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HIGH DIVERSITY AND SENSITIVITY TO COASTAL DEVELOPMENT OF FISH AND INVERTEBRATES OF THE NOVIGRAD AND KARIN SEAS: A METACOMMUNITY STUDY IN THE NORTHERN ADRIATIC, CROATIA

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ABSTRACT

Demersal fish and benthic macroinvertebrates were censused in spring 2009 in six embayments and one open Adriatic shallow water location. Relative faunal abundance and species richness, diversity, and evenness were calculated and compared across bays and across natural and developed coastline within bays. We found that the faunal communities of the most enclosed bays, the Novigrad Sea and the Karin Sea, (1) exhibit significantly higher fish richness and faunal diversities than any of the other bays, (2) were the most dissimilar from the open Adriatic community, (3) experienced significant reductions in biodiversity at developed compared to natural coastlines and (4) harbor two threatened fish species and highest densities of juvenile fish. Their diversity, uniqueness, and sensitivity to development make the Novigrad and Karin seas candidates for legal protection.

Key words: metacommunity, faunal diversity, visual census, Adriatic embayments, coastal development

ALTA DIVERSITÀ E SENSIBILITÀ ALLO SVILUPPO COSTIERO DI PESCI ED INVERTEBRATI DEL MARE DI NOVIGRAD E KARIN: STUDIO SULLE METACOMUNITÀ DELL'ADRIATICO SETTENTRIONALE, CROAZIA

SINTESI

Il censimento dei pesci demersali e dei macroinvertebrati bentonici è stato eseguito nella primavera del 2009 in sei baie e una località di acque basse aperte dell'Adriatico. L'abbondanza faunistica relativa, la ricchezza di specie, la diversità e l'uniformità sono state calcolate al fine di confrontare le diverse baie, alcune con la linea di costa naturale altre invece soggette a cambiamenti antropogenici. I risultati evidenziano che le comunità faunistiche delle baie semichiuse nel mare di Novigrad e Karin (1) presentano una ricchezza di specie ittiche e una diversità faunistica significativamente più alta rispetto alle altre baie, (2) presentano le più alte differenze con le comunità di acque aperte dell'Adriatico, (3) hanno subito significative riduzioni nella biodiversità nei tratti di costa modificata rispetto ai tratti di costa naturale, e per finire (4) ospitano due specie ittiche minacciate e alte densità di stadi ittici giovanili. La loro diversità, l'unicità e la sensibilità allo sviluppo costiero rendono le baie di Novigrad e Karin idonee per la protezione legale.

Parole chiave: metacomunità, diversità faunistica, visual census, baie dell'Adriatico, sviluppo costiero

INTRODUCTION

Regional *vs.* local factors influencing bay diversity

Within a system of connected and partially enclosed coastal embayments, faunal community structure is determined by local and regional processes (Caley & Schluter, 1997). The latter affect the likelihood of available species dispersing into a bay, and include interactions with biotic and abiotic landscape variables and individual species' traits, both of which affect the potential of species dispersal and migration (Harrison & Cornell, 2008). Local processes affect the likelihood of arriving species establishment within a bay, and include interactions with the local biotic and abiotic environments (Hillebrand & Blenckner, 2002).

Local and regional processes can interact (Hiltunen *et al.*, 2006). Regional processes can strongly depend on each bay's hydrological connectivity and degree of enclosure and on its distance from the primary species source (Bouvier *et al.,* 2009). Local processes are driven by abiotic variables, including salinity and temperature, diversity and complexity of habitats, and faunal interactions (predation, competition, parasitism, and facilitation), which can differ even within a bay.

If hydrological connectivity (distance and level of enclosure) with the primary species pool dominates community assembly, one would expect open bays to be richer in species than enclosed bays, and that bays closer to the source are richer than those farther away. Furthermore, in the absence of strong species interactions or in unsaturated communities, species with the highest dispersal and reproductive potential will tend to dominate the community, resulting in low evenness and thereby in potentially low diversity despite high richness (Mouillot, 2007). Conversely, if local interactions and species sorting by niche partitioning are dominant, then bays with the most diverse abiotic conditions (*e.g.*, spatial salinity range) and the highest habitat diversity should exhibit the highest richness/diversity (Mouillot, 2007).

In practice, the relative importance of regional versus local processes might differ from bay to bay. For instance, the diversity within hydrologically well-connected and open bays similar in abiotic conditions may be primarily driven by regional processes while the diversity of more isolated or enclosed bays, or those with higher habitat diversity, may be set primarily by the outcomes of local interactions (de Macedo-Soares *et al.*, 2010).

