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EVIDENCE FOR SEAGRASS COMPETITION IN A CENTRAL CROATIAN ADRIATIC LAGOON

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ABSTRACT

Evidence for competition between two co-occurring seagrass species, Zostera noltii *and* Z. marina*, was found along an isobath transect in the Novigrad Sea, Central Croatian Adriatic. The transect included developed (marina) and undeveloped regions of shoreline. Each species' coverage and presence was evaluated using DGPS-tracked underwater videography. Seagrass shoot density was estimated from SCUBA samples. The two* Zostera *species exhibited opposite significant changes correlated with the environmental gradient:* Z. marina *cover and shoot density decreased while* Z. noltii *cover and shoot density increased with distance from marina. Significantly more of the spatial variation was explained by species interaction than by environmental variables. We conclude that competition is a major process structuring the distribution of* Zostera *species in the Novigrad Sea.*

Key words: *Zostera*, seagrass competition, environmental gradient, DGPS-supported videography, Adriatic

EVIDENZA DI COMPETIZIONE TRA FANEROGAME MARINE NELLA LAGUNA DELL'ADRIATICO CENTRALE (CROAZIA)

SINTESI

L'articolo tratta la competizione esistente fra due specie di fanerogame marine, Zostera noltii *e* Z. marina*, che coabitano nel mare di Novigrad (Adriatico centrale). Il transetto, effettuato lungo un'isobata, ha compreso zone sviluppate (marina) e non sviluppate della costa. La presenza e la copertura di ogni specie sono state valutate con l'aiuto della videografia subacquea sostenuta da DGPS. La densità dei ciuffi è stata calcolata dai campioni raccolti durante l'immersione. Per le due specie di* Zostera *sono state riscontrate variazioni significanti opposte correlate con il gradiente ambientale. La copertura e la densità dei ciuffi di* Z. marina *diminuiscono, mentre la copertura e la densità dei ciuffi di* Z. noltii *aumentano con la distanza dalla marina. La variazione nello spazio delle specie è stata significativamente chiarita meglio considerando l'interazione fra le specie che le variabili ambientali. Gli autori sostengono che la competizione sia il fattore principale che influenza la distribuzione delle specie di* Zostera *nel mare di Novigrad.*

Parole chiave: *Zostera*, competizione tra fanerogame marine, gradiente ambientale, videografia sostenuta da DGPS, Adriatico

INTRODUCTION

Much information is available on the spatial distribution of seagrasses as a result of the interplay between seagrass and the physical environment, such as light attenuation (reviewed by Leoni *et al.*, 2008), nutrient concentrations (reviewed by Touchette & Burkholder, 2000), sediment grain size and organic content (reviewed by de Boer, 2007), salinity (reviewed by Touchette, 2007), temperature (reviewed by Lee *et al.*, 2007), wave exposure (reviewed by Cabaço *et al.*, 2008), air exposure during low tides, benthic slope, and depth. These responses are interpreted as an outcome of physiological tradeoffs during the process of adaptation to these physical conditions and resources. Fewer studies have incorporated both physical and biological processes, such as competition and their effect on spatial distribution and abundance (Fourqurean *et al.*, 1995; Laugier *et al.*, 1999; Tanaka & Kayanne, 2007), and seemingly none have done so within a single analysis.

Our study focuses on two co-occurring *Zostera* species, *Z. noltii* and *Z. marina*, along a 3-m isobath transect spanning a developed area (residential and tourist housing, light commercial business, seawall, marina, agricultural fields), to an undeveloped shoreline. The restriction to the 3-m isobath ensured that (i) neither species was investigated at its lower or upper depth limit (depth distribution for both species ranges from 0.25-4.5 m in the study area; Schultz *et al.*, 2009), that (ii) depth related variation in physical environmental variables was ignored, and (iii) that the two species were co-occurring within most of the study transect and associated plots. This gave us the opportunity to investigate spatial variation of the two species in relation both to physical environmental gradients along the transect and to each other's presence.

Much is known about the two *Zostera* species, although the majority of studies have been carried out outside the Adriatic and even the Mediterranean. In the Adriatic, *Z. noltii* is described as a widely distributed species mainly found in the shallow benthos of a range of habitats from sheltered low energy to higher energy environments with more wave and current activity (Widdows *et al.*, 2008). *Z. marina* in the Adriatic is described as the species with the more restricted and irregular distribution, requiring sheltered places and freshwater input (Guidetti, 2000). Although *Z. noltii* is considered the more marine species, both species are known to have great euryhalinity tolerance (den Hartog, 1970) and both have been found to benefit from decreased salinities (Hootsmans *et al.*, 1987; Vermaat *et al.*, 2000; Charpentier *et al.*, 2005). *Z. noltii* appears to prefer sandy sediments, whereas *Z. marina* tends to be found on muddier ground with a higher organic content (Duarte & Kalff, 1988; Caniglia *et al.*, 1992; Koch, 2001). *Z. marina* as the larger species is expected to be more tolerant of low light conditions, *e.g.* as a consequence of sediment re-suspension, as it has greater light-absorbing surface area and higher resource-storing volume. Both species have been shown to respond positively to addition of ammonium and nitrate in N-limited environments (Marba *et al.*, 1996), a situation that can be expected near residential areas and freshwater inflow.

