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SEASCAPE CONTEXT AS A DRIVER OF THE FISH COMMUNITY STRUCTURE OF *Posidonia oceanica* MEADOWS IN THE ADRIATIC SEA

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ABSTRACT

Marine underwater habitats dominated by seagrass *Posidonia oceanica* play an essential role in fish community assembly, affecting taxonomic and functional diversity, abundance and fish behavior. The value of seagrasses as habitat depends on the spatial arrangement of the seascape elements and the availability of alternative habitats. Little is known about the effect of the seascape context of *P. oceanica* meadows on fish assemblages in the Mediterranean Sea. To identify *P. oceanica* meadows' relative importance as a habitat for fishes, fish communities in the Croatian Adriatic Sea were investigated, using SCUBA lure-assisted visual census. The results show a significant effect of different arrangements of *P. oceanica* meadows' seascape elements and surrounding habitats on fish community structure. Fragmented mosaic meadows with *P. oceanica* growing directly on and between rocky-algal reefs/boulders had significantly higher fish abundances compared to both types of continuous meadows (bordering rock and bordering sand). Continuous meadows bordering sand harbored the highest number of unique species. Evidence that alternative structured habitats within proximity to seagrass beds may affect the community structure of associated fish assemblages is provided, highlighting the need to consider *P. oceanica* meadows' seascape context in conservation management and experimental design for fish community structure.

How to Cite

INTRODUCTION

Seagrasses represent one of the most productive and diverse shallow-water marine habitats; they form extensive and dense beds with high structural complexity (Duarte and Chiscano, 1999), which increases their value as a nursery/spawning and feeding ground for many fish, invertebrate and bird species (Orth et al., 1984; Nagelkerken et al., 2001). Seagrasses are identified as being "ecosystem engineers" for providing habitat for diverse fauna and for delivering numerous ecosystem services, such as slowing down water movement, stabilizing the sediment, protecting the shores from erosion, increasing sedimentation rates, and having high denitrification, nitrogen burial and carbon burial rates (Bos et al., 2007; Eyre et al., 2011; McLeod et al., 2011). Despite their value, seagrasses are among the most endangered habitats worldwide; their decline rates are as high as those of coral reefs or mangroves (estimated loss of 110 km^2 yr^{-1} between 1980 and 2006) (Waycott et al., 2009). The known extent of *Posidonia oceanica* L. Delile 1813 within the Mediterranean in 2015 was a minimum of 12,247 km^2, with an estimated loss of 10% or 1,241 km^2 over the past 50 years (Telesca et al., 2015). However, the report mentioned above lacks information on the presence or absence of *P. oceanica* for almost half of the Mediterranean coastline (primarily the southeastern Mediterranean).

Posidonia oceanica is an endemic Mediterranean seagrass that forms large monospecific meadows (Hemminga and Duarte, 2000) present between the surface and 44 meters of depth (Den Hartog, 1979; Borg and Schembri, 1995; Procaccini et al., 2003). Fish assemblages associated with *P. oceanica* meadows have been well studied (Bell and Harmelin-Vivien, 1982; Francour, 1997; Moranta et al., 2006; Boudouresque et al., 2012; Zubak et al., 2017), and the high degree of spatial and temporal variation in the structure of fish assemblages have been documented (Guidetti, 2000; Deudero et al., 2008; Kalogirou et al., 2010). Existing studies of the community structure and the differences in fish assemblages focus on comparing *P. oceanica* meadows to other nearshore habitats (Mouillot et al., 1999; Guidetti, 2000). To the best of our knowledge, there are no published studies on how *P. oceanica* fish assemblages are influenced by the seascape context, especially by the surrounding or adjacent habitats. Published studies in tropical and temperate areas outside the Mediterranean region have documented interactions among seagrass, mangrove and coral reef habitats (Nakamura and Sano, 2004; Dorenbosch et al., 2006; Gilby et al., 2018). Coral reefs and mangroves affect the tropical and subtropical fish assemblages in adjacent habitats (Dorenbosch et al., 2006; Kopp et al., 2007; Olds et al., 2013). Similarly, the proximity of seagrass beds in subtropical estuaries provides complex habitats and increases the number of species and individuals in nearby habitats (Gilby et al., 2018). Species diversity and abundance of associated fauna can be positively affected by a higher habitat structural complexity (Graham and Nash, 2013; Henderson et al., 2017), and the combination of shelter, food resources and protection from predation are the main factors that shape the animal communities (Connolly and Hindell, 2006). Seagrasses can be nurseries from which juvenile fish move to adjacent habitats or serve as feeding or sheltering grounds (Nagelkerken, 2000; Dorenbosch, 2004; Nakamura and Sano, 2004). Within seagrass habitats, fish communities can be affected, among other factors, by seagrass patch size and shape (Salita et al., 2003), but also by the seascape context — the spatial organization of the various elements of the submarine landscape, including the availability of adjacent alternative structured habitats (Dorenbosch et al., 2007; Pittman et al., 2007; Unsworth et al., 2008).