Sensitivity to coastal development

Bays that are open and well connected to a regional species pool and diversity of which is primarily regulated by regional factors, such as dispersal and hydrological connectivity, are likely to be less prone to reductions in richness as a result of coastal development. Here, species lost through the negative effects of development are likely to be replaced, perhaps quickly, by new arrivals (the dominance of dispersal over local processes is termed its »mass effect«; Mouillot, 2007). Development-related stress may instead affect primarily the equilibrium relative abundance of species, based on the balance between their tolerance and speed of dispersal rescue (Uchida & Inoue, 2010), and this balance in turn affects species evenness and thereby faunal diversity.

Bays housing saturated communities that are enclosed and poorly connected to the species pool are expected to experience larger reductions in richness due to anthropogenic disturbances, as taxa lost are not easily replaced from the species source and any species loss will have a relatively large effect due to interactions within the community. Furthermore, coastal development often reduces habitat diversity and causes abiotic changes within water and sediment, both of which can have profound effects on species diversity in locally-controlled locations.

Study design and predictions

Demersal fish and benthic macroinvertebrates were censused in spring 2009 in six Adriatic embayments and at one outer-coast shallow water location representing a gradient in hydrological connectivity, distance from the marine species pool, and in level of enclosure. Relative faunal abundance and species richness, diversity, and evenness were calculated and compared across bays and across natural and developed coastlines within each bay.

We predicted that (1) faunal richness is higher in hydrologically well connected, open bays which are more frequently reached by marine species from the source location; (2) species uniqueness and evenness is higher in enclosed and less hydrologically connected bays as they may be more influenced by local interactions, »species sorting«, than by species arrival from the marine source location; and (3) faunal communities of enclosed bays exhibit the highest diversity reductions in developed relative to natural coastlines.

MATERIAL AND METHODS

Study area and sample locations

The study area included seven shallow water bodies (»locations«) in the northern Adriatic, Zadar region of Croatia (Fig. 1). Within each location a natural coastline site and the nearest developed coastline site, in all cases a marina with seawall, were selected for detailed study, resulting in total of fourteen study sites.

Tab. 1: Hydrological distance of the six embayment locations from the open Adriatic location and their level of enclosure.
Tab. 1: Oddaljenost šestih zalivov od lokacije na odprtem morju v Jadranu in opis oprtosti/zaprtosti zaliva.

	Nin Bay	Ljubac Bay	Miocic Bay	Rovanjska Bay	Novigrad Sea	Karin Sea
Distance from Privlaka (km)	9	18	18	40	46	52
Level of enclosure	open	open	open	open	enclosed	enclosed

The six embayments, Nin Bay, Ljubac Bay, Miocic Bay, Rovanjska Bay, Novigrad Sea, and Karin Sea differed in their hydrological connectivity to the open Adriatic location (Privlaka) and in their degree of enclosure (Tab. 1, Fig. 1).

Visual census transects

Fish and invertebrates large enough to be detectable by naked eye were censused along SCUBA 2-m belt transects without disturbing the habitat (Nagelkerken *et al.*, 2000; Horinouchi *et al.*, 2005, Schultz *et al.*, 2009). All individuals of all taxa were recorded but for the presented calculations of relative abundance, diversity, and evenness, and for statistical analyses, observational units called »groups« were used, defined as one or more individuals of the same species occurring in close spatial proximity and observed at the same instant (Kruschel & Schultz, 2010). Transects were followed at a steady speed of approximately 0.3 m/sec. Transects started and ended at the shore and were comprised of two linear paths forming an open triangle with the tip at 6 m depth. Due to differences in slope and coastline shape at the 14 locations under investigation, transect lengths ranged from 450 m to 1400 m.