The placement of the transect within the study area offered (i) significant variation in physical environmental variables, including salinity, wave exposure, sediment characteristics, distance from anthropogenic influence and freshwater due to the change in geographical location (without depth interference), and (ii) an opportunity to investigate the two *Zostera* species within a continuous mixed bed. This allowed us to compare the relative importance of the physical environment and species interactions for each species' spatial distribution.

MATERIALS AND METHODS

Study area

The Novigrad Sea, Croatia (44°12'N, 15°30'E), is a protected estuarine embayment of 29 km^2 (approximately 8 × 5 km at longest axes) in the eastern Adriatic Sea (Fig. 1). It is connected to the Velebit Channel in the north by a narrow strait (the Maslenica Channel), and is receiving freshwater inflow from the Zrmanja River in the northeast, by underground springs, a few small seasonal creeks, and a canal draining water from the agricultural area near the town of Posedarje (Sinovčić *et al.*, 2004; Figs. 1 and 2). Benthic habitats include dense macroalgae/rock, unconsolidated bare sediments (gravel, sand, and mud) and sparse to dense seagrass belonging to three species *Zostera noltii*, *Z. marina*, and *Cymodocea nodosa*. The present study was carried out in spring 2007 (salinity measurements in fall and winter) in the low gradient westernmost portion of the Novigrad Sea where the seagrass cover is a continuous meadow extending from the developed north side of the bay (town of Posedarje) to the undeveloped south side (Fig. 2). Here the water is shallower than 5 m and the bottom is muddy to sandy.

DGPS/videography and video analysis

Along a constant depth (3-m isobath) transect of 1167 m length, a video sensor (Sony, 480 colour TVL) continuously recorded the sea bottom. Simultaneously overlaid on the video image was the satellite time recorded every two seconds. Depth was monitored by a 200 KHz, 11°, single-beam transducer. Horizontal DGPS coordinates were taken with real-time submeter accuracy from radio beacon transmissions to a GPS antenna held by kayak operator directly above the video sensor visible from the surface (Norris *et al.*, 1997;

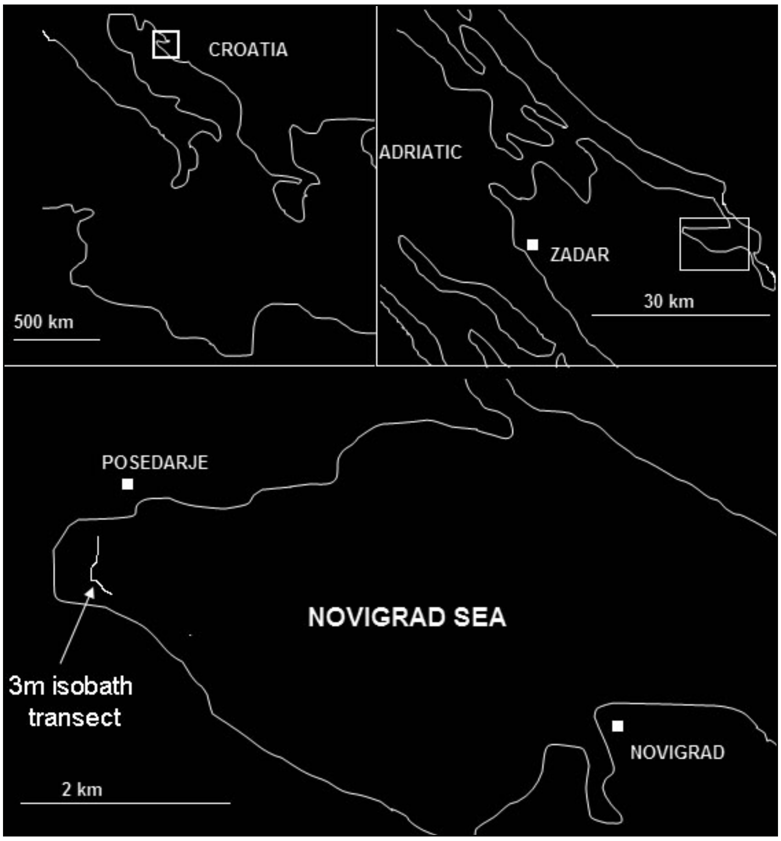

Fig. 1: Approximate location of the 3 m isobath transect at the Novigrad Sea, Croatia.
Sl. 1: Približna lokacija trimetrskega izobatnega transekta v Novigrajskem morju, Hrvaška.

