RELATIONS OF MACROFAUNAL DIVERSITY WITH HABITAT DIVERSITY IN A CENTRAL CROATIAN ADRIATIC LAGOON

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ABSTRACT

The macrofauna of the shallow benthos (0–6 m) in the Novigrad Sea, the Central Croatian Adriatic, was censused in three seasons and over five habitat types at ten sites in 2007/8. The relative abundances of all animal taxa identified within the resulting fifty habitats x site combinations were subjected to a cluster analysis. There was a strong tendency for habitats to cluster together indicating that unique associations of fauna with their preferred habitat exist and that they are spatially stable. Sub-clustering within four of the main habitat types coincided with site variability in faunal richness and diversity. Regardless of clustering, habitat diversity explained 29% of faunal diversity across rock sites and 39% across sparse seagrass sites, while faunal abundance explained 46% of faunal diversity in rock habitats (positive correlation) and 32% at unconsolidated sediments (negative correlation).

Key words: habitat diversity, faunal diversity, visual census, GPS, videography, Adriatic Sea

RELAZIONE FRA DIVERSITÀ MACROFAUNISTICA E DIVERSITÀ DI HABITAT IN UNA LAGUNA CROATA NELL'ADRIATICO CENTRALE

SINTESI

La macrofauna bentonica di acque superficiali (0–6 m) nel mare antistante Novigrad, in Adriatico centrale, è stata campionata durante tre stagioni in cinque tipi di habitat e 10 siti di campionamento, fra il 2007 ed il 2008. Le abbondanze relative di tutti i taxa animali identificati all'interno delle 50 combinazioni habitat x sito, sono state sottoposte alla cluster analysis. I risultati evidenziano una forte tendenza degli habitat a raggrupparsi, il che indica una marcata relazione fra la fauna e l'habitat preferenziale, nonché la stabilità su scala spaziale. I sotto-raggruppamenti all'interno di quattro habitat principali coincidono con la variabilità dei siti in termini di ricchezza faunistica e diversità. A prescindere dalla cluster analysis, la diversità di habitat spiega il 29% della diversità faunistica in siti di fondo duro, e il 39% in siti con fanerogame marine sparse. L'abbondanza faunistica invece spiega il 46% della diversità faunistica in habitat rocciosi (correlazione positiva) ed il 32% su sedimenti non-consolidati (correlazione negativa).

Parole chiave: diversità di habitat, diversità faunistica, censimenti visivi, GPS, videografia, mare Adriatico

INTRODUCTION

Biodiversity is rapidly being lost in a world increasingly transformed by human activities and there is a need to understand the factors mediating species coexistence and local biodiversity. Shallow enclosed lagoons simultaneously provide nursery habitat for fish and invertebrates, but are especially vulnerable because they have limited exchange of water and fauna with the open sea and already experience natural stresses such as large annual salinity variations, which shape the unique fauna and habitats. Understanding the drivers of diversity permits predictions regarding the influence of anthropogenic activities. Environments with steep gradients in habitat characteristics allow for spatial niche segregation among species and species sorting by habitat (Mouillot, 2007). In such a situation faunal diversity depends primarily on the availability of niches, those directly related to habitat as well as resource niches indirectly related to habitat, such as trophic niches (Wilson, 1999). The total number of niches then is determined by habitat diversity, whose components are habitat heterogeneity and habitat complexity (Ziv, 1998; Guidetti & Bussotti, 2002). Habitat heterogeneity refers to the relative abundance of the various structural components within a habitat, and their variability, while complexity deals with the absolute abundance of the various structural components.

For example, the presence of seagrass at a location often has a positive effect on faunal diversity due both to its structural complexity (Hori et al., 2009) and its heterogeneity, which includes spatial variability in seagrass species, shoot density, and shoot morphology (Bell & Westoby, 1986a, b). Likewise, rock habitats are known to have high faunal diversity of cryptobenthic species such as Blennidae and Gobiidae, which increases with increasing complexity and heterogeneity (Macpherson & Zika, 1999; Gratwicke & Spreight, 2005; La Mesa et al., 2006; Lingo & Szedlmayer, 2006; Orlando-Bonaca & Lipej, 2007). Even sediments, lacking three dimensional complexity on a scale of macrofaunal body size, are nevertheless reported to support a more diverse macrofauna when heterogeneous in particle size (Hilbig & Blake, 2000; Jayaraj et al., 2008). This is because particle size influences physical variables, including water and organic matter content (Kruschel et al., 2009), oxygen concentration (Rosenberg et al., 2002), and sediment resuspension rates (Rutzler et al., 2000), which all influence the habitat choice of infauna and surface organisms (Alongi & Christofferson, 1992). Generally, increased habitat diversity (complexity and heterogeneity) is expected to increase the number of food resource niches, e.g. epifauna and epiphytes on seagrass (Sirota & Hovel, 2006) and rock (Consoli et al., 2008) or infauna (Sciberras et al., 2009) in heterogeneous sediments, thereby increasing faunal diversity through reduced

competition when diet overlap is low (Moreno-Rueda et al., 2009).

The shallow benthos of the Novigrad Sea is spatially heterogeneous. Fundamentally different habitats with three-dimensional structure (macroalgae, rock, seagrass) and unconsolidated sediments occur in a patchy mosaic at the scale of a few meters. If species sorting and niche availability were in fact the main drivers of faunal assembly and diversity in the Novigrad Sea lagoon, we would predict to observe (1) habitat specific faunal assemblages that are spatially stable (across sites), and that (2) site variability in faunal diversity for each of the basic habitat associated assemblages can be explained by the site variability in habitat diversity.

MATERIAL AND METHODS

Geographical location and sample locations

The Novigrad Sea, Croatia (44°12′N, 15°30′E) is a protected lagoon of 29 km^2 (approximately 8.5 km long) in the eastern Adriatic Sea. It is connected to the open Adriatic by the Velebit Channel via a narrow strait, the Maslenica Channel (Fig. 1). The study area is influenced by freshwater inflow from the Zrmanja River, a few small seasonal creeks, and a canal in the far western corner (Sinovčić et al., 2004; Matić-Skoko et al., 2007).
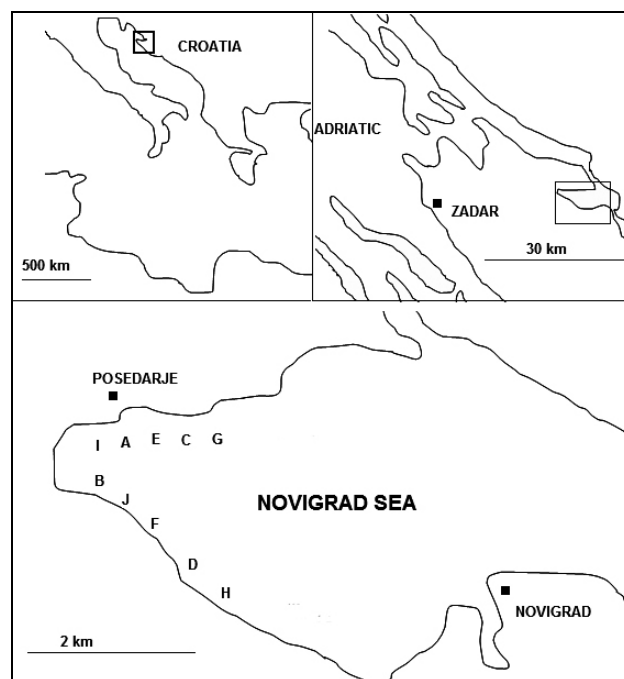