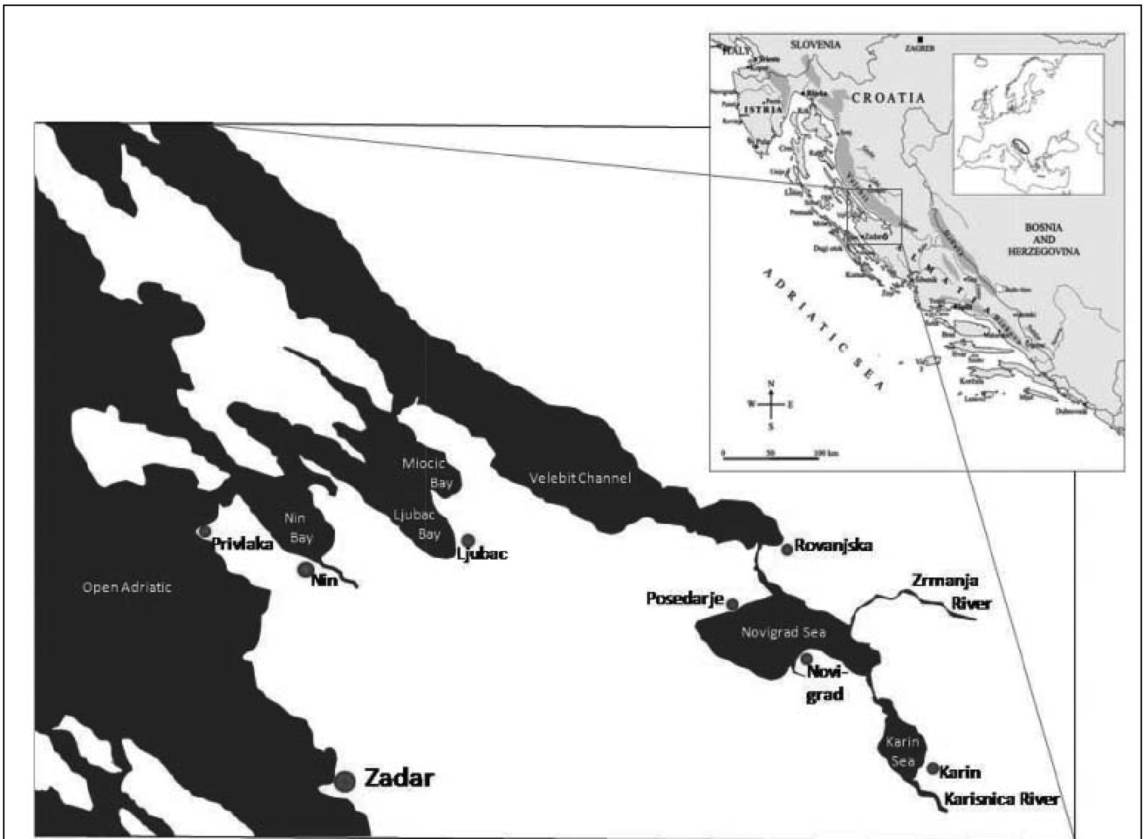

Fig. 1: Approximate location of the seven study locations in the northern Adriatic, Croatia (Zadar area).
Sl. 1: Približna lokacija sedmih obravnavanih območij v severnem Jadranu, Hrvaška (področje Zadra).

Tab. 2: List of 85 taxa identifiable to some taxonomic level below animal order and indication for their presence in the seven study locations. Legend: K = Karin Sea, L = Ljubac, M = Miocic, Ni = Nin, No = Novigrad Sea, P = Privlaka, R = Rovanjska.

Tab. 2: Seznam 85 taksonov, identificiranih na eni od taksonomskih stopenj pod/nižji od živalskim redom in z označbo prisotnosti na sedmih obravnavanih lokacijah. Legenda: K = Karinsko morje, L = Ljubac, M = Miocic, Ni = Nin, No = Novigrajsko morje, P = Privlaka, R = Rovanjska.

Taxa	Location	Taxa	Location
Porifera		**Echinodermata**	
Anchinoe tenacior	Ni	*Antedon mediterranea*	P
Aplysina aerophoba	MNiP	*Arbacia lixula*	LP
Axinella spp.	L	*Astropecten aranciaca*	R
Chondrilla nucula	MP	*Holothuria forskali*	P
Chondrosia spp.	P	*Holothuria tubulosa*	RMLNIP
Suberites domuncula	Ni	*Marthasterias glacialis*	R
unidentified sponges	RMLNiP	*Ocnus planci*	LNiP
Cnidaria		*Paracentrotus lividus*	MP
Adamsia palliata	RL	*Sphaerechinus granulosus*	P
Andresia partenopea	R	**Tunicata**	
Anemona viridis	NoRLNi	*Clavelina* spp.	P
Balanophyllia europaea	L	*Phallusia mammillata*	MLNiP
Calliactis parasitica	RMNiP	**Teleostei**	
Cerianthus membranaceus	KNoP	*Anguilla anguilla*	KNo
Cereus pedunculatus	RP	*Atherina* spp.	KNoRMP
Condylactis aurantiaca	P	*Callionymus pusillus*	LNiP
Phymanthus pulcher	P	*Coris julis*	M
Mollusca		*Diplodus annularis*	KNiP
Aporrhais pespelecani	No	*Diplodus vulgaris*	MP
Aplysia punctata	LNiP	*Gobius bucchichi*	RML
Arca noae	P	*Gobius geniporus*	KNoLP
Cerastoderma glaucum	KNo	*Gobius niger*	KNoRMLNiP
Cerithium vulgatum	KNoRMLNiP	*Gobius paganellus*	KRMNiP
Charonia tritonis variegata	Ni	*Hippocampus ramulosus*	No
Chlamys varia	R	juvenile fish < 3cm	KNo
Crassostrea gigas	M	juvenile *Gobius*	KNoMLNi
Hexaplex trunculus	KNoRMLNiP	*Lipophrys pavo*	KNo
Loligo vulgaris	Ni	*Parablennius incognitos*	NoRMLNiP
Monodonta turbinata	NoRMLNi	*Parablennius gattorugine*	NoR
Murex brandaris	RMLNiP	*Parablennius tentacularis*	R
Mytilus spp.	No	*Pomatoschistus bathi*	KNoRNiP
Ostrea edulis	KNoMLNi	*Pomatoschistus marmoratus*	KRMLP
Pecten jacobaeus	KNoRNiP	*Pomatoschistus minutus*	KNoLNi
Pinna nobilis	NoRMLNiP	*Pomatoschistus pictus*	P
Sepia officinalis	P	*Pomatoschistus quagga*	No
Annelida		*Serranus hepatus*	R
Myxicola infundibulum	R	*Serranus scriba*	P
Sabella spp.	RMLNiP	*Spicara maena*	P
Serpulidae	KNoRMLNiP	*Syngnathus* spp.	KNoR
Venus verrucosa	K	*Symphodus cinereus*	KNoRMLNiP
Crustacea		*Symphodus ocellatus*	KNoMNiP
Brachyura	NoMLP	*Symphodus roissali*	NoR
Dardanus arrosor	RNi	*Symphodus rostratus*	M
Inachus dorsettensis	RP	*Trachinus draco*	P
Maja crispata	P	*Tripterygion* spp.	P
Mysidacea	P	*Zostrisessor ophiocephalus*	KNoRMLNi
Pagurus spp.	KNoRMLNiP		
Palaemon elegans	KNoM		