Dauwalter *et al.*, 2006; Schultz, 2008). Subsequent analysis of every second of the recorded video allowed for calculation of the linear coverage for all seagrass species present.

Seagrass and sediment sampling and processing

Following over the DGPS tracks of the video transect by submeter real-time navigation, a SCUBA diver was led to 32 stations evenly spaced along the previously followed video transect. At each station, the diver harvested all seagrass from three replicate circular plots of 0.085 m^2 each, as well as 3 sediment cores (100 ml syringes with stopper) of 3 cm diameter inserted into the bottom to a depth of approximately 8–10 cm. Seagrass and sediment samples were kept refrigerated. Seagrass was processed within 48 hours, sediment within 6 hrs. The uppermost 5 cm of sediment were placed in plastic containers, homogenized by stirring and kept air tight and refrigerated until further processing (within 72 hours), when a portion of the sediment (approximately 30 g) was wet-weighed and then dried at 60ºC until constant dry weight. Water content of the sediment was calculated as the weight loss in percent. Loss-on-ignition (LOI) analysis was used to measure the sediment organic matter content. Small samples of sediment (mean weight 9 g) were dried overnight at 105ºC until weight constancy and then combusted at 530ºC for 2 h. Organic content was calculated as the weight loss in percent. In seagrass samples from each of the 3 plots at each of the 32 stations the shoots of all species present *(Z. marina, Z. noltii, Cymodocea nodosa)* were counted. Ten shoots (or less if less available in the sample) from each species were randomly chosen and the length (ruler) and width (dissecting scope) of the longest intact leaf of each shoot was measured and the leaf area calculated.

Salinity, bottom slope, and wave exposure

Water samples were taken from the surface and salinity immediately measured with a refractometer. All samples were taken from a kayak and approximately every 10 m while tracking the 3-m isobath transect with submeter accuracy. Bottom slope was calculated from the shortest distance between the 2 m isobath line and the 4 m isobath line passing through each of the 32 sampling stations on the 3-m isobath line. All isobath lines were identified by kayak-based DGPS tracking with the depth continuously monitored as described above. Depth-dependent wave exposure (REI_d) was calculated

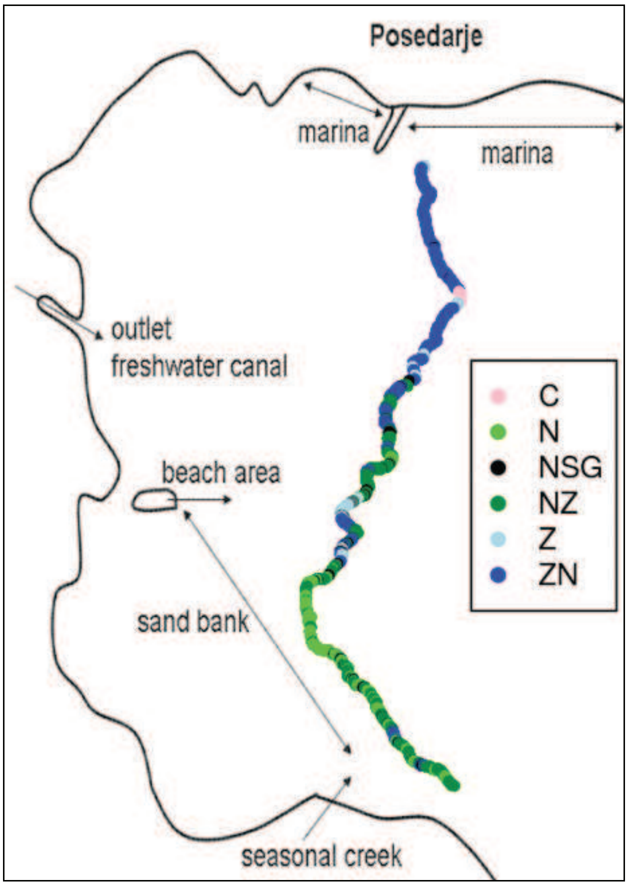

Fig. 2: Detailed view of the 1,167 m long 3 m isobath transect in the westernmost section of the Novigrad Sea, Croatia. Colour code identifies seagrass species and relative visual presence for individual units of approximately 0.3 m. Legend: C = *Cymodocea nodosa*, ***N =*** *Zostera noltii*, ***Z =*** *Zostera marina*, ***NZ = mixed*** *Zostera* ***with*** *Z. marina* ***observed within a 0.3 m unit but not in every video frame, ZN = mixed bed with*** *Z. marina* ***present in every video frame, NSG = no seagrass (unconsolidated sediments).***
Sl. 2: Podroben prikaz 1.167 m dolgega in 3 m širokega izobatnega transekta v najzahodnejšem delu Novigrajskega morja na Hrvaškem. Vrsti sta označeni z različnima barvama v posameznih približno 0,3 m velikih enotah. Legenda: C = *Cymodocea nodosa*, ***N =*** *Zostera noltii*, ***Z =*** *Zostera marina*, ***NZ = obe vrsti, pri čemer se*** *Z. marina* ***pojavlja v 0,3 m veliki enoti, vendar ne v vsakem video-okvirju. NSG = brez morskih trav (nestrjene usedline).***