Fig. 1: Approximate location of the ten study sites (A–J) in the Novigrad Sea.
Sl. 1: Približne lokacije desetih obravnavanih območij (A–J) v Novigrajskem morju.

The total water volume is approximately 0.5 km^3 and reaches maximum depth of 35 m near the channel mouth. Tidal differences are 30 cm or less. Wave heights up to about 1 m occur under strong winds. The shallow benthic habitats (less than about 6 meters depth) include dense macroalgae/rock, unconsolidated sediments, and sparse to dense seagrass on mud, sand, or gravel. The seagrass is most expansive in the low gradient western portion near Posedarje (Schultz *et al.,* 2009). It was this area chosen for the study due to the presence of equal representation of each of the major benthic habitats of shallow protected waters of the Adriatic (seagrass, rock from pebble to bedrock, macroalgae, unconsolidated sand and gravel), all intermixed and neighboring each other on a small spatial scale along a shoreline several kilometers in length (Bakran-Petricioli *et al.,* 2006, Janeković *et al.,* 2006).

Ground cover/habitat distribution

Along visual census SCUBA transects a total of 5930 m of macroalgae (A), 5500 m of bare rock (R), 9300 m of dense seagrass (SD), 9400 m of sparse seagrass (SS), and 8400 m of bare, unconsolidated mud, sand or gravel (U) were encountered, with each category scored at a resolution of about 0.3 m. All seagrass vegetation occupied mud, sand or gravel. Algae (*Cystoseira* and a few unidentified brown and green algae), were attached to rocks of all sizes. For a detailed description of the structural heterogeneity within the five basic habitat categories see Table 1. While all five ground cover types were observed at all sampled depths, algae and rock dominated the shallowest sampling zone (0–2 m), bare unconsolidated ground the intermediate zone (1.5–3.5 m), and seagrass the deepest zone (2.5–5 m) (Fig. 2). Three parallel to the shore transects, one in each sampling zone, where investigated at ten study sites (A–J) that varied in the observed proportions of the five basic ground covers averaged across all three zones (Fig. 3).

Visual census transects

The abundance of macrofauna was censused along 2-m wide SCUBA belt transects (Nagelkerken *et al.,* 2000; Horinouchi *et al.,* 2005). Visual census allows quantification of habitat occupation by each individual

Tab. 1: Key to the identification of microhabitats within the basic habitats. Seagrass is identified by species and visual density (ground coverage proportion), unconsolidated sediments by grain size, algae by species and rock by size and cover. The sediment grain size and rock size categorization is a modified version of Larsonneur (1977) (in UNEP, 1998).

Tab. 1: Ključ za identifikacijo mikrohabitatov znotraj osnovnih habitatov. Habitat morske trave je določen z vrstami in vizualno ocenjeno gostoto (delež pokrovnosti tal), neutrjeni sedimenti z velikostjo delcev, alge z vrstami in skale z velikostjo in poraščenostjo. Kategorizacija velikosti delcev pri sedimentih in velikosti skal po prirejeni Larsonneur verziji (1977) (v UNEP, 1998).

seagrass (sparse, SS and dense, SD with matching ground coverage proportions: 0 – 1)			
N *Zostera noltii*		1 = SS	0 – 0.25
Z *Z. marina*		2 = SS	0.25 – 0.5
C *Cymodocea nodosa*		3 = SD	0.5 – <1
combinations, sequence = dominance		4 = SD	1
ZZ = either NZ or ZN (see Table 2)			
unconsolidated sediments		**algae**	
	1 = mud (< 50 μm)	A1	*Cysoseira* spp
	2 = sand (50 μm – 0.2 mm)	A$_{oth}$	other algae
	3 = sandgravel (0.2 – 2mm)		
U	4 = gravel (2 mm – 2cm)		
	5 = sand within rocks		
	6 = gravel within rocks		
D	sediment covered with dead seagrass		
H	human wastes		
bare rocks			
R	bare rock	1 = pebble (2cm - fist)	
RT	rock covered in algal turf	2 = cobble (fist - head)	
MR	rock covered in *Mythilus*	3 = rock (head - body)	
		4 = boulder (> body)	
		5 = bedrock	

Fig. 2: Relative abundance of the five basic habitats (U: unconsolidated sediments, SS: sparse seagrass, SD: dense seagrass, R: bare rocks, A: algae) across depth related zones (A/R: algae and rocks, U: unconsolidated sediments, SG: seagrass) in which macrofauna was visually censused along parallel transects (one per zone).
Sl. 2: Relativna številčnost petih osnovnih habitatov (U: neutrjeni sedimenti, SS: redka morska trava, SD: gosta morska trava, R: neporaščene skale, A: alge) po globinskih območjih (A/R: alge in skale, U: neutrjeni sedimenti, SG: morska trava), v katerih je bila makrofavna vizualno popisana vzdolž paralelnih transektov (eden na območje).
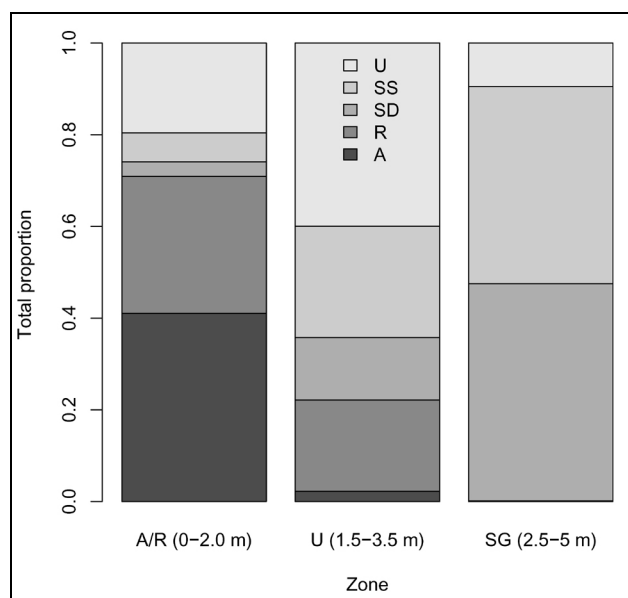