Along the east coast of the Adriatic Sea (Croatia), *Posidonia oceanica* beds occur at depths ranging from 0 to about 36 meters on unconsolidated sediments and flat rock or rock boulders (Zubak et al., 2020). The meadows can be very diverse and most often occur as dominant habitat in one of the three types of the spatial organization of the seascape elements: (i) continuous meadows bordering bare unconsolidated sediments, (ii) continuous meadows bordering rocky algal reefs/boulders, and (iii) mosaic meadows growing on rocky algal reefs/boulders — a particular case where seagrasses grow anchored in the crevices of rocks and between rocky boulders (Fig. 1). The effects of the different seascape contexts of *P. oceanica* meadows on fish assemblage descriptors were predicted. The idea that individual fish species exhibit significant differences in *P. oceanica* meadows' preference depending on the meadows' seascape context was proposed to test the null hypotheses that there were no differences in species composition, species richness and abundance of fish assemblages occurring over different seascape contexts of *P. oceanica* meadows.

MATERIALS AND METHODS

Survey locations and methods

Fish assemblages within seagrass meadows of *Posidonia oceanica* were surveyed during 2011 (June-September) and 2012 (March-September), along the eastern coast of the Adriatic Sea, Croatia (Fig. 2). Fifty-five lure-assisted visual census belt transects (details in S1 Table) were performed, following the procedure described in Kruschel and Schultz (2010, 2012), using SCUBA diving along 10-meter isobaths. All transects were performed during the daytime, with calm waters, no wind (0-1 Beaufort), and at high underwater visibility (>15 m).

The diver (always the same individual observer, IZČ) moved along each georeferenced transect (Garmin GPSMAP 60CSx Handheld GPS Navigator attached to a buoy above the diver) and observed and recorded all fishes appearing within a water column defined by its
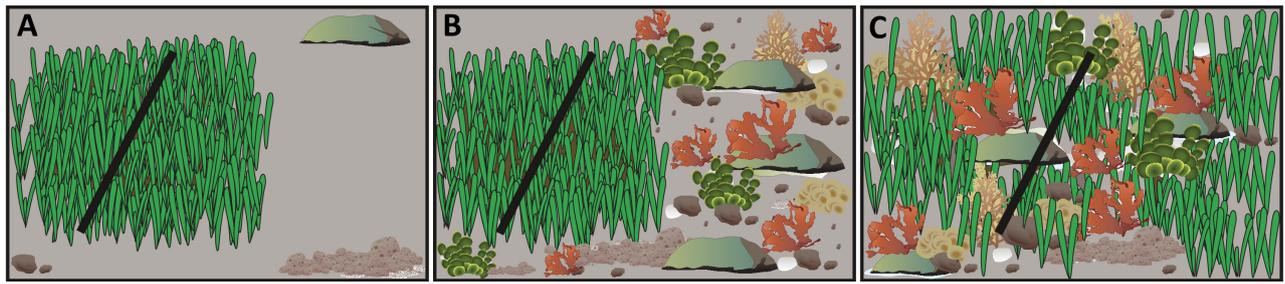
Fig 1. Three spatial organization types of *Posidonia oceanica* seascape elements.