using the formulas given in Krause-Jensen *et al.* (2003). Necessary data on wind direction, velocity and frequency were provided by the Croatian Meteorological and Hydrological Service. Fetch distances were measured as the distance between a sampling point and the nearest shoreline in each of eight compass directions (N, NW, W, SW, S, SE, E, NE) as measured on satellite photos with resolution 2.5 m per pixel (Google Earth 5.0, 2009).

Data analysis

Effects of physical variables on shoot densities were tested with single- and multiple-factor analysis of variance (ANOVA) on untransformed response variables, which were not significantly different from those normally distributed. Significance of individual coefficients in the ANOVA multiple-factor was evaluated with t-tests. F-test was used to compare the results of two nested analyses of variance that differed only in the presence or absence of seagrass shoot density. Relationships among variables were visualized with a standard biplot of the results of principal components analysis based on correlations among all variables.

RESULTS

Seagrass visual cover along the transect

Along the 1,167 m transect, three seagrass species were observed (Fig. 2). *Z. noltii* was present over 974 m (83.5% of the transect), *Z. marina* over 877 m (75.1%) and *C. nodosa* over 17 m (1.5%). *C. nodosa* was restricted to one small section of the transect. The *Zostera* species mostly co-occurred in mixed communities (781 m linear coverage, 66.9% of the transect). Near the marina development, *Z. marina* had greater visual presence and *Z. marina* blades were frequent and observed in every video frame (Fig. 2: "ZN", coded dark blue). Further away from the marina, fewer blades of *Z. marina* were observed within the *Z. noltii*-dominated seagrass bed (*Z. marina* present within each base unit of approximately 0.3 m which equals one second of video, but not in every video frame (Fig. 2: "NZ", coded dark green). Monospecific patches of *Z. marina* (Fig. 2: "Z", coded light blue, 96 m accumulative coverage, 8.2% of the transect) were generally rare and occurred either near the marina or along a heavily frequented beach area (Fig. 2). Monospecific patches of *Z. noltii* (Fig. 2: "N", coded light green, total coverage 193 m, 16.5%) were twice as common as those of *Z. marina*, but basically restricted to the natural side, where they were most expansive along the sand bank (Fig. 2) located in the southwest of the study area. *Z. marina* visual presence increased again (Fig. 2 shift from "NZ" to "ZN") in the area directly influenced by a seasonal creek at the very south end of the transect (Fig. 2).

Tab. 1: Description of the general environment along the transect. For references with geographical locations refer to figure 2.
Tab. 1: Opis okolja vzdolž transekta. Glede podrobnosti o geografskih lokacijah na preučevanem območju glej sliko 2.

Geographical location	Description of the environment
North	Transect located within the marina, a concreted area that experiences regular small boat traffic and mooring, as well as freshwater drainage and wastewater input.
Northwest	Near transect enters a freshwater canal, which receives drainage from agricultural fields and some residential waste water. The mouth of the canal is characterized by dense growth of marsh plants, such as *Phragmites* spp.
West	Transect near a low-gradient shallow beach area experiencing frequent bathing and boating/anchoring traffic from May to October.
Southwest	Transect follows the edge of a shallow sand bank, an area where the benthic slope at 3 m is highest.
South	Transect ends near the mouth of a seasonal creek off an undeveloped rocky shore (freshwater entering mainly in early spring).

Tab. 2: Summary of variables representing the changes in physical environment along the transect. For references with geographical locations refer to figure.2.
Tab. 2: Povzetek parametrov, ki ponazarjajo spremembe v fizičnem okolju vzdolž transketa. Glede podrobnosti o geografskih lokacijah na preučevanem območju glej sliko 2.

