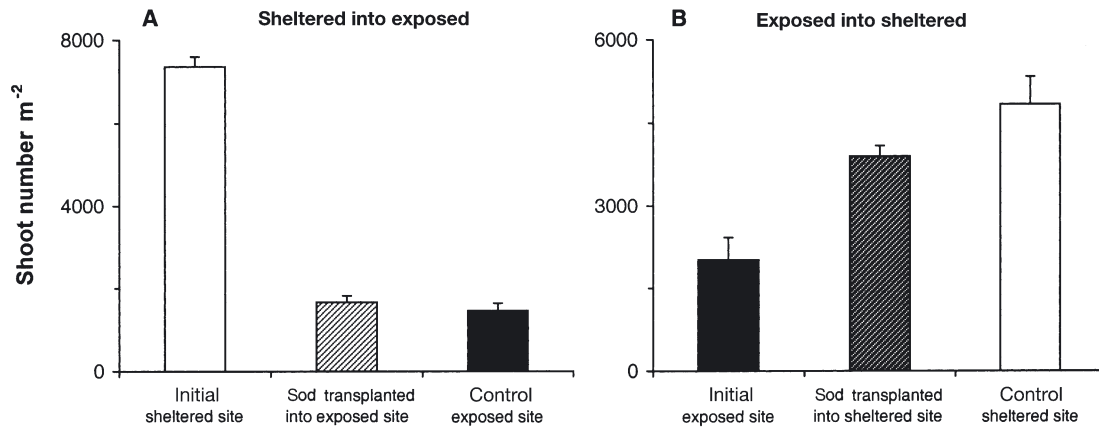


Fig. 3. Transplantation effect on seagrass density after 6 wk. (A) Initial shoot number (mean \pm SE, $n = 6$) drastically decreased after transplantation of sheltered seagrasses into the exposed site. (B) Initial density of exposed seagrass shoots (mean \pm SE, $n = 6$) distinctly increased after transplantation into the sheltered site

plants (Fig. 4B & Table 3). Seagrass transplants had significantly shorter shoots (Tukey's test, $p < 0.05$) and leaves (Tukey's test, $p < 0.001$) than the surrounding sheltered seagrasses after 6 wk. There were no differences in the leaf width or in the number of leaves per shoot between initial values and seagrass sections transplanted from exposed into the sheltered seagrass bed (Fig. 4B, Table 3). However, the leaf width of transplanted, exposed seagrasses significantly exceeded that of the surrounding sheltered seagrasses by 10% after 6 wk (Tukey's test, $p < 0.0001$) (Fig. 4B).

Enclosed seagrasses

Table 3. Split-plot ANOVA for effects of transplantation and enclosure experiments on the seagrass density and shoot morphology (number of leaves per shoot, shoot length, leaf length and leaf width)

Treatment	df	MS	F	p
Transplantations				
Sheltered into exposed				
Shoot density	2	67 162 792	298.61	<0.0001
Leaf number per shoot	2	5.733	16.28	<0.0001
Shoot length ^a	2	8.559	159.80	<0.0001
Leaf length ^a	2	29.757	109.50	<0.0001
Leaf width ^a	2	0.023	87	<0.0001
Exposed into sheltered				
Shoot density	2	12 335 332	13.83	<0.001
Leaf number per shoot	2	0.128	1.57	ns
Shoot length ^a	2	1.088	32.43	<0.0001
Leaf length ^a	2	7.473	32.93	<0.0001
Leaf width ^a	2	0.002	104.54	<0.0001
Enclosures				
Leaf length ^a	2	0.003	80.68	<0.0001
Leaf width ^a	2	0.002	135.68	<0.0001

^aLogarithmic transformation

The enclosures significantly increased the length and width of seagrass leaves within the exposed seagrass stand (Fig. 5, Table 3). Both the enclosed, exposed seagrasses and the enclosed seagrasses transplanted from the sheltered into the exposed site produced distinctly longer and wider leaves than ambient seagrasses without cages within 6 wk (Fig. 5, Table 3). Surprisingly, the leaf length of all 'caged' seagrasses at the exposed seagrass site became as long as seagrass leaves in the sheltered stand within 6 wk (ANOVA, $F = 1.157$, $df = 1$, $p = 0.284$, pooled data of enclosures). However, the leaf widths within both enclosure treatments were slightly greater than the leaf widths of seagrasses in the sheltered area after the experimental period (ANOVA, $F = 80.68$, $df = 1$, $p < 0.0001$, pooled data of enclosures).