Calculation of fauna and habitat related variables

Relative abundance of unique species within each transect was calculated as the absolute abundance divided by the total abundance of all species. Faunal diversity was calculated as one minus Simpson's concentration, the probability that two random observations of fauna are the same species, and as the Simpson's reciprocal index, which is the multiplicative inverse of Simpson's concentration. The latter is referred to as the »effective« number of species or the number of species at the location if they are all equally abundant, given the observed probability that two random observations are the same unique species. Species evenness was calculated as the standard Pielou index. Proportion of species at location A overlapping with those at location B was calculated as the number of species shared by locations A and B, divided by the total number of species in location A.

Diversity index values were compared among sites using the t-test on ranked data, which is equivalent to the non-parametric Kruskal-Wallis test. Dendrograms of community dissimilarity were constructed using beta diversity as the dissimilarity index, which is equivalent to Simpson's dissimilarity, and to the Bray-Curtis dissimilarity based on binary data (Lande, 1996). Non-metric multidimensional scaling on double-standardized species data was performed to ordinate the locations and species in two dimensions, using beta diversity as the dissimilarity measure (Minchin, 1987).

RESULTS

Observed taxa

Table 2 lists the 85 faunal taxa that were identifiable to some level above class and their presence/absence in the seven locations. In addition, 38 visually distinctly unique taxa identifiable with less taxonomic certainty were observed, most of which were sponges, tunicates, and anemonies, totalling 123 observed taxa.

Location similarities by faunal richness and relative taxon abundance

Table 3 lists the number of species observed in each of the 7 locations. The highest richness was observed at the open Adriatic location, Privlaka (P). The lowest richness was found in the furthest removed and most enclosed Karin Sea (K).

Table 3 also lists the species similarities of each location (rows) with each of the other locations (columns). These values indicate that the two neighbouring bays most enclosed and furthest removed from the open Adriatic, the Novigrad Sea (No) and the Karin Sea (K), are most similar to each other, sharing 63% and 76% of their species respectively. Transects of the open bays that are geographically closer to the open Adriatic and hydrologically more connected to it, including Rovanjska (R), Miocic (M), Ljubac (L), and Nin (Ni), shared only 46–61% of their species with each other, and only 34–46% with the two enclosed bays. The Novigrad Sea shared fewer species with the open Adriatic location (46%) than any of the other bays (55–61%).

Tab. 3: Community overlap based on proportion of species in each bay (rows) shared with each of the other bays (columns; for abbreviations see Table 2). Proportions were calculated by dividing the number of species shared by bay A (rows) and bay B (column) by the total number of species in bay A (rows). Note that this matrix is not symmetrical because the proportion of species in bay A that are shared with bay B is not the same as the proportion of species in bay B that are shared with bay A.

Tab. 3: Prekrivanje združb glede na delež vrst v vsakem od zalivov (vrstice), kot so te prisotne v drugih zalivih (stolpci; za kratice glej Tabelo 2). Delež je bil izračunan z delitvijo števila vrst, prisotnih v zalivu A (vrstice) in zalivu B (stolpci), s skupnim številom vrst v zalivu A (vrstice). Matrica ni simetrična, ker delež vrst iz zaliva A, ki so prisotne tudi v zalivu B, ni enak deležu vrst iz zaliva B, ki so prisotne tudi v zalivu A.