Physical environmental variable	Summary of results based on measurements
Benthic slope	Generally low, ranges from 0.8 to 1.8 %, lowest values in the north and highest in the southwest.
Sediment organic-matter content and water content	Organic-matter content ranged from 3.0 to 10.9%, water content ranged between 32 and 65%, with highest values in and near the marina and lowest values in the south and along the sand bank (southwest). Sediment organic-matter and water content were highly positively correlated ($p = 2.2x10^{-16}$, $R^2 = 0.94$).
Salinity	Ranged between 9 to 14 ppt in the winter and 32 and 34 ppt in the fall. In the fall salinity was significantly highest in the center of the transect, in winter salinity was significantly highest near the natural side (south).
Depth-dependent wave exposure index	Ranged between 6.90 and 6.99 and significantly increased with distance from the north and the south ends, but was slightly higher within the marina (6.95) than at the South end (6.90).

Seagrass responses to the physical environment

Mean shoot density of *Z. noltii* was 656 shoots/m^2 and significantly higher than that of *Z. marina* (111 shoots/m^2, $p = 5.9 \times 10^{-8}$). *Z. noltii* shoot density significantly increased with distance from marina ($p = 0.035$, $R^2 = 0.11$, Fig. 3) and was positively affected by bottom slope ($p = 0.45$, $R^2 = 0.093$; Tab. 3). Sediment characteristics, like organic and water content, had a marginally negative effect, while distance to a sandbank had a marginally positive effect (Tab. 3). On the contrary, *Z. marina* shoot density decreased with distance from marina ($p = 0.0003$, $R^2 = 0.34$; Fig. 3), was lowest near (alongside) the sand bank ($p = 0.0074$, $R^2 = 0.30$), and was negatively affected by benthic slope ($p = 0.033$, $R^2 = 0.11$; Tab. 4). *Z. marina* shoot density correlated positively with sediment organic content ($p = 0.0056$, $R^2 = 0.20$) and water content ($p = 0.0037$, $R^2 = 0.22$; Tab. 4).

The physical environment along the transect

The 3-m isobath transect reaches north to south from the town of Posedarje to the opposite natural shore (Fig. 2). Tables 1 and 2 summarize and describe changes of the overall environment and specific aspects of the physical environment along the transect.

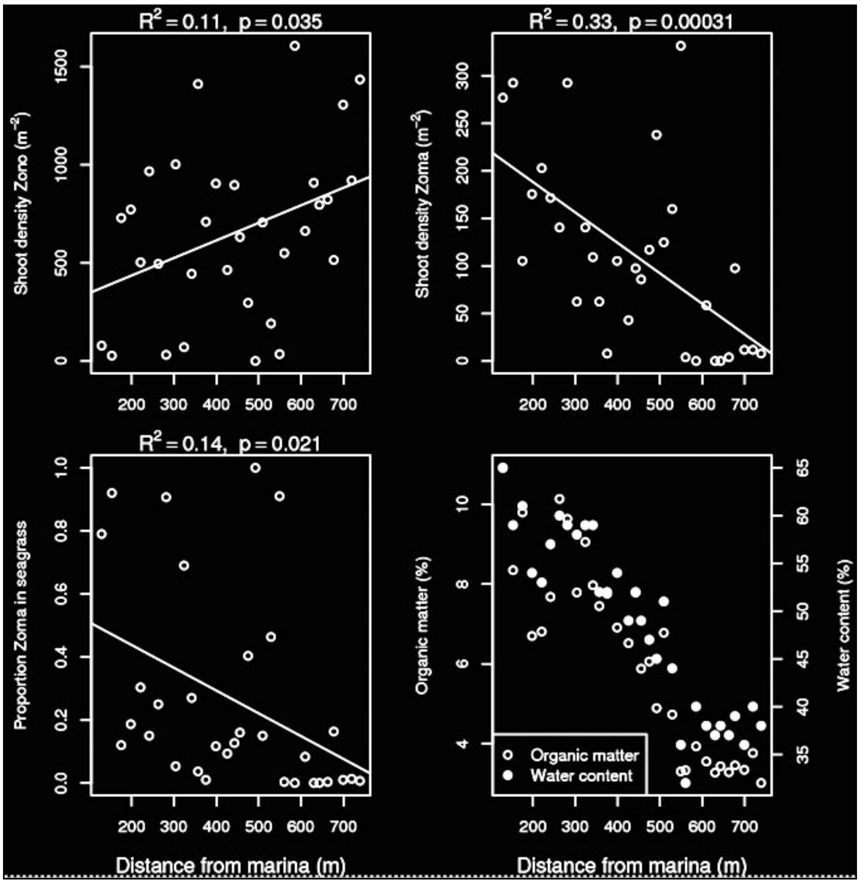

Fig. 3: Scatterplots, regression lines, and ANOVA results (distance from marina) for *Z. noltii* ***and*** *Z. marina* ***shoot densities, proportion of seagrass that was*** *Z. marina****, and sediment organic matter and water content.***
Sl. 3: Razpršeni diagrami, regresije in rezultati ANOVE (razdalja od marine) za gostoto šopov vrst *Z. noltii* ***in*** *Z. marina****, delež morske trave, ki je bila*** *Z. marina****, organske usedline in vsebnost vode.***