Fig. 3: Relative abundance of the five basic habitats (U: unconsolidated sediments, SS: sparse seagrass, SD: dense seagrass, R: bare rocks, A: algae) along long transects within sites (A–J).
Sl. 3: Relativna številčnost petih osnovnih habitatov (U: neutrjeni sedimenti, SS: redka morska trava, SD: gosta morska trava, R: neporaščene skale, A: alge) vzdolž dolgih transektov znotraj območij (A–J).

animal, at all substrates and on a small scale (body size; Lipej & Orlando-Bonaca, 2006). This is not possible for other popular methods such as trawl or seine net sampling (Gray *et al.*, 1998; Hindell & Jenkins, 2005; Horinouchi *et al.*, 2005). Macrofauna observed comprised all fish species and all invertebrates large enough to be detectable by naked eye and without physically disturbing the habitat. All individuals of all taxa were recorded but for the presented analyses, observational units called "groups" were used, defined as spatial clusters of 1 or more individuals of the same species observed at the same moment. For statistical tests, the appropriate unit of replication is probably the group, since individuals within a group are not independent observations, and ninety-eight percent of all groups observed comprised 10 or less individuals. Transects were followed at a speed of approximately 0.3 m/sec during the day and 0.15 m/sec during the night. Transect length ranged from 160 m to 360 m.

DGPS/videography

During the daytime sampling, the diver carried a video sensor (Sony, 480 color TVL) that continuously recorded the sea bottom. Simultaneously overlaid on the video image was satellite time recorded every two seconds. Depth was recorded by a 200 KHz, 11.208, single-beam transducer. Horizontal DGPS coordinates (2006 Trimble Pro XRS) 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; Dauwalter *et al.*, 2006; Schultz, 2008). The night dives followed the same transects as the day dives usually within 24 hours, by submeter real-time navigation over the DGPS tracks of that day's dive transects. This had the advantage of not using underwater survey markers or tape measures which have been observed to attract fish. The proportion of each microhabitat, defined as subhabitats within the five basic habitats: rock (R), algae (A), dense seagrass (SD), sparse seagrass (SS), and unconsolidated sediments (U), occupying the transect, was

measured by analysis of the video (for microhabitat identification key see Table 1). Each second of the video was identified as representing one of these microhabitats, and then the linear extent of transect occupied by each of the microhabitats was calculated from the associated DGPS positions (Schultz, 2008). One second of video represents approximately 0.3 m of transects.

Calculation of fauna and habitat related variables

Total abundance of a faunal species was defined as the number of observational units or groups encountered per meter of visual census transect. Relative abundance of a species within a site/habitat combination was equal to the absolute abundance in that combination divided by the total abundance of all species within that combination. Faunal diversity was calculated as the Simpson's reciprocal index, equal to the multiplicative inverse of the probability that two random groups of fauna are the same species. This we refer to as the "effective" number of species or the number of species in the site/habitat if all species were equally abundant, given the observed probability that two random groups are the same species. Habitat diversity – again as Simpson's reciprocal index, in this case the reciprocal of the probability that two random seconds of transect video showed the same bottom microhabitat. This is referred to in the text as the "expected" number of microhabitat types for a site/habitat combination. Total microhabitat abundance was equal to the number of video seconds showing a particular microhabitat type within a transect. Relative microhabitat abundance within a given site/habitat was equal to its absolute abundance divided by the total number of seconds in the transect video.

Data analysis

All confirmatory statistical tests were conducted within general linear models, including unequal variance *t*-tests, single-factor ANOVA and linear regression, after checking for normality and homoscedasticity.

RESULTS

As reported in a previous publication (Schultz *et al.,* 2009), over a total dive transect length of 39 km accomplished in 60 hours of diving, 61,713 animals have been observed: 54,043 fish belonging to 39 taxa and 7670 invertebrates belonging to 46 taxa. Individuals have been recorded in 10,359 observational fish groups and 4,309 observational groups of invertebrates. The total faunal density was 1.6 animals per transect meter (1.4 fish and 0.20 invertebrates), or 0.38 observational units per transect meter (0.27 fish and 0.11 invertebrate).

Habitat specific faunal assemblages

The cluster analyses of the site specific relative abundances of faunal taxa observed in each of the site/habitats revealed seven main significant clusters (Fig. 4), with each cluster representing one of the five basic habitats, including: sparse seagrass (SS, cluster 5), dense seagrass (SD, clusters 1 and 6), rock (R, clusters 2 and 3), unconsolidated sediments (U, cluster 4), and algae (A, cluster 7). For each of the seven main clusters Table 2 gives information on total faunal and microhabitat richness and taxon dominance and indicates in which of the five basic habitats (A, R, SS, SD, U) taxa reach their highest relative abundance. The number of dominant taxa (comprising 90% of the total faunal abundance) within each main cluster positively correlated with sub-cluster habitat richness (Tab. 2). Faunal richness and habitat richness was highest at bare sediment (cluster 4), in sparse seagrass (cluster 5), and in dense seagrass (cluster 6). Taxa comprising 90% of the total faunal abundance in the sparse seagrass (cluster 5) and in the rock habitat (cluster 3) were most even in their relative abundances, whereas the faunal assemblage at bare sediments was dominated by *Gobius niger* and gobiid juveniles, comprising more than 50% of the total faunal abundance (Tab. 2).

Rock habitat (clusters 2 and 3)

Gobiids *(Gobius cobitis* (Goco), *G. paganellus* (Gopa), *G. cruentatus* (Gocr), and *G. bucchichii* (Gobu) reached their highest relative abundance in the rock habitat and several blennids *(Parablennius sanguinolentus, P. incognitos, P. gattorugine* (Paga), *Lipophrys dalmatinus,* and *L. pavo),* and *Serranus scriba* was found there exclusively. Invertebrates found solely on rocks were the squad lobsters of the genus *Galathea,* the crab *Eriphia verrucosa,* the urchin *Paracentrotus lividus,* and oysters (Ostreidae). The shrimp *Palaemon elegans* (Pael) had its highest relative abundance here, while labrids *(Symphodus ocellatus* (Syoc) and *S. roissali* (Syroi)) were very common, yet had an even higher relative abundance in algal vegetation.