A: Continuous meadow bordering sand. B: Continuous meadow bordering rocky-algal reef. C: *Posidonia oceanica* mosaic meadow on rocky substrates and between boulders with macro-algae. The thick black line represents a single transect performed within each of the surveyed meadows (illustration created by Ivana Zubak Čižmek with the courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/); authors: Diana Kleine, Joanna Woerner, and Tracey Saxby)
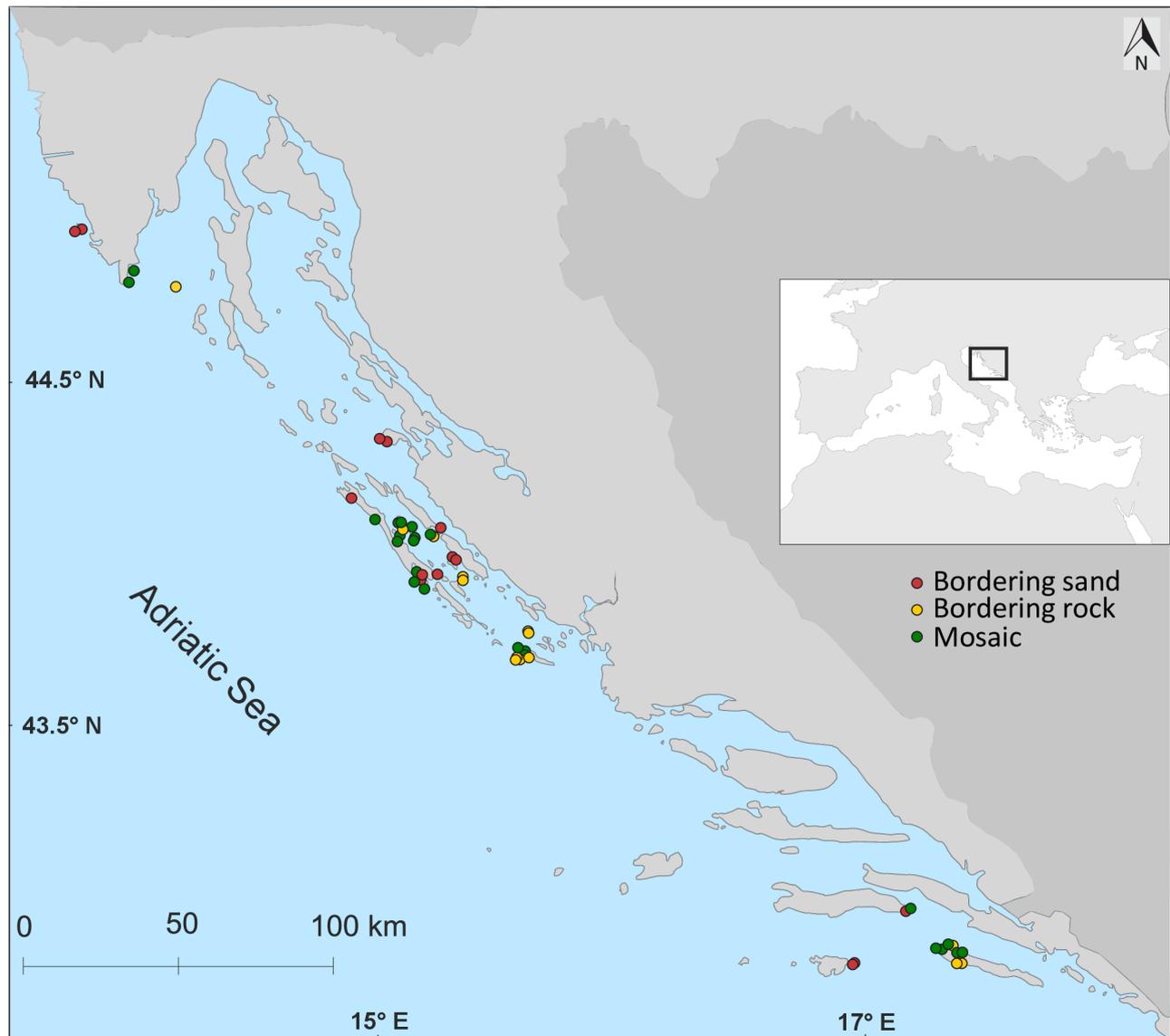
Fig 2. Locations of surveyed fish assemblages within *Posidonia oceanica* seagrass meadows in the Eastern Adriatic Sea, Croatia

width (1 m to both sides of the lure line's path) and the height (extending from the bottom upward to the diver's eyes, approximately 2 m). The lure was a small (2* 1 cm) piece of lead tied to a 2 m long fishing line, wrapped around a Styrofoam® board. The lure was positioned and moved approximately 5 cm above the substrate's surface. The transects were time standardized to 10 minutes (the length varied between 61 and 99 m; mean 79.88 m (SD 11.05)). Time standardized transects were chosen because lure use requires sufficient time to allow fish to approach the lure. If transects varied in timespan, the error variance in the abundance of approaching fish would increase, and if transects tended to occupy different time spans in different habitats, then timespan would be a confounding factor with habitat. The addition of a lure to visual fish counts along transects increases the probabilities to see fishes and reduces bias due to differences in size, mobility, tendency to hide/camouflage (Kruschel and Schultz, 2010, 2012). The diver took the following data on individual fish along each transect: taxon (usually species level), developmental stage (adult/juvenile), and abundance. In some analyses, juvenile fish were treated as being different from their conspecific adults since it has been shown that many differences in fish behavior (habitat selection, feeding, anti-predator response) may depend on the ontogenetic stage (Jones, 1984; Laegdsgaard and Johnson, 2001). If the observed individuals were grouping/schooling, individual fish observations were considered non-independent; such groups were defined as two or more individuals of the same taxon observed at the same moment (i.e., observations). Individuals were counted to 20 fish, while abundance in larger groups was estimated in increments of 10 up to 100 fish and in increments of 100 up to the maximum observed group size of 200. The diver simultaneously recorded the visually estimated proportion of *P. oceanica* cover (p1 < 25%, 25% <p2 ≤ 50%, 50% < p3 ≤ 75%, 75% < p4 ≤ 100%) for each transect. The height of the *P. oceanica* canopy was uniform across all transects (approximately 80 cm). Other predictor variables that potentially influence the fish assemblage structure included seawater temperature (°C), the shore's slope calculated from the distance to the shore and transect depth (°), and coastline geography (embayment vs. open shore). Fish assemblages were characterized by documenting the absolute and relative abundance of adult and juvenile fish, fish taxonomic diversity, and fish species composition.