The proportion of seagrass showed that *Z. marina* was significantly correlated with the same predictor variables and in the same direction as *Z. marina* shoot density. Total shoot density showed less significant correlations with any of the predictor variables, but the directions of all responses were equal to those for *Z. noltii* shoot density. In a biplot (Fig. 4b), the first two principle components were the distance from the marina and the distance from the freshwater canal outlet (see in Fig. 2). Again, *Z. marina* shoot density is negatively correlated with the distance from marina and the freshwater canal, while *Z. noltii* is positively correlated with these two variables. In addition, *Z. marina* shows positive correlation with wave exposure and negative correlation with the slope, while the opposite is true for *Z. noltii*.

Tab. 3: ANOVA results for *Zostera noltii* ***shoot density; Df = 1.1. Statistically significant results are highlighted (bold).***
Tab. 3: Rezultati analize variance (ANOVA) za gostoto šopov vrste *Zostera noltii****; Df = 1,1. Statistično značilni rezultati so poudarjeni (mastne črke).***

Predictor variables	***Zostera noltii* shoot density**		
	F	**p**	**R^2**
distance from marina	4.86	**0.035**	0.11
distance from sand bank	3.1	0.088	0.064
distance from beach area	1.01	0.32	0.00037
distance from canal	3.32	0.078	0.060
wave exposure	3.72	0.063	0.080
salinity fall	0.11	0.74	-0.029
salinity winter	0.25	0.62	-0.025
bottom slope	4.18	**0.05**	0.093
sediment organic matter %	3.74	0.063	0.081
sediment water content %	3.03	0.092	0.061

Seagrass interactions

Z. marina shoot density was highly negatively and significantly correlated with *Z. noltii* shoot density ($p = 9 \times 10^{-11}$, $R^2 = 0.35$; Fig. 4a). When all physical variables were combined in a multiple regression analysis ($p = 0.0019$, $F = 3.14$, $Df = 10, 85$), only 18% of the variation in *Z. noltii* shoot density was explained and only fall salinity had an independent significant effect. A subsequent multiple regression analysis with *Z. marina* shoot density, added as one of the predictor variables ($p = 1.0 \times 10^{-7}$, $F = 6.51$, $Df = 11, 84$), significantly improved the model ($p = 5.14 \times 10^{-7}$, $F = 29.06$, $Df = 84, 85$ in comparison to the nested ANOVAs; Tab. 5) and explained additional 20.5% of the variation. The only physical variables having an independent significant effect on *Z. noltii* shoot density were fall salinity (positive), wave exposure (negative), sediment organic content (negative), and distance from a sand bank (negative).

Tab. 4: ANOVA results for *Zostera marina* ***shoot density; Df = 1.1. Statistically significant results are highlighted (bold).***
Tab. 4: Rezultati ANOVE za gostoto šopov vrste *Zostera marina****; Df = 1,1. Statistično značilni rezultati so poudarjeni (mastne črke).***

Predictor variables	*Zostera marina* shoot density		
	F	p	R^2
distance from marina	16.6	**0.00031**	0.33
distance from sand bank	14.12	**0.00074**	0.3
distance from beach area	8.4	**0.007**	0.19
distance from canal	1.29	0.26	0.0093
wave exposure	3.4	0.075	0.072
salinity fall	0.19	0.67	-0.027
salinity winter	2.51	0.12	0.047
bottom slope	5	**0.033**	0.11
sediment organic matter %	8.89	**0.0056**	0.2
sediment water content %	9.91	**0.0037**	0.22