Algae habitat (cluster 7)

The algal vegetation assemblage is characterized by two species of labrids *S. ocellatus* (Syoc) and *S. roissali* (Syroi), and the shrimp *P. elegans* (Pael) all of which also associate with rocks. Algal assemblages of different locations vary primarily in the relative abundances of these labrids and shrimp: as labrids increase the shrimp decreases and vice versa. Like the two labrids, *Atherina* spp. (Ath) reaches its highest abundance in the algal habitat where at night individuals or small groups hover in canopy gaps within stands of large *Cystoseira* individuals.

Tab. 2: Comparison of the main site/habitat clusters (Fig. 4) by relative abundance of common taxa (comprising 90% of the total abundance) and total faunal richness (above) and by relative abundance of microhabitats and microhabitat richness. For microhabitat identification refers to Table 1. Highlighted abbreviations for common animal taxa (see text for full species names) indicate in which habitat taxa reached their peak relative abundance.

Tab. 2: Primerjava glavnih skupin območje/habitat (Sl. 4) z relativno številčnostjo glavnih vrst (90% celotne številčnosti) in celotnega bogastva favne (zgoraj) ter z relativno številčnostjo mikrohabitatov in bogastva mikrohabitatov. Za identifikacijo mikrohabitatov glej Tabelo 1. Poudarjene okrajšave za glavne živalske vrste (glej besedilo za polno ime vrste) označujejo habitat, v katerem je vrsta dosegla največjo relativno številčnost.

SD (dense seagrass)				R (rocks)				U (sediments)		SS (sparse seagrass)		A (algae)	
Cluster 1	prop.	Cluster 6	prop.	Cluster 2	prop.	Cluster 3	prop.	Cluster 4	prop.	Cluster 5	prop.	Cluster 7	prop.
relative faunal abundances													
Psmi	0.529	Ath	0.240	**Pael**	0.341	Goni	0.120	**Goni**	0.337	Goni	0.190	**Ath**	0.360
Zoop	0.090	Psmi	0.171	Goni	0.138	**Gobu**	0.119	**Gojuv**	0.166	Zoop	0.114	**Syoc**	0.198
Ath	0.072	**Zoop**	0.131	Gojuv	0.114	**Goco**	0.113	Ath	0.140	Ath	0.111	**Syroi**	0.162
Pael	0.050	Pael	0.085	Ath	0.071	Ath	0.112	Pagurus	0.063	**Brachyura**	0.106	Pael	0.147
Ansu	0.045	**Ansu**	0.062	Brachyura	0.066	Pael	0.111	Pael	0.045	*Pagurus*	0.100	Brachyura	0.036
Hetr	0.038	Brachyura	0.059	Zoop	0.066	Syroi	0.090	Brachyura	0.044	Gojuv	0.068		
Brachyura	0.034	Goni	0.053	Syoc	0.048	**Gocr**	0.089	**juv2**	0.022	Pael	0.063		
Pagurus	0.032	*Pagurus*	0.035	**Paga**	0.048	Syoc	0.073	Gobu	0.021	**Hetr**	0.044		
		Anan	0.028			Brachyura	0.052	Syroi	0.017	Ansu	0.024		
		Syoc	0.028			**Gopa**	0.033	Syoc	0.015	Psmi	0.024		
								Goco	0.013	Syoc	0.016		
								Hetr	0.010	Gobu	0.011		
								Gocr	0.008	Syroi	0.010		
								juv1	0.008	juv2	0.009		
+ 19 taxa	0.099	+ 43 taxa	0.108	+ 4 taxa	0.110	+ 28 taxa	0.087	+ 45 taxa	0.091	+ 43 taxa	0.108	+ 28 taxa	0.097
relative habitat abundances													
ZZ3	0.584	ZZ3	0.386	R1	0.440	R2	0.428	U2	0.244	N2	0.353	A1	0.993
N3	0.196	N3	0.245	R2	0.425	RT3	0.221	U3	0.208	ZZ2	0.175	Aoth	0.007
C3	0.168	C2	0.099	R3	0.108	R3	0.165	D	0.111	N1	0.137		
ZZ4	0.052	ZZ4	0.070	RT2	0.022	R1	0.076	U5	0.107	R2	0.104		
		N2	0.048	RT3	0.006	RT4	0.054	U4	0.093	C2	0.078		
		N4	0.042			RT2	0.045	R2	0.063	R1	0.067		
		C3	0.034			R4	0.005	R1	0.060	Z2	0.022		
		ZZ2	0.023			MR4	0.003	U6	0.050	ZZ1	0.018		
		Z2	0.022			MR3	0.001	R3	0.020	Z1	0.011		
		N1	0.016			R5	0.001	RT3	0.020	RT2	0.009		
		Z1	0.008					RT2	0.006	RT3	0.006		
		C1	0.006					RT5	0.005	RT1	0.006		
		ZZ1	0.001										
								+ 6 habitats	0.013	+ 3 habitats	0.010		

Unconsolidated sediment habitat (cluster 4)

Common inhabitants on bare sand/gravel near the rocks in shallow water are the goby *Gobius niger* (Goni) and hermit crabs of the genus *Pagurus*. Common inhabitants on bare sand/gravel near the lower limits of the *Cymodocea nodosa* beds in deeper water include the bivalve *Pecten jacobeus*, the gastropod *Hexaplex trunculus* (Hetr), and the fish *Symphodus cinereus*. Taxa common in more expansive areas of bare sand/gravel include small gobiids, mainly *Pomatoschistus* spp., juveniles of *G. niger* (Gojuv), and bentho-pelagic juvenile fish with schooling behavior (juv1 and juv2).