	richness	K	No	R	M	L	Ni	P
Karin Sea	29		0.76	0.48	0.48	0.45	0.55	0.55
Novigrad Sea	35	0.63		0.49	0.43	0.49	0.49	0.46
Rovanjska	41	0.34	0.41		0.57	0.46	0.57	0.60
Miocic	39	0.34	0.38	0.51		0.56	0.54	0.62
Ljubac	37	0.35	0.46	0.51	0.59		0.59	0.57
Nin	41	0.39	0.41	0.49	0.51	0.54		0.61
Privlaka	61	0.26	0.26	0.34	0.39	0.34	0.41	

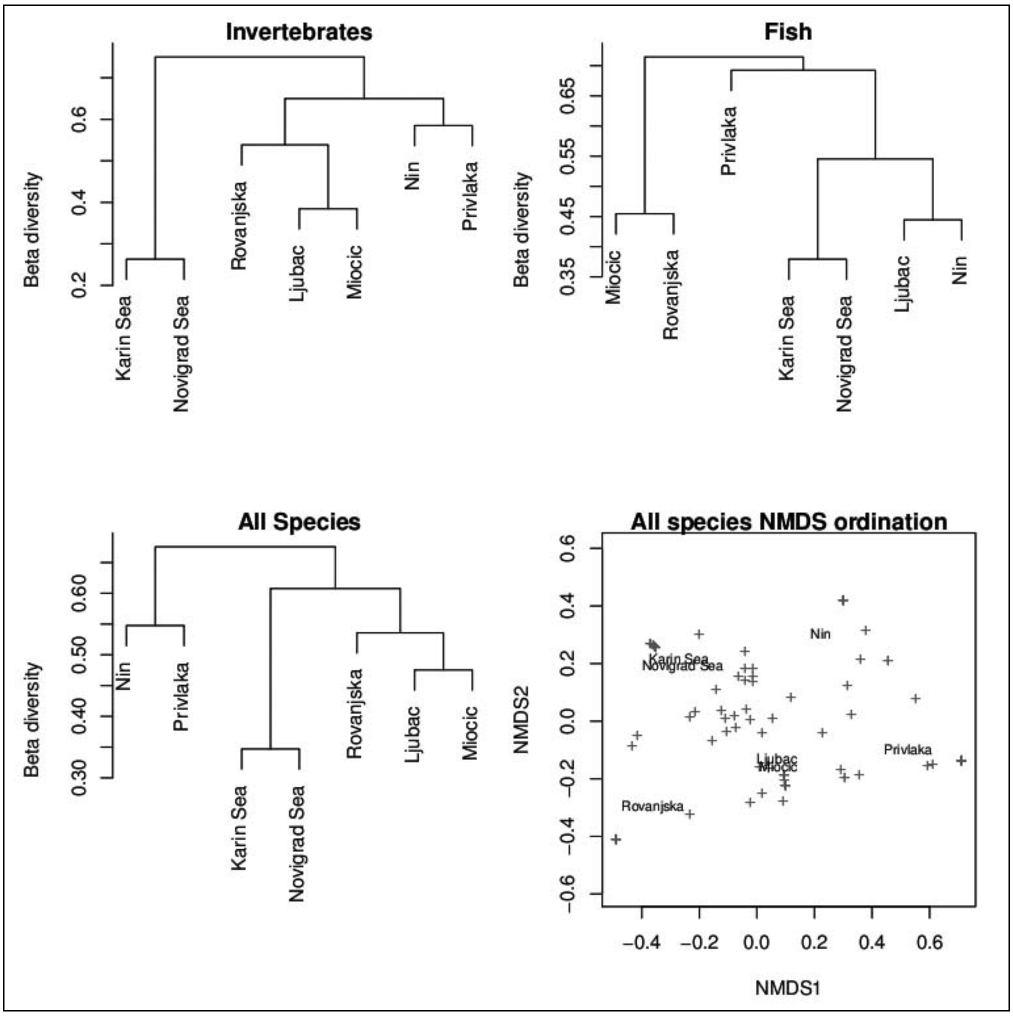

Fig. 2: Dendrograms of community dissimilarity for invertebrates only, fish only, and all species combined, and non-metric multidimensional scaling ordination based on all species combined. Locations are indicated as text, species by »+«. Total stress for the ordination was 2%.
Sl. 2: Dendrogrami razlik med združbami za nevretenčarje, ribje vrste in vse vrste skupaj ter nemetrično več-dimenzionalno umerjanje za vse vrste skupaj. Območja so označena z besedami, vrste s simbolom »+«. Totalni stres umerjanja je 2%.

The dendrogram of community dissimilarity clearly separates the enclosed bays Novigrad Sea and Karin Sea, as a distinct cluster from all other locations, and places Privlaka with Nin, its direct neighbor bay. Rovanjska is clustered with Ljubac and Miocic, which are more similar to each other than to Rovanjska (Fig. 2, lower left; all species).