Data analysis

All statistical analyses were conducted using R v.3.4.2. (R Development Core Team and R Core Team, 2017) and RStudio 1.1.383. For all analyses, significance levels were set at α = 0.05. Analysis of variance (ANOVA) using the aov function (Chambers et al., 2017) was performed to test for differences in abundance and richness among the three different seascape contexts of *Posidonia oceanica* meadows, among the different *P. oceanica* covers and

among different temperature values. The analyses were based on a one-way model and the residuals were checked for normality using the Shapiro-Wilk test. Tukey HSD post-hoc test using the TukeyC and TukeyHSD functions (Faria et al., 2018) was performed to explore the differences in the abundance among all pairs of levels of the selected factor (e.g., seascape context).

Because transects varied in length and were time standardized, abundance was expressed and analyzed as the abundance per m³ of each transect (m³; volume = length * width (2 m) * height (2 m)). To compare fish assemblages found associated with the three different seascape contexts of *P. oceanica* meadows, permutational multivariate analysis of variance, PERMANOVA (Anderson, 2001; McArdle and Anderson, 2001) was used, which is a non-parametric confirmatory statistics method. The predictor variables of interest were the meadow's seascape context (bordering bare sand, bordering rocky-algal reefs, or mosaic rocky-algal substratum), *P. oceanica* cover, and temperature. The response matrix was the matrix of relative fish abundances in each community at each transect, with the transect being the statistical sample replicate (N = 55). The fish community matrix was converted to the Bray-Curtis distance matrix before analysis. The similarities among communities grouped by the primary predictor variable (seascape context of the meadow) were presented visually with unconstrained, non-metric multidimensional scaling using Bray-Curtis distances; double Wisconsin standardization was used and the solution with the lowest stress was reported; 2D nMDS, using the metaMDS function in the vegan package of R (Faith et al., 1987; Minchin, 1987). The variation in the abundance of each species within and among the meadows' seascape contexts was further partitioned, using an analysis of deviance for the generalized linear (quassi-Poisson) model.

RESULTS

The diversity and abundance of fishes

A total of 2010 observations of 6842 fish individuals belonging to 45 taxa (59 when treating juveniles differently from their conspecific adults) were identified in the *Posidonia oceanica* meadows in the Croatian Adriatic Sea. Fifteen fish families were recorded and, in terms of species richness, Labridae, Gobiidae and Sparidae were the most diverse, with 12, 9 and 7 recorded taxa, respectively. Labridae and Sparidae contained 73% of all observed individuals (Table 1).

The most frequently recorded species in the whole dataset (including juveniles) were *Coris julis* (394 observations of 495 individuals), *Symphodus ocellatus* (364 observations of 778 individuals), *Chromis chromis* (155 observations of 2740 individuals) and *Diplodus annularis* (117 observations of 129 individuals). Nine taxa were observed on a single occasion (Table 2).

Table 1. The total number of fish observations, the number of recorded taxa in each fish family and their relative abundances observed in *Posidonia oceanica* meadows in the Adriatic Sea, Croatia. Abbreviated taxa names are given in the parentheses following the full taxon name