Sparse seagrass (cluster 5)

Species frequently observed in sparse seagrass are associated either with shallower *Zostera* beds (*Zosterissessor ophiocephalus* (Zoop) and *Anemonia viridis* (Anvi)) or deeper *Cymodocea* beds and the adjacent deep unvegetated sediments *(H. trunculus* (Hetr), *P. jacobaeus, S. cinereus, Spicara smaris)*.
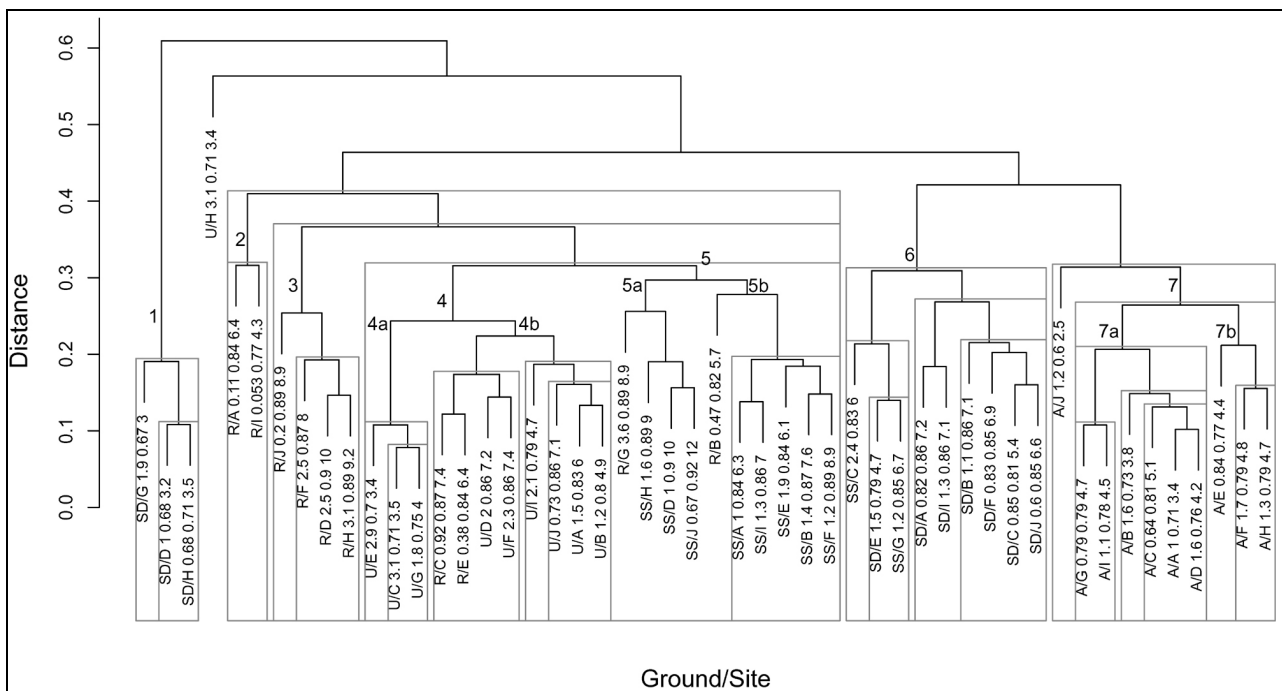
Fig. 4: Dendrogram of site/habitat combinations based on taxa abundance per linear transect meter relative to the total within each of the five substrates, all sampling times (diel, seasonal) and all sites (A–J) pooled. Significant clusters (multiscale bootstrap resampling probability >0.95) are enclosed in rectangles. Main subclusters representing one of the five basic habitats (see Fig. 3) are numbered. Primary subclusters within main habitat clusters are indicated with the letters "a" and "b" in addition to the cluster number. Total faunal abundance (1st value) and diversity indices (probability, 2nd value, and effective number of taxa, 3rd value) were displayed along with the name of each of the fifty site/habitat combinations.

Sl. 4: Dendrogram kombinacij območje/habitat na podlagi številčnosti taksonov na meter linearnega transekta glede na celoto znotraj vsakega od petih substratov, vseh časov vzorčenja (dnevnih, sezonskih) in vseh območij vzorčenja (A–J). Statistično značilne skupine** (multiscale bootstrap resampling **verjetnost >0,95) so označene z okviri. Glavne podskupine, ki predstavljajo enega od petih glavnih habitatov (glej Sl. 3), so oštevilčene. Glavne podskupine znotraj glavnih habitatnih skupin so označene s črkami "a" in "b" poleg številke skupine. Celotna številčnost (1. vrednost) in diverzitetni indeks (verjetnost, 2. vrednost, in dejansko število taksononv, 3. vrednost) so pripisani imenu vsake od petdesetih kombinacij območje/habitat.

Dense seagrass (clusters 1 and 6)

The dense seagrass assemblage is characterized by the highest relative abundances of two invertebrates, the snakelock anemone *A. viridis* (Anvi) and the green urchin *Psammechinus microtuberculatus* (Psmi), although the abundance of the urchin is seasonal (highest in winter) and patchy (see Fig. 3, cluster 1 is separated from all others on the basis of high relative "Psmi" abundance). Likewise *A. viridis* (Anvi) have been observed to increase temporarily in spring when they cover seagrass blades in dense patches. Fish taxa reaching their peak abundance in dense seagrass are two seagrass resident predators, the European eel, *Anguilla anguilla* (Anan), and the grass goby, *Z. ophiocephalus* (Zoop). Although the labrid *S. cinereus* prefers deeper sparse *Cymodocea* and adjacent sediments for foraging, nests of this species

(identified by the presence of a territorial male) are associated with dense seagrass. While *Atherina* spp. (Ath) frequently and quickly passes in schools over all habitats during the day with little preference, it noticeably seeks out dense seagrass at night, hovering in small groups or individually at a distance above the canopy.

Site variability in habitat specific faunal richness, diversity, and abundance

Rock habitat (clusters 2 and 3)

The two main rock assemblages (clusters 2 and 3) were markedly different in taxon richness (12 *vs.* 38 taxa) (Tab. 3), yet the likewise large difference in mean diversity (*e.g.*, 5.4 *vs.* 9 effective taxa) was not quite significant (Tab. 3), while mean faunal abundance was sig-

Tab. 3: Summary of the comparisons of mean site diversity and mean total site abundance within sub-clusters of basic habitats, with t test results given in columns 4–7. In addition sub-cluster richness (column 3), sub-cluster relative proportion of main habitats (column 8), and microhabitat heterogeneity indicators and their relative abundance for each sub-cluster are listed (column 9).