The ordination plot (Fig. 2, lower right; all species) further illustrates these relationships. The Novigrad Sea and the Karin Sea are again a very close group, and so are the direct neighbours Miocic and Ljubac. Privlaka and Nin, which are clustered together in the dendrogram, are actually quite different from each other according to this ordination, and Rovanjska is also substantially dissimilar from Ljubac and Miocic.

The two separate dendrograms based on invertebrates and fish (Fig. 2) are substantially different from each other. The invertebrate communities of Privlaka and Nin, which are near the open Adriatic, are most dissimilar of all communities from the cluster of the Novigrad and Karin seas. This may be a simple reflection of the fact that these are most geographically distant from each other and hydrologically isolated. Clustered with Privlaka and Nin are the three remaining open bays (Miocic, Ljubac, Rovanjska), which are in terms of distance closer and hydrologically more open to Privlaka and Nin than the Novigrad and Karin seas. These relationships are less obvious in the fish community dendrogram, where Privlaka is clearly dissimilar from all other communities and the open bays no longer have a clear geographical relationship. However, like the invertebrate dendrogram, the Novigrad and Karin seas are highly similar and constitute a single cluster separate from the other communities.

Variability in faunal diversity and evenness across locations

Table 4 shows how the natural coastlines of the seven study locations differ in fish and invertebrate richness, diversity and evenness. The Novigrad Sea and the Karin Sea have the significantly highest invertebrate and fish diversity and evenness among the six bay locations and also harbor the highest fish richness, while invertebrate richness is low. The open Adriatic location, Privlaka, has of all locations the second highest (following the Novigrad Sea) invertebrate and the highest fish diversity but the lowest invertebrate and relatively low fish evenness.

Differences in faunal diversity and evenness comparing developed and natural coastlines

The significantly largest losses (56 and 53%) in invertebrate diversity in developed relative to natural coastline transects have been observed in the Karin Sea and the Novigrad Sea, the enclosed bays (Tab. 5). While almost the same number of species was present at developed and natural sites, evenness was reduced by half. All other locations, except for Miocic, exhibited increased invertebrate diversity at developed sites, which in all cases was primarily due to substantial increases in evenness, while the numbers of species remained the same. Fish diversity loss at developed sites was recorded at five of the seven locations (41% to 6%), including the Karin Sea and the Novigrad Sea. In the Karin Sea this change was due to loss in richness (55%) and in the Novigrad Sea due to lowered evenness (43%).

Protected species and juvenile fish

The threatened European eel, *Anguilla anguilla*, was observed only in the Novigrad Sea and the Karin Sea, while the sea horse *Hippocampus ramulosus* was observed only in the Novigrad Sea. The protected bivalve *Pinna nobilis* was present in all bays except the Karin Sea but was by far most abundant in Miocic and Ljubac. Although juvenile fish were present at all locations, differences in relative abundance can be inferred by the higher likelihood of observing juvenile fish < 3cm along the Novigrad Sea and Karin Sea transects.

Tab. 4: Simpson diversity, Simpson reciprocal index, Shannon evenness, and species richness of invertebrates and fish and the ranked t-test results comparing rankings based on the two diversity indices and evenness for the six bays (for abbreviations see Table 2); values for Novigrad Sea (No) and Karin Sea (K) are highlighted.
Tab. 4: Simpsonov indeks diverzitete, recipročni Simpsonov indeks, Shannonov indeks poravnanosti in vrstno bogastvo nevretenčarjev in rib ter razvrstitev rezultatov t-testa, ki primerjajo razvrstitev glede na oba diverzitetna indeksa in vrstno poravnanost za vseh šest zalivov (za kratice glej Tabelo 2); vrednosti za Novigrajsko morje (No) in Karinsko morje (K) so krepko natisnjene.

Bay	Simpson diversity	Simps. recipr. index	df	t-value	p-value	Bay	Shannon evenness	Bay	richness
Invertebrates (natural sites)			3.692	-3.6742	0.0245				
No	**0.81**	**5.19**				**K**	**0.72**	P	31
P	0.73	3.71				**No**	**0.59**	L	21
K	**0.73**	**3.66**				R	0.27	Ni	21
Ni	0.65	2.85				L	0.25	R	19
M	0.60	2.51				M	0.23	M	18
R	0.53	2.14				N	0.18	**No**	**11**
L	0.41	1.68				P	0.06	**K**	**9**
Fish (natural sites)			3.692	-3.6742	0.0245				
P	0.91	11.04				**K**	**0.86**	P	18
K	**0.88**	**8.03**				**No**	**0.71**	**K**	**16**
No	**0.86**	**7.17**				P	0.42	**No**	**13**
M	0.85	6.64				M	0.33	M	13
Ni	0.80	5.01				Ni	0.30	Ni	11
R	0.64	2.78				R	0.30	R	9
L	0.44	1.79				L	0.28	L	7

Tab. 5: Ranked ratios (developed site/natural site) of diversity, evenness and species richness for invertebrates and fish and the t-test results comparing diversity rankings, values for Novigrad Sea and Karin Sea are highlighted.
Tab. 5: Razvrstitev razmerij (umetno oblikovano obrežje/naravno obrežje) diverzitete, poravnanosti in bogastva vrst za nevretenčarje in ribe ter rezultati t-testa s primerjavo razvrstitve diverzitete; vrednosti za Novigrajsko morje in Karinsko morje so krepko natisnjene.