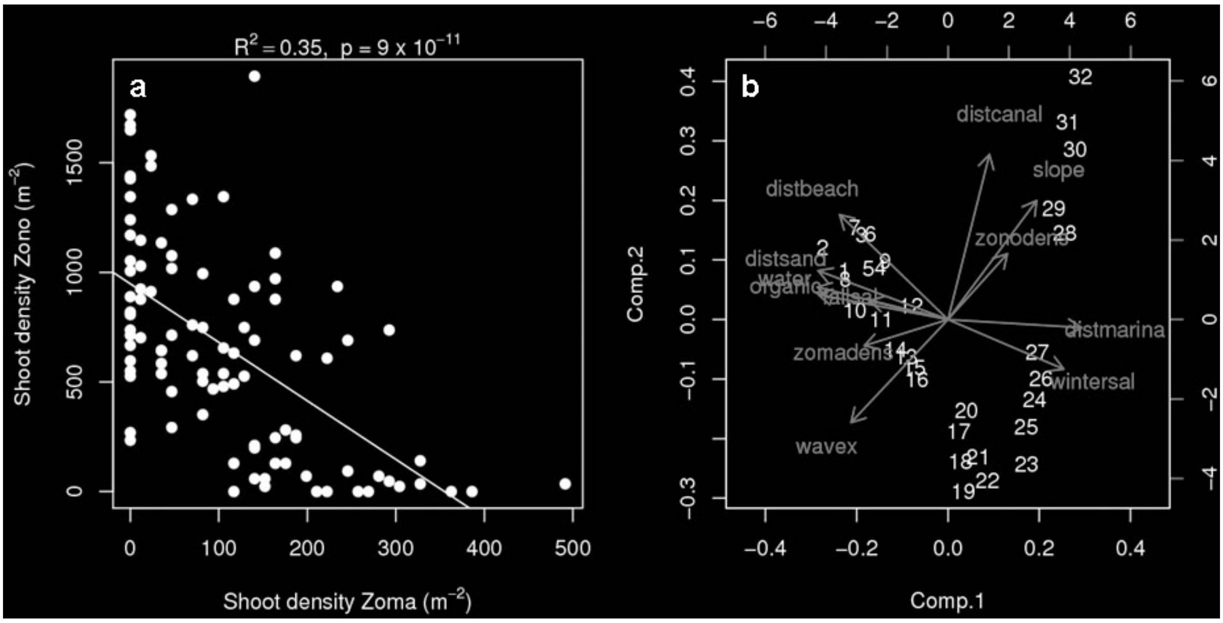

Fig. 4: (a) Scatterplot, regression line, and ANOVA results (*Z. marina* ***shoot density) for*** *Z. noltii* ***shoot density. (b) Standard biplot of the results of a principal components analysis (PCA) based on correlation among all variables. Legend: "dist" = distance, "sal" = salinity, "wavex" = wave exposure index, zoma =*** *Z. marina****, zono =*** *Z. noltii****, dens = shoot density, water = sediment water content, organic = sediment organic content.***
Sl. 4: (a) Razpršeni diagram, regresija in rezultati ANOVE (gostota šopov vrste *Z. marina****) za gostoto šopov vrste*** *Z. noltii****. (b) Standard biplot-grafikon rezultatov analize glavnih komponent (PCA) sloni na korelaciji spremenljivk. Legenda: "dist" = razdalja, "sal" = slanost, "wavex" = indeks izpostavljenosti valovom, zoma =*** *Z. marina****, zono =*** *Z. noltii****, dens = gostota šopov, water = vsebnost vode v sedimentu, organic = vsebnost organske mase.***

DISCUSSION

Both *Zostera* species were present and mostly co-occurred along the entire transect. There was no obvious spatial segregation, although *Z. noltii* was the species present over a larger linear distance than *Z. marina* and at a higher mean shoot density. The shoot densities of *Z. noltii* (range 0–1600 shoots/m^2) compare well with those found in mixed beds by Laugier *et al.* (1999) in a French Mediterranean lagoon (range 50–2,500 shoots/m^2), but were an order of magnitude lower than those found in a monospecific *Z. noltii* bed in a lagoon in southern Portugal (6,000–8,000 shoots/m^2; Cabaço *et. al.*, 2008). Similarly, *Z. marina* shoot density in the Novigrad Sea (range 0–333 shoots/m^2) was lower than described by Guidetti (2000) from monospecific *Z. marina* beds in the northwestern Adriatic (range 280–775 shoots/m^2), but compared well with shoot densities of *Z. marina* in mixed *Zostera* beds in a coastal lagoon in France (100–180 shoots/m^2; Laugier *et al.*, 1999).

Tab. 5: Results of a nested analyses of variance (Df = 11.84) of *Zostera noltii* ***shoot density with*** *Z. marina* ***shoot density included as one of the (otherwise physical environmental) predictor variables. Statistically significant results are highlighted (bold).***
Tab. 5: Rezultati vgnezdene analize variance (Df = 11,84) gostote šopov vrste *Zostera noltii****, kjer je gostota šopov vrste*** *Z. marina* ***vključena kot ena izmed (sicer fizično okoljskih) prediktorskih parametrov. Statistično značilni rezultati so poudarjeni (mastne črke).***

Predictor variables	***Z. noltii* shoot density**		
	estimate	**t**	**p**
Z. marina shoot density	-2.54	-5.44	**5.14x10^{-7}**
distance from marina	11.88	1.38	0.17
distance from sand bank	31.14	1.68	0.096
distance from beach area	-29.84	-1.11	0.27
distance from canal	6.28	0.33	0.74
wave exposure	-13817.4	-1.68	0.096
salinity 1	-101.45	-2.34	**0.022**
salinity 2	-166.78	-1.54	0.13
bottom slope	-20029.9	-0.71	0.48
sediment organic matter %	-161.31	-2.15	**0.034**
sediment water content %	3465.96	1.54	0.13