Flume experiment

The flume experiments showed no differences in the grain size distribution of the sediments within the lanes of different current flow (ANOVA, $F = 0.486$, $df = 2$, $p = 0.624$). The sediment consisted of medium and very well sorted sand.

The density, the shoot length and the leaf length of *Zostera noltii* decreased with increasing currents (Fig. 6, Table 4; pooled data of August and September). The shoot number decreased by 21% from the lane with the lowest to the lane with mean flow rates, and was further reduced by 28% between lanes of mean and highest current velocities (Fig. 6, Table 4; pooled data of August and September) (Tukey's test, $p < 0.05$ between lanes of highest and lowest currents). Length of shoots decreased only slightly from reduced to mean current flow (Tukey's test, $p = 0.34$), but was reduced

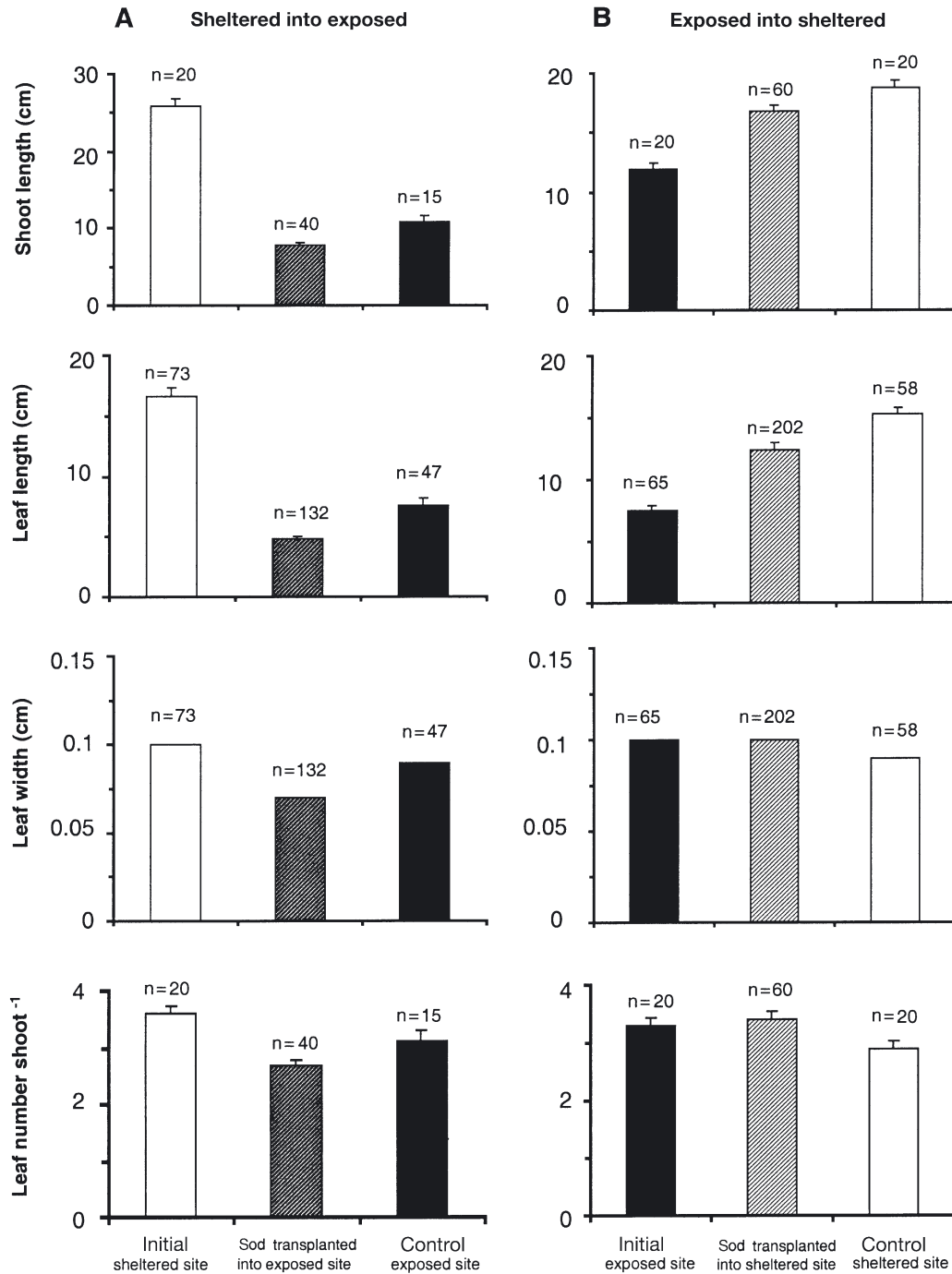


Fig. 4. (A,B) Transplantation effect on seagrass plant morphology after 6 wk. (A) Initial length of shoots, length and width of leaves, and the leaf number per shoot significantly decreased after transplantation of sheltered seagrasses into the exposed site (mean \pm SE). (B) Initial shoot length and leaf length significantly increased after transplantation of exposed seagrasses into the sheltered site, whereas no changes could be observed in leaf width and in the number of leaves per shoot (mean \pm SE). Leaf

by 16% between the lanes of mean and highest current velocities (Tukey's test, $p < 0.01$). The leaf length was reduced by nearly 10% from reduced to mean current flow (Tukey's test, $p = 0.28$) and decreased by 17%

between lanes of mean and highest velocities (Fig. 6, Table 4; pooled data of August and September) (Tukey's test, $p < 0.001$ between lanes of highest and lowest currents). Leaf width and number of leaves per

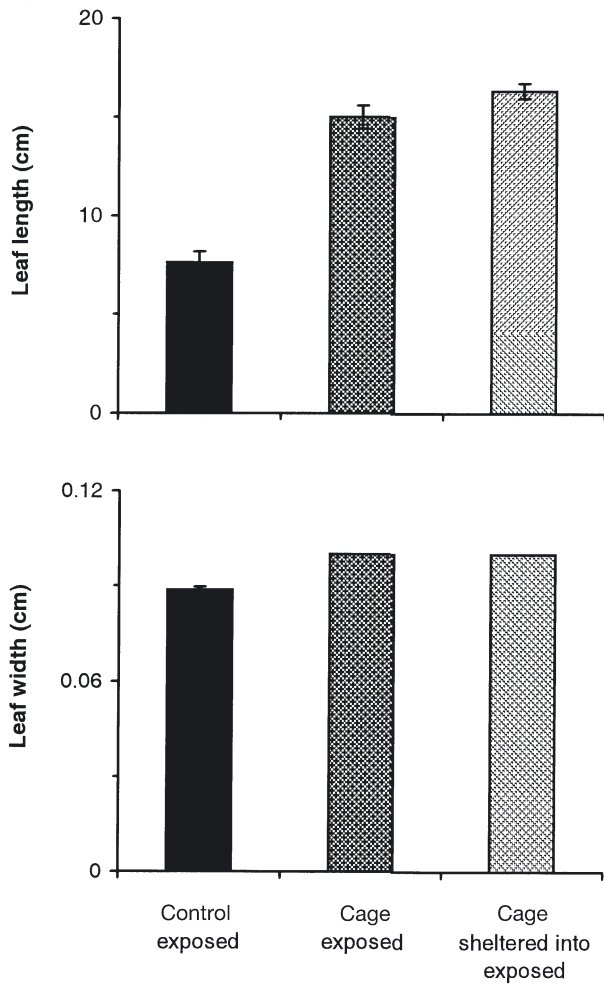


Fig. 5. Enclosure experiments in exposed seagrasses (exposed seagrasses with and without cages, and cages on seagrasses transplanted from sheltered into exposed site). Leaf length and width within the enclosures (widths SE = 0) distinctly increased after 6 wk (mean \pm SE, n = 50)

shoot did not differ between seagrasses within the flume and the ambient seagrasses outside (Table 4; pooled data of August and September).