Bay	Simpson diversity	df	t-value	p-value	Bay	Shannon evenness	Bay	richness
Invertebrates		3.692	3.6742	0.02450				
Karin sea	**0.44**				**K**	**0.43**	L	0.81
Novigrad Sea	**0.47**				**No**	**0.50**	R	0.84
Miocic	0.64				M	1.09	P	0.87
Nin	1.11				Ni	1.59	**K**	**0.88**
Privlaka	1.11				R	1.64	M	0.94
Rovanjska	1.49				L	2.33	Ni	1.00
Ljubac	2.08				P	5.56	**No**	**1.18**
Fish		3.888	1.2603	0.2779				
Miocic	0.59				**No**	**0.57**	M	0.38
Karin Sea	**0.79**				**K**	**0.85**	Ni	0.45
Privlaka	0.83				R	1.01	P	0.50
Novigrad Sea	**0.88**				P	1.18	**K**	**0.56**
Nin	0.94				Ni	1.27	L	0.85
Ljubac	1.16				M	1.82	R	1.22
Rovanjska	1.22				L	1.96	**No**	**1.32**

DISCUSSION

This study confirms the prediction (1): invertebrate richness is higher in open bays easily accessed by passively dispersed species (e.g. invertebrate larvae). In contrast, richness of fish species was highest in the two most distant and least hydrologically connected bays, the Novigrad Sea and the Karin Sea. This observation is consistent with the fact that fish are more likely than invertebrates to disperse actively, *e.g.,* as adults during migration into enclosed estuarine bays specifically for reproduction (Sinovčić *et al.,* 2004; Matić-Skoko *et al.,* 2007). While invertebrate richness and diversity in bays may be primarily the result of mass effects and lack of saturation, fish diversity may be better explained by local interactions then by the regional predictor variables investigated in this study. Abundances of both invertebrates and fish were more even in the Novigrad Sea and the Karin Sea than in the open bays. This may suggest communities closer to equilibrium and community structuring by predictor variables not investigated in this study.

Prediction (2) was confirmed: the Novigrad Sea and the Karin Sea clustered separately from all other bays by fish, invertebrate, and total dissimilarity. It is interesting that the clustering by invertebrate dissimilarity closely matches dissimilarities in distance and hydrological connectivity, while this is not as clearly the case with fish community dissimilarities. Again one can argue that invertebrate community dissimilarities are more likely the outcome of regional dispersal, affected by distance and connectivity, while fish communities are more likely to be shaped by local forces, such as habitat availability or faunal interactions, because they are highly motile and more flexible in dispersal than the mostly sedentary invertebrates that are dispersed easily only as larvae. The two clusters of open bay fish communities Ljubac/Nin and Rovanjska/Miocic may be indicative of differences in habitat availability in these locations. According to Stiefel (2009), study sites in Ljubac/Nin are strongly dominated by unconsolidated or sparsely vegetated sediment reaching to the shore, while at sites in Miocic/Rovanjska bays such sediments are fringed by rocky shores.

While highly similar to each other, the Novigrad Sea and the Karin Sea shared the least species with the open Adriatic source location (Privlaka), and were less similar to any other bay than any of the other bays were to each other (Tab. 3). Stiefel (2009) reports that the three open bays Nin, Ljubac, and Miocic have significantly lower diversity and complexity of habitat than the Novigrad and Karin seas. This comparison supports the hypothesis that the fauna of the enclosed bays may be shaped by local interactions, and it further confirms the uniqueness of the Novigrad and Karin Sea among the study locations. Future analyses of existing data will test hypotheses about the relative effect of local factors, *e.g.,* habitat diversity and heterogeneity, on fish and invertebrate descriptors in the seven locations.

The study also confirmed prediction (3): we detected the largest changes in invertebrate diversity between developed and natural coastlines in the Novigrad Sea and the Karin Sea, primarily because increased relative abundances of few species caused a decreased species evenness. Substantial changes in fish diversity were likewise observed, due to richness loss in the Karin Sea and increased abundance of a few taxa in the Novigrad Sea. In contrast, at the open Adriatic location and in the open bays, invertebrate diversity was not affected, or even positively affected, by development, primarily because highly uneven communities became more even due to lowered abundances of the more common species. The effect of development on fish diversity is less obvious, yet fish diversity at developed coastlines is reduced everywhere, not only in the Novigrad and Karin Sea. The only two bays not experiencing fish diversity loss were Rovanjska and Ljubac, which naturally harbor significantly lower fish diversities.