Tab. 3: Povzetek primerjave povprečne diverzitete območja in povprečne številčnosti celotnega območja znotraj podskupin osnovnih habitatov, pri čemer so rezultati t testa zapisani v stolpcih 4–7. Dodane so vrednosti za bogastvo podskupin (3. stolpec), za relativni delež glavnih habitatov po podskupinah (8. stolpec) in indikatorji mikrohabitatne heterogenosti ter njihova relativna številčnost za vsako podskupino (9. stolpec).

habitat	Cluster (richness)	site specific variables	mean	df	t value	p	site habitat proportions	heterogeneity	prop
dense seagrass	1 (27)	Index probability	3.233333 0.687	10 4.146	-9.8011 -10.4844	1.910e-06 0.0003877	0.05 – 0.15	*Z. noltii* *Z. marina/C. nodosa*	0.613 0.386
		abundance	1.193333	2.938	-0.0193	0.9858	mean 0.09	very dense seagrass	0.015
	6 (53)	Index probability abundance	6.411111 0.840 1.201111				0.7 – 0.36 mean 0.22	*Z. noltii* *Z. marina/C. nodosa* very dense seagrass	0.856 0.14 0.144
rocky groundcover	2 (12)	Index probability abundance	5.350 0.8050 0.0815	1.323 1.065 3.012	-3.257 -2.32 -3.1079	0.1389 0.2467 0.05269	0.14 – 0.22 mean 0.18	pebbles/cobbles turf covered boulders	0.886 0.027 none
	3 (38)	Index probability abundance	9.025 0.8875 2.0750				0.18 – 0.35 mean 0.23	pebbles/cobbles turf covered boulders	0.550 0.320 0.062
unconsolidated sediments	4a (44)	Index probability abundance	3.633333 0.72000 2.60000	8.933 4.116 2.003	-6.404 -6.3876 4.3565	0.0001289 0.002796 0.04874	0.24 – 0.39 mean 0.31	gravel within rocks dead seagrass	0.255 0.258 0.006
	4b (47)	Index probability abundance	6.387500 0.83875 0.83875				0.08 – 0.27 mean 0.19	gravel within rocks dead seagrass	0.235 0.159 0.201
sparse seagrass	5a (41)	Index probability abundance	9.975000 0.9000000 1.717500	5.608 7.911 3.523	3.516 3.7551 0.7395	0.01406 0.005697 0.5058	0.19 – 0.28 mean 0.23	*Z. noltii* *Z. marina* *C. nodosa*	0.636 0.220 0.144
	5b (50)	Index probability abundance	6.933333 0.8533333 1.211667				0.18 – 0.33 mean 0.25	*Z. noltii* *Z. marina* *C. nodosa*	0.898 0.042 0.060
algae	7a (29)	Index probability abundance	4.283333 0.7483333 1.121667	6.669 6.79 3.849	1.2528 2.1152 0.531	0.2524 0.07345 0.6245	0.10 – 0.31 mean 0.18	*Cystoseira* spp.	0.988
	7b (30)	Index probability abundance	4.633333 0.8066667 1.280000				0.16 – 0.20 mean 0.18	*Cystoseira* spp.	1.000

nificantly higher for sites in cluster 3. Habitat composition differed in the two groups of rock sites: cluster 2 sites were dominated by pebbles and cobble sized rocks (89%) and lacked boulders, while sites in cluster 3 were to 45% occupied by rocks larger than pebbles and cobbles, of which 6% were boulders (Tab. 3). Also a higher proportion of rocks in cluster 3 sites were covered in turf algae and *Mytilus* than in cluster 2-sites (turf: 32% *vs.* 3%, *Mytilus:* 0.4% *vs.* none) Considering all rock sites, regardless of their cluster position, 29% of the variation among sites in faunal diversity was explained by rock diversity (Fig. 5, Tab. 4). Rock faunal abundance was positively correlated with faunal diversity and explained 46% of its variance (Tab. 4).

Unconsolidated sediment habitat (sub-clusters 4a and b)

The two main unconsolidated sediment assemblages differed significantly in faunal diversity (Tab. 3), yet they had equal taxon richness (44 and 47). Sites in cluster 4a had a significantly higher mean faunal abundance, primarily due to the high abundance of *Gobius niger* and juvenile gobiids (1.25 and 0.4 per transect meter), comprising 64% of the total faunal abundance. Sediments in 4a-sites did not differ as much in grain size from sediments in 4b-sites (26% *vs.* 24% coarse sand and gravel) as in spatial relation to neighboring habitats (rock *vs.* seagrass) (Tab. 3). More of the unconsolidated sediment in 4a-sites than in 4b-sites comprised small patches

Tab. 4: Site faunal diversity as a function of a site's habitat diversity in the rock and sparse seagrass habitat. For each habitat 12 microhabitat types were defined (for details see Table 1) and quantified in DGPS assisted videos of the benthos. Significance of correlation is indicated by p values which are given along with r^2 values.
Tab. 4: Favnistična diverziteta območja kot funkcija habitatne diverzitete območja za habitat skal in habitat redke morske trave. Za vsak habitat smo določili 12 mikrohabitatnih tipov (za podrobnosti glej Tabelo 1) in jih količinsko opredelili z DGPS video meritvijo dna. Značilnost korelacije je podana v vrednosti p in r^2.