DISCUSSION

Direct impact of stronger hydrodynamics on seagrasses

The comparison of different seagrass sites in the Sylt-Rømø Bight indicates that hydrodynamics may impact intertidal seagrass characteristics at the population level (extent, biomass and density) as well as on the individual level (leaf number per shoot, shoot and leaf length). All seagrass characteristics recorded from 1997 to 1999 (except the leaf width) were distinctly

lower at the exposed site than in the sheltered area. Even the belowground biomass was almost half as high in exposed stands, in contrast to studies that found a tendency to larger belowground biomass in exposed versus sheltered areas (Kautsky 1987, Coops et al. 1991, Fonseca & Bell 1998). The decrease in belowground biomass might be the consequence of decreasing nutrient concentrations within the sediments caused by intense water movements washing out sediment porewater (Koch 1999). Although a relation between higher water flow and the enhanced

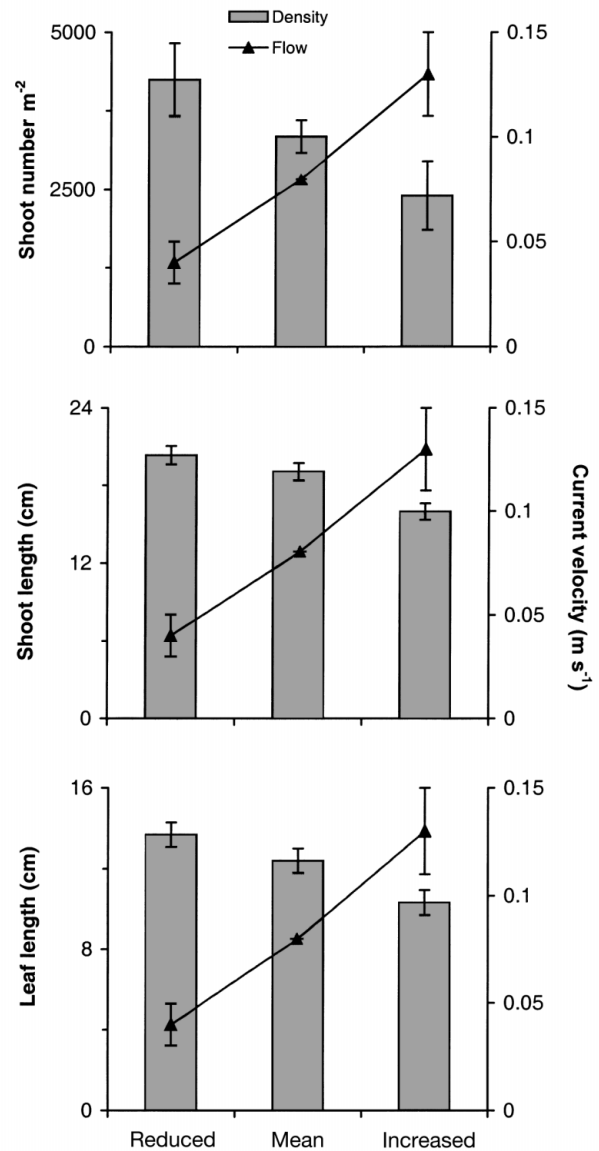


Fig. 6. Effects of reduced-, mean- and increased-flow treatments within the 'three-current flume'. Shoot number (n = 6), shoot length (n = 42) and leaf length (n = 132) (mean \pm SE) decreased with increasing current velocities