Overall our study suggests that the faunal communities of the two enclosed bays, the Novigrad Sea and the Karin Sea, are most diverse, most different and most sensitive to coastal development. Our observations suggest that these bays may be more controlled by local ecological interactions than regional mass effects, and therefore that local alterations of ecological interactions, such as those caused by shoreline development, are likely to have a greater impact on the community than in the more open bays in our study.

Published results from detailed studies of the Novigrad Sea support the significantly higher sensitivity to coastal development: (1) coastal development – the replacement of natural coastline with human structures, including seawalls in marinas – reduce the availability of rocky reefs, the most complex habitat harboring the highest faunal diversity (Kruschel & Schultz, 2010); (2) anthropogenic stressors associated with coastal development, such as wastewater and run-off pollution, boat traffic, and tourism, alter sediment properties and negatively affect water clarity, substantially altering benthic habitats (Kruschel *et al.*, 2009). The seagrass *Cymodocea nodosa,* which occupies the deeper benthos (4–6 m) and harbors the highest invertebrate diversity (Schultz *et al.,* 2009) disappears due to lowered light penetration. *Zostera marina*, most tolerant to sediment resuspension and organically enriched sediments, invades the more natural *Z. noltii* meadows (0–4 m) causing both loss and unusually high abundances of some invertebrates, thus negatively affecting diversity through richness and evenness reduction (Stiefel, 2009). In addition, dense seagrass patches invaded by *Z. marina* have been shown to harbor the lowest fish richness, diversity, and abundance (Schultz *et al.,* 2009; Kruschel & Schultz, 2010).

Enclosed estuarine bays of eurythermal and euryhaline character, such as the Novigrad Sea and the Karin Sea, are known to function as fish nurseries, especially the shallow, low-gradient regions near river mouths (Matić-Skoko *et al.*, 2007). Higher abundances of juvenile fish than in non-estuarine bays are expected here. Our observations confirm this prediction, and small juvenile fish (< 3 cm) have been more often encountered in the Novigrad and Karin seas. Taxa observed only in these bays included the red-listed fish *Anguilla anguilla* and the rare *Hippocampus ramulosus.*

CONCLUSIONS

Within a regional network of connected embayments, the faunal communities of more isolated and enclosed bays were the most diverse and more distinct than in less isolated open bays. This may have to do with the fundamentally different processes (regional *vs.* local) structuring these communities. Isolated enclosed bays experience higher abiotic variability (*e.g.*, in temperature and salinity) and in the case of the Novigrad Sea and the Karin Sea, higher habitat diversity (Stiefel, 2009) which indicates that they may be primarily controlled by local interactions. In contrast, communities of more open and hydrologically connected bays may be primarily shaped by regional processes.

The faunal communities of the two enclosed bays, the Novigrad Sea and the Karin Sea, have also been identified as being significantly more sensitive to coastal development than faunal communities in other locations of the region. We therefore recommend the Novigrad and Karin seas as excellent candidates for formal legal status as protected natural areas within the Croatian Natura 2000 network.

VISOKA DIVERZITETA IN OBČUTLJIVOST NA RAZVOJ OBALNEGA OBMOČJA PRI RIBAH IN NEVRETENČARJIH V NOVIGRAJSKEM IN KARINSKEM MORJU: ŠTUDIJA METAZDRUŽB V SEVERNEM JADRANU, HRVAŠKA

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POVZETEK

Popis pridnenih ribjih vrst in bentoških nevretenčarjev je bil izveden pomladi 2009 v šestih zalivih in eni lokaciji v plitvi vodi odprtega Jaranskega morja. Izračunana je bila relativna številčnost favne, pa tudi bogastvo, diverziteta ter poravnanost vrst; podatke smo primerjali med zalivi in naravnim ter umetno oblikovanim obrežjem zalivov. Ugotovljeno je bilo, da favnistični združbi dveh najbolj zaprtih zalivov, Novigrajskega in Karinskega morja (1) izkazujeta občutno večje bogastvo ribjih vrst in večjo diverziteto od katerega koli drugega zaliva, (2) se najbolj razlikujeta od združbe na lokaciji na odprtem morju, (3) sta doživeli izrazitejše zmanjševanje biodiverzitete, če primerjamo podatke za naravno in umetno oblikovano obrežje in (4) nudita zavetje dvema ogroženima ribjima vrstama in najvišji gostoti mladostnih primerkov rib. S svojo diverziteto, edinstvenostjo in občutljivostjo na razvoj obalnega območja sta Novigrajsko in Karinsko morje kandidata za pravno zaščito.

Ključne besede: metazdružba, favnistična diverziteta, vizualno štetje, jadranski zalivi, razvoj obalnih območij

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