	df	t value	p value	F	r^2 value
Response: faunal diversity rocky habitat (R)					
habitat diversity	8	1.395	0.0612	4.736	0.2934
faunal abundance	8	2.924	0.0192	8.549	0.4562
Response: faunal diversity sparse seagrass habitat (SS)					
habitat diversity	8	2.620	0.0307	6.862	0.3944
Response: faunal diversity unconsolidated sediment habitat (U)					
faunal abundance	8	-2.277	0.05232	5.184	0.3174
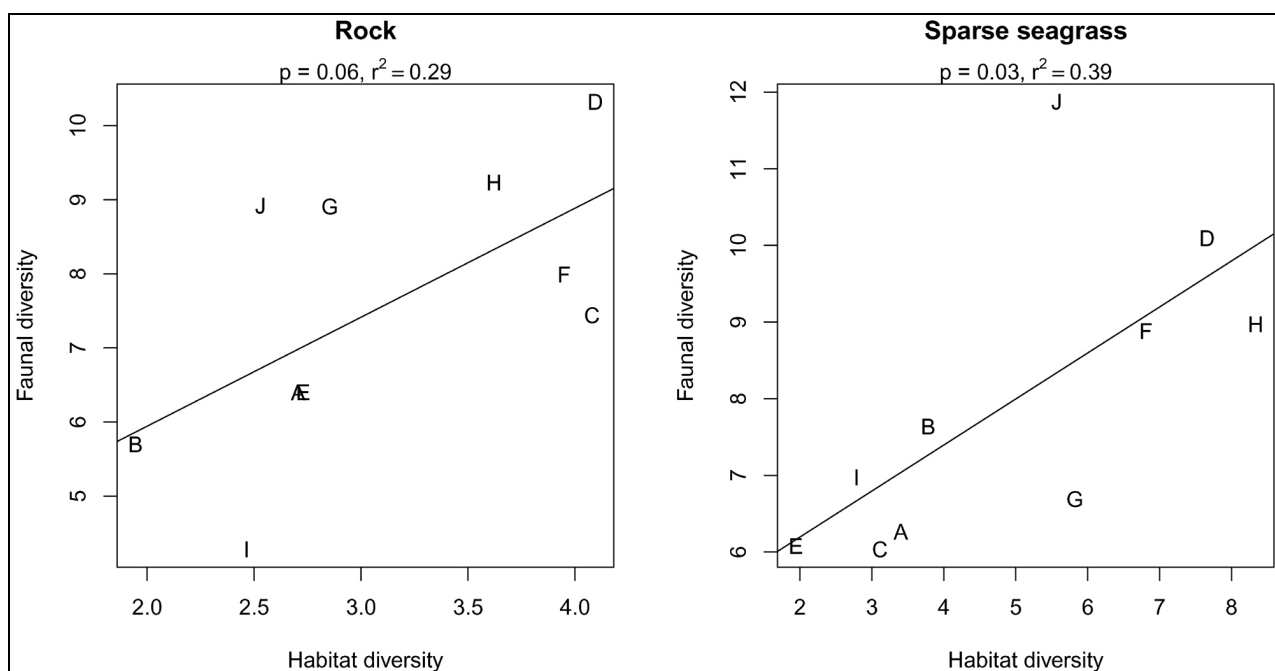
Fig. 5: Site/habitat taxon diversities (effective number of taxa) for the rock (right) and sparse seagrass (left) habitat as a function of a site's habitat diversity (effective number of microhabitats). Each of the 10 sites is represented by a letter (A–J). For site location see Fig. 1, for microhabitat categorization within basic habitats refers to Table 1. Microhabitats were quantified for each second (0.3 m) in DGPS assisted videos of the benthos. Significance of cor-relation is indicated by p values given along with r^2 values on top of each figure (for details of the ANOVA results see Table 4).
Sl. 5: Vrstna diverziteta za območje/habitat (dejansko število vrst) za habitat skal (desno) in redke morske trave (levo) kot funkcija habitatne diverzitete za posamezno območje (dejansko število mikrohabitatov). Vsako od 10 območij je označeno s črko (A–J). Za lokacijo območja glej Sl. 1, za kategorizacijo mikrohabitata znotraj osnovnih habitatov glej Tabelo 1. Mikrohabitati so bili količinsko opredeljeni za vsako sekundo (0,3 m) v DGPS video meritvi dna. Značilnost korelacije je podana v vrednosti p in r^2 na vrhu vsakega grafa (za podrobnosti ANOVA rezultatov glej Tabelo 4).

among rocks (26% *vs.* 16%) while less sediment in 4a-sites than in 4b-sites was covered in dead seagrass (0.6% *vs.* 20%) (Tab. 3). Considering all sediment sites, regardless of their cluster location, faunal abundance is negatively correlated with faunal diversity and explains 32% of its variation (Tab. 4).

Sparse seagrass (sub-cluster 5a and b)

The two main sparse seagrass assemblages (sub-clusters 5a and b) significantly differed in faunal diversity (Tab. 3) which coincided with marked differences in the sparse seagrass habitat composition. Sparse seagrass in 5b-sites was to 90% comprised of *Zostera noltii*, the seagrass occupying the shallower benthos (0–2.5 m), while sites clustered in 5a had significantly higher proportions of other seagrass species than 5b-sites: deep (4.5–6m) sparse *Cymodocea* (2.5 times higher) and sparse *Z. marina* (4 times higher) (Tab. 3). Considering all sparse seagrass sites, regardless of their association with cluster, site variability in sparse seagrass habitat diversity was significantly correlated with and explained 29% of the site variability in faunal diversity (Fig. 5, Tab. 4).

Dense seagrass (clusters 1 and 6)

The two main dense seagrass assemblages (clusters 1 and 6) significantly differed in faunal diversity (Tab. 3) and in faunal richness (27 *vs.* 53), which coincided with marked differences in the dense seagrass site coverage (9% *vs.* 22%), density, and relative abundance of seagrass species. Sites in cluster 6 were dominated by *Z. noltii* (86%) and had a higher proportion of very dense seagrass (per transect meter coverage =1) than cluster 1-sites (14% *vs.* 1.5%) (Tab. 3).

Algae (clusters 7a and b)

The sites of the two main algal clusters did not significantly differ in faunal diversity, faunal abundance, or algal habitat diversity (Tab. 3).

DISCUSSION

The study area indeed comprised habitat specific faunal assemblages (Fig. 4). Each of the five basic habitats, algae (A), rock (R), sparse (SS) and dense (SD) seagrass and unconsolidated sediment (U) were clearly dominated by a different set of taxa *(e.g.,* labrids in the algae, four associated gobies in the rocky habitat, *Psammechinus tubercularis* (Psmi) and *Zosterisessor ophiocephalus* (Zoop) in seagrass, and juvenile fish (gobiids and various unidentified) at bare sediments (Tab. 2). Also, all habitats were home for a number of exclusive taxa, *e.g., Anguilla anguilla* (Anan) in seagrass, various blennids and invertebrate species in the rock habi-

tat, and mollusks such as *Pecten jacobeaus* and *Hexaplex trunculus* (Hetr) in sparse *Cymodocea nodosa* and adjacent sediments. These findings are in agreement with habitat preferences calculated by Schultz *et al.* (2009) for the Novigrad Sea shallow benthos taxa. The observed habitat specific faunal assemblages were spatially stable; taxa did not exhibit different habitat associations at different sites. However, the diversity of the basic assemblages did vary among sites (Tab. 3), which was correlated with microhabitat diversity which to some extent was correlated with site variability in faunal abundance (positive in the rock habitat, negative at bare sediments). Within the Novigrad Sea rock habitat, rock size variability and the coverage with ratio of bare rocks versus rocks covered with turf and mussels may be the most important microhabitat descriptors in explaining faunal diversity variability. In sparse seagrass the most important factor may be seagrass species diversity, which in the Novigrad Sea is linked to depth. In dense seagrass patches site area coverage and density may be most important, while at bare sediments the influence of neighboring habitats (rock *vs.* seagrass) rather than grain size coincided with differences in faunal diversity. Faunal diversity has been reported to positively respond to a variety of rock characteristics, including: rugosity (Luckhurst & Luckhurst, 1978), turf coverage (Feireirra *et al.*, 2001), coverage with habitat engineering sessile animals, *e.g.* mussels (Feireirra *et al.*, 2001; Buschbaum *et al.*, 2008), vertical relief (Gratwicke & Spreight, 2005), and interstitial space variety (Schmude *et al.*, 1998). For the Mediterranean Sea positive relationships between rock habitat diversity and faunal diversity have been found for blennioids by Macpherson & Zika (1999) and for blennioids and other cryptobenthic fish by Patzner (1999). Blennioid diversity has been investigated in greater detail in shallow Adriatic habitats by Orlando-Bonaca & Lipej (2007) who discovered that among other microhabitat descriptors the presence/absence of turf algae and sessile invertebrates, rock size, and the precise position at boulders, all resulted in blenny assemblage variability. A study including a variety of families of rock resident crypto-benthic fish concluded that habitat choice was almost entirely based on whether rocks were covered in vegetation or bare (La Mesa *et al.*, 2006). Letourneur *et al.* (2003) found for the north-western Mediterranean that rock cover *per se* and within the rock habitat variability in rock size were most powerful in explaining fish distribution. Garcia-Charton & Ruzafa (1998, 2001) reported from the south-western Mediterranean a positive relation between habitat complexity and fish richness and abundance, with the size variability of boulders, especially the number of large boulders having the largest positive effect on richness and abundance, and Consoli *et al.* (2008) compared three rocky shores exhibiting significant differences in rock habitat complexity in the central Mediterranean where the most