Table 4. *F*-values and significance levels (*p*) of ANOVA for effects of the *in situ* flume experiment on seagrass density and shoot morphology (number of leaves per shoot, shoot length, leaf length and leaf width) within the 'three current-flume'

	df	MS	<i>F</i>	<i>p</i>
Shoot density	3	27 791 132	24.443	<0.0001
Leaf number per shoot	3	0.397	0.904	ns
Shoot length	3	135.993	7.526	<0.001
Leaf length	3	399.567	8.635	<0.0001
Leaf width	3	0.002	1.191	ns

development of seagrass belowground biomass (which anchors the plants firmly and prevents the shoots from being washed away) is suspected (Cooper & McRoy 1988, Peralta et al. 2000), no difference in the leaf/rhizome ratio between the sites was found in the present study. However, the lower values of the seagrass biomass and density, as well as the smaller differences between the study sites in 1997 compared to the following years, are presumably attributable to the effects of the severe winter in 1995/1996, initially causing a strong decline in many intertidal benthic populations, due to ice drift (driven by tidal currents and wind) (e.g. Günther & Niesels 1999, Armonies et al. 2001).

The cross transplantation experiments revealed a negative impact of strong water dynamics, by drastically reducing the initial density and shoot morphology after transplanting sheltered seagrasses into the exposed site, thereby supporting the recorded seagrass pattern. In the Dutch Wadden Sea, van Katwijk & Hermus (2000) consistently observed the complete loss of unprotected transplants after transplanting *Zostera marina* to a greater depth, where water dynamics were more severe. Stronger hydrodynamics trigger erosion processes which may detach roots and rhizomes from sediments, thereby thinning out seagrass stocks (Kirkman & Kuo 1990). Severe damage to seagrass beds has also been reported due to wave action and/or sand abrasion after hurricanes (Birch & Birch 1984, Poiner et al. 1989, Preen et al. 1995). Additionally, the decrease of seagrass leaf length in exposed areas might be caused by strong water dynamics (too low to remove whole plants), causing leaf loss, presumably due to increased leaf drag (van Katwijk & Hermus 2000). However, shorter leaves have also been recorded to have developed as a morphological adaptation, being more robust to exposure and light (Cooper & McRoy 1988). In contrast, after transplanting exposed seagrasses into the sheltered area, the initial seagrass density doubled and the length of shoots and leaves increased distinctly. Worm & Reusch (2000) recorded an increased shoot growth

in relation to higher initial shoot density in *Z. marina* patches, suspected to be linked to reduced current velocity (Fonseca et al. 1982), sediment stabilisation and physiological processes among shoots (Olesen & Sand-Jensen 1994). In agreement with the findings of van Katwijk & Hermus (2000), the enclosure experiments at the exposed seagrass bed (which artificially created a sheltered situation due to the gauze of the cages) led to an increase in the length and width of seagrass leaves within the enclosures, thereby supporting the results of the transplants within the sheltered sites. Additionally, these findings contribute to exclude other possible site-specific differences, e.g. changes in average water depth and differences in light availability and nutrients, thus supporting the indicated impact of hydrodynamics.

Hydrodynamics versus biotic and abiotic factors

Bioturbation (Philipart 1994, Valentine et al. 1994, Townsend & Fonseca 1998) and burrowing of polychaetes and crabs (Davis et al. 1998, Hughes et al. 2000) has been shown to inhibit development and transplantation success of seagrasses. However, the effect of these processes on *Zostera noltii* transplants can be excluded, as higher abundances of adult lugworms *Arenicola marina* (Schanz unpubl. data) and crabs *Carcinus meanas* (Polte 2000, Schanz et al. 2000) were recorded in sheltered seagrass sites, where seagrasses are well developed.

Although epiphyte cover on seagrass leaves dominates at exposed seagrass sites, a decrease in seagrass development due to epiphyte shading (Neckles et al. 1993, Williams & Ruckelshaus 1993) can also be excluded. Both the exposed seagrass covered by epiphytes and the transplanted sheltered seagrasses without visible epiphytes (but associated epiphyte-grazing snails) showed distinctly higher leaf values within the enclosures than in the ambient, exposed seagrasses without cages after 6 wk. Within the enclosures, artificial shading may have been caused by the gauze. In contrast, epiphyte cover on exposed seagrasses might have enhanced leaf drag due to the heavy load, thereby reducing leaf flexibility and leading to severance of plant parts (Jernakoff et al. 1996, Verduin & Backhaus 2000). Consequently, it is assumed that the lower density and plant morphology at exposed seagrass sites may be at least partly influenced by epiphytes, which were indirectly influenced by strong hydrodynamics, which, in turn, reduce the density of grazers (Schanz et al. 2002).