In agreement with the two species' description worldwide, *Z. marina* was the larger species, with longer and broader leaves, and thus a larger mean leaf area (*Z. noltii* : 480 mm^2, *Z. marina*: 1385 mm^2, $p = 8.2 \times 10^{-14}$), also indicating a larger biomass per shoot. Individually, physical variables such as salinity, wave exposure, and bottom slope explained none or only very little of the variation in shoot density of *Z. marina* (0–11%, Tab. 4) and *Z. noltii* (0–8%, Tab. 3), while sediment characteristics did so to a larger extent (*Z. marina*: 20–22%, *Z. noltii*: 6–8%, Tabs. 3 and 4). *Z. marina* was positively affected by finer sediments with higher organic and water content, while the opposite was true for *Z. noltii*. Caniglia *et al.* (1992) showed a similar distribution of *Z. marina* and *Z. noltii* in the Venice lagoon based on grain size; *Z. noltii* occurred on coarse textured sediment (sand), while *Z. marina* inhabited finer substrate with higher organic content.

Z. marina reached highest shoot density, and highest relative abundance near the marina. This is consistent with the hypothesis that the marina environment increased the competitive ability of *Z. marina* within the mixed *Zostera* bed. The taller *Z. marina* may have been the better competitor in a low light environment associated with frequent sediment re-suspension (muddier sediment, more frequent disturbance), conditions that could have resulted in what we observed: both species grew tallest shoots within and near the marina (data not shown). In contrast to *Z. marina*, *Z. noltii* shoot density was highest outside the marina where *Z. marina* was absent or very sparse. The strong negative correlation of the two *Zostera* species' shoot densities could be evidence for competition; they explained a higher percentage of variation than any other predictor variable tested, and had an effect with far higher statistical significance than any of the other physical variables in the multiple regression (Tab. 5). We conclude that *Z. noltii* beds of the Novigrad Sea are likely to be successfully invaded by *Z. marina* in areas where sediments have a higher organic and water content and/or experience more mechanical disturbance (wave exposure and more frequent anthropogenic traffic). Here *Z. marina* may be better suited to tolerate mechanical stress by means of deeper and larger rhizomes that are more likely to remain after a severe disturbance *(e.g.* anchoring) allowing for quick re-growth of new shoots. The occurrences of small monospecific *Z. marina* patches may be the direct result of such disturbances. *Z. noltii* appears to be the better competitor on coarser and less disturbed sediments, where its high shoot density may prevent the establishment of *Z. marina* shoots. Among species with a seasonal growth pattern, the smaller species are known to show faster increase in shoot density than larger species (Marba *et al.*, 1996). Our findings corroborate the description of *Z. noltii* as the species tolerating high and low energy environments and a broad range of salinities in the Adriatic (den Hartog, 1970). Our results, however, somewhat contradict the finding that *Z. marina* requires protected areas (Guidetti, 2000). Most relatively wave protected areas in Adriatic bays are actually under anthropogenic use, and experience boat traffic and residential drainage carrying organic particles and sediment, which combined result in lowered light attenuation that could then be the more direct cause of *Z. marina* being able to invade or even replace *Z. noltii*. Future research should address the mechanisms allowing coexistence of the two species on the scale of centimetres across the wide range of physical conditions observed in this study.

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DOKAZI O TEKMOVALNOSTI MED MORSKIMI TRAVAMI V LAGUNI SREDNJEGA JADRANA (HRVAŠKA)

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POVZETEK

Avtorji članka so na izobatnem transektu v Novigrajskem morju (Hrvaška, srednji Jadran) našli dokaze o tekmovalnosti med sobivajočima morskima travama Zostera noltii *in* Z. marina*. Transekt je vključeval razvita (marina) in nerazvita območja obrežnega pasu. Pokritost s posameznima vrstama morske trave je bila ugotovljena s podvodno videografijo DGPS, medtem ko je bila gostota poganjkov ocenjena na osnovi primerkov, ki so jih nabrali potapljači. Izkazalo se je, da se vrsti na okolje odzivata povsem drugače: medtem ko sta se pokrovnost in gostota šopov vrste* Z. marina *zmanjševali z razdaljo od marine, sta se pokrovnost in gostota šopov vrste* Z noltii *povečevali. Prostorsko razširjenost vrst je bilo mogoče v precej večji meri pojasniti z vzajemnim delovanjem in vplivanjem dveh vrst kot pa z okoljski parametri. Sklep avtorjev je bil, da je tekmovalnost med dvema vrstama poglavitni proces, ki določa razširjenost obeh vrst iz rodu* Zostera *v Novigrajskem morju.*

Ključne besede: *Zostera*, tekmovalnost med morskimi travami, okoljski parametri, DGPS-videografija, Jadran

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