complex habitat harbored the most abundant fish fauna most likely as a result of increased spatial and trophic niches.

The presence of three seagrass species as well as their high shoot densities in the Novigrad Sea is unique compared to nearby embayments less separated from the open Adriatic and less influenced by fresh water (Stiefel, 2009). Seagrass adapted search-and-attack and ambush predators, such as *A. anguilla* and *Z. ophiocephalus* benefit from this situation (Schultz *et al.*, 2009), as well as the green urchin which comprises >50% of the faunal abundance in sites with high *Zostera marina* proportions (Tab. 2). In the Novigrad Sea such elevated proportions of *Z. marina* are a sign of disturbance (Kruschel *et al.*, 2009), which may come along with taxon dominance and reduced faunal diversity (Neira *et al.*, 2007). In the Novigrad Sea the distribution of seagrass species is depth dependent and shallow *Zostera* seagrass beds support a different fauna from deep *Cymodocea* beds (Schultz *et al.*, 2009).

Two possible reasons for the observed differences in faunal diversity are that (1) deeper seagrass seems to attract a variety of invertebrates absent from shallower waters, and (2) *Zostera* beds are avoided by fish taxa such as labrids and gobiids in favor of algal and sediment habitats because of the higher risk of predation posed by the *Zostera* resident predators *A. anguilla* and *Z. ophiocephalus* (Kruschel & Schultz, 2010; Schultz & Kruschel, 2010). Algal-associated labrids such as *Symphodus ocellatus* (Syoc) and *S. cinereus* as well as the sediment-associated *Gobius niger* (Goni) are known to prefer seagrass in other locations (Wiederholm, 1987; Guidetti, 2000, 2002; Stiefel, 2009). Diversity differences in the unconsolidated sediment fauna are primarily driven by evenness rather than species richness, as the relative abundance of the most common species *G. niger* (adults and juveniles) tends to peak in abundance on sediments near rock rather than near seagrass. This distribution may be a response to the risk of predation by and/or to spatial competition with the larger and more successful predator *Z. ophiocephalus* as has been demonstrated in field and tank experiments by Schultz & Kruschel (2010) and Kruschel & Schultz (2010). Similar cases of competition- and predation-driven niche partitioning among gobiid species has been reported else-

where (Wiederholm, 1987; Schofield, 2003; Malavasi *et al.*, 2005).

CONCLUSIONS

In agreement with our prediction, the Novigrad Sea contains habitat-specific faunal assemblages, and the microhabitat diversity within four of the five basic habitats coincides with site differences in diversity of the associated faunal assemblages. Yet, only in the rock habitat may species diversity be directly linked to microhabitat niche availability. In the seagrass habitat, negative interactions between seagrass resident predators and their potential prey, and depth-related differences in seagrass microhabitat composition may be responsible for the species sorting. Similarly, taxon diversity differences among sediment sites may be a result of species competition (Gobidae) and/or avoidance of predation in the potentially available neighboring seagrass habitat (Gobiidae and juvenile fish). Overall faunal diversity in the Novigrad Sea seems to be driven by habitat diversity, either through increased availability of spatial and resource niches or through facilitation of spatial avoidance of competitors or predators.

Protection of faunal diversity in the Novigrad Sea should therefore focus on maintenance of the mosaic-like distribution of the five basic habitats and their microhabitats. The loss of the rocky-algal habitat would likely result in a greater reduction in biodiversity than the loss of other habitats, as through shoreline development, especially the conversion of the natural sublittoral habitat to concrete seawall. The loss of deep *Cymodocea nodosa* would also result in the loss of unique biodiversity, as it comprises a unique invertebrate fauna and does not support resident predators such as *Zosterisessor ophiocephalus* or *Anguilla anguilla*. *C. nodosa* in the Novigrad Sea is threatened by competition with *Zostera* species, which are stimulated by anthropogenic disturbance (Kruschel *et al.*, 2009), and is most sensitive to increased turbidity due to its restriction to deeper areas. The loss of shallow water sediment patches, the preferred habitat of a variety of juvenile fish, *e.g.*, through *Zostera* expansion, would likely cause a reduction in the nursery function of the Novigrad Sea, leading eventually to a reduction of fish diversity and abundance.

RAZMERJA MED PESTROSTJO VRST MAKROFAVNE IN PESTROSTJO HABITATOV V LAGUNI V OSREDNJEM HRVAŠKEM JADRANU

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POVZETEK

Popis bentoške makrofavne plitvih predelov (0–6 m) Novigrajskega morja v osrednjem hrvaškem Jadranu je bil izveden v treh letnih časih 2007/08 in v okviru petih habitatnih tipov na desetih območjih. Relativno številčnost vseh identificiranih živalskih vrst v okviru petdesetih habitat x lokacija kombinacij smo obravnavali s klastersko analizo. Pokazala se je močna tendenca grupiranja habitatov, kar kaže na izredno povezanost favne z njenim prednostnim habitatom ter njuno prostorsko stabilnost. Pod-razvrščanje znotraj štirih glavnih habitatnih tipov se ujema z variabilnostjo območja v številu vrst in diverziteti. Ne glede na klastersko analizo pa lahko s habitatno diverziteto pojasnimo 29% favnistične diverzitete na skalnatih lokacijah in 39% na lokacijah, redko poraslih z morsko travo, medtem ko številčnost favne pojasni 46% favnistične diverzitete v skalnih habitatih (pozitivna korelacija) in 32% na neutrjenih sedimentih (negativna korelacija).

Ključne besede: pestrost habitatov, pestrost vrst, GPS, videografija, Jadransko morje

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