The temporal change in leaf colour (into red-brown) after transplanting seagrasses into the exposed area presumably resulted from stress due to higher irradi-

ance caused by the sparse seagrass cover (Pérez-Lloréns & Niel 1993). This is supported by brighter green leaves at the exposed area, compared to the darker green of sheltered leaves (Schanz pers. obs.) attributed to a higher concentration of photosynthetic pigments (Peralta et al. 2000). As the density of exposed seagrasses was too low to retain a water layer during low tide, as observed in dense, sheltered beds (Polte 2000), this may expose seagrasses to higher radiation and desiccation, and, in turn, might limit seagrass development in the upper tidal zone (Leuschner et al. 1998).

However, with the 'three-current flume', which altered the tidal currents within one seagrass stand, the possible impacts of the animal-plant interactions and radiation stress on the seagrass pattern could be separated from those caused by current velocities. This experiment clearly demonstrated the inverse relation between increasing tidal current velocities and seagrass development and morphology under the same habitat conditions (as changes of the environmental condition within the different lanes were not expected; even sediment composition remain unaltered).

In the northern Wadden Sea, seagrasses are generally distributed along the sheltered sides of the barrier islands, protected from stronger currents and waves. In accordance with recent studies of Fonseca & Bell (1998) and van Katwijk & Hermus (2000), changes in seagrass distribution are related to depth gradients at the study sites, attributed to increasing current velocities caused by deeper tidal channels within the Sylt-Rømø Bight. In addition, hydrodynamics may also control the structural pattern of seagrass beds on a horizontal scale, as the extent and biomass of *Zostera noltii* beds increased with increasing distance from the deep tidal channel at the entrance of the bight, attributed to more moderate tidal current velocities deeper inside the bay (Schanz unpubl. data).

As hydrodynamics affect various processes in the seagrass system (Gerard & Mann 1979, Wheeler 1980, Ackermann 1986, Fonseca & Kenworthy 1987, Koehl & Alberte 1988, Koch 1994), increasing hydrodynamics might contribute directly as well as indirectly to deterioration or even loss of seagrass beds. This raises the question whether a certain threshold exists between water dynamics and the development of seagrass beds. Conover (1964, 1968) and Fonseca & Kenworthy (1987) reported that a current speed $>0.5 \text{ m s}^{-1}$ is critical for the standing stock of subtidal *Zostera marina*, whereas Fonseca et al. (1983) estimated an upper limit of approximately 1.2 to 1.5 m s^{-1} velocity that *Z. marina* is able to tolerate. In our field experiments a significant reduction of shoot morphology and density of *Z. noltii* was observed at current velocities $>0.08 \text{ m s}^{-1}$ within the 'three-current flume', whereas the maximum cur-

rent speeds which *Z. noltii* is able to tolerate may be $>0.33 \text{ m s}^{-1}$, as recorded at the exposed area. Once a seagrass bed has been severely damaged, e.g. by heavy storms, many years will pass before subsequent recovery has taken place (Patriquin 1975, Zieman 1976, Birch & Birch 1984, Poiner et al. 1989, Williams 1990).

In the Wadden Sea, hydrodynamics changed dramatically during the last century, presumably attributed to coastal engineering and a rise in sea level (Führböter & Jensen 1985, Hemminga & Duarte 2000), and this has led to increasing erosion processes and drastic losses of shore biotopes (Asmus & Asmus 1998, Reise et al. 1998). In agreement with de Jonge & de Jong (1992), our findings may contribute to explaining the failure of re-establishment of seagrasses at sites where they once occurred as extended beds and where they were diminished due to the wasting disease in the early 1930s. However, since changes in environmental conditions are ongoing (rise in sea level, higher storm frequency), hydrodynamics have to be considered in future research as one of the driving forces controlling seagrass bed development.

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