Family	Taxon	N observations	Relative abundance
Labridae (12)	**Total**	**1021**	**0.508**
	Coris julis (coju)	394	
	Symphodus cinereus (syci)	93	
	Symphodus doderleini (sydo)	17	
	Symphodus melanocercus (symel)	84	
	Symphodus mediterraneus (seme)	25	
	Symphodus melops (symelo)	8	
	Symphodus sp.	12	
	Symphodus ocellatus (syoc)	364	
	Symphodus roissali (syro)	2	
	Symphodus rostratus (syros)	11	
	Symphodus tinca (syti)	9	
	Thalassoma pavo (thpa)	2	
Sparidae (7)		**393**	**0.196**
	Boops boops (bobo)	50	
	Diplodus annularis (dian)	117	
	Diplodus vulgaris (divu)	90	
	Oblada melanura (obme)	85	
	Sarpa salpa (sasa)	2	
	Sparus aurata (spaau)	7	
	Spondyliosoma cantharus (spca)	42	
Serranidae (3)		**176**	**0.088**
	Serranus cabrilla (seca)	43	
	Serranus hepatus (sehe)	33	
	Serranus scriba (sesc)	100	
Pomacentridae (1)		**155**	**0.077**
	Chromis chromis (chch)	155	
Centracanthidae (2)		**136**	**0.068**
	Spicara maena (spma)	62	
	Spicara smaris (spsm)	74	

Continued

Family	Taxon	N observations	Relative abundance
Gobiidae (9)		**63**	**0.031**
	Gobius sp.	15	
	Gobius bucchichi/incognitus (gobu)	23	
	Gobius cruentatus (gocr)	8	
	Gobius fallax (gofa)	2	
	Gobius geniporus (goge)	3	
	Gobius auratus (goau)	1	
	Gobius niger (goni)	1	
	Gobius vittatus (govi)	8	
	Pomatoschistus sp.	2	
Mullidae (1)		**13**	**0.006**
	Mullus surmuletus (musu)	13	
Blennidae (1)		**5**	**0.002**
	Parablennius sp.	5	
Scorpaenidae (3)		**4**	**0.002**
	Scorpaena notata (scno)	2	
	Scorpaena porcus (scpo)	1	
	Scorpaena scrofa (scsc)	1	
Atherinidae (1)		**1**	**<0.001**
	Atherina hepsetus (athe)	1	
Carangidae (1)		**1**	**<0.001**
	Seriola dumerili (sedu)	1	
Congeridae (1)		**1**	**<0.001**
	Conger conger (coco)	1	
Moronidae (1)		**1**	**<0.001**
	Dicentrarchus labrax (dila)	1	
Muraenidae (1)		**1**	**<0.001**
	Muraena helena (muhe)	1	
Unidentified		**39**	**0.019**
Total (45)		**2010**	

Table 2. Taxa observed exclusively in one seascape context (bordering sand/bordering rock/mosaic) of *Posidonia oceanica* meadows, observed on more than one occasion (their abundance is shown in parentheses)

Seascape context		
Bordering sand	**Bordering rock**	**Mosaic**
Mullus surmuletus (13)	*Gobius vittatus* (8)	*Scorpaena notata* (2)
Symphodus melops (8)		
Spondyliosoma cantharus juv. (6)		
Pomatoschistus sp. (2)		
Sarpa salpa (2)		
Symphodus rostratus (2)		
Thalassoma pavo (2)		

The abundance of recorded fish varied significantly between the three seascape contexts of the *P. oceanica* meadows (Table 3, p = 0.009, F = 5.128); it was higher in mosaic meadows than in the meadows bordering sand and meadows bordering rock (Fig. 3). A statistically significant difference was found between mosaic meadows and meadows bordering rock (Tukey p = 0.032), and between mosaic meadows and meadows bordering sand (Tukey p = 0.011). There was no significant difference in the abundance per m³ between the two types of continuous meadows (Tukey p = 0.999).

No statistically significant difference was observed in species richness between the three observed seascape contexts of *P. oceanica* meadows (p = 2.24, F = 1.48). The highest species richness and abundance were observed at the following sites: Fulija West (91 observations of 285 individuals belonging to 22 taxa), Žut (53 observations of 256 individuals belonging to 19 taxa) and Galijola (86 observations of 836 individuals belonging to 17 taxa). The transects mentioned above were all placed in mosaic *P. oceanica* meadows.

Community structure in three meadow types

All three seascape contexts of the *P. oceanica* meadows shared a species pool; 25 of 59 taxa (42% including juveniles) co-occurred in the three meadow types and the meadows bordering sand had the highest number of unique taxa (Fig. 4).

Analysis of the fish community using nMDS showed the separation of three seascape contexts of the meadows (Fig. 5), with nMDS stress 0.20. Further analysis showed that 11 taxa showed significant variation in the abundance across the meadow types (Table 4).

	Bordering sand	Mosaic	Bordering rock
Unique taxa	10	5	8
Unique taxa; N>1	7	1	1
Total taxa	42	34	44
Taxa shared between two meadow types	25	32	29
Taxa shared among three meadow types		25	
Total number of taxa (including juveniles)		45 (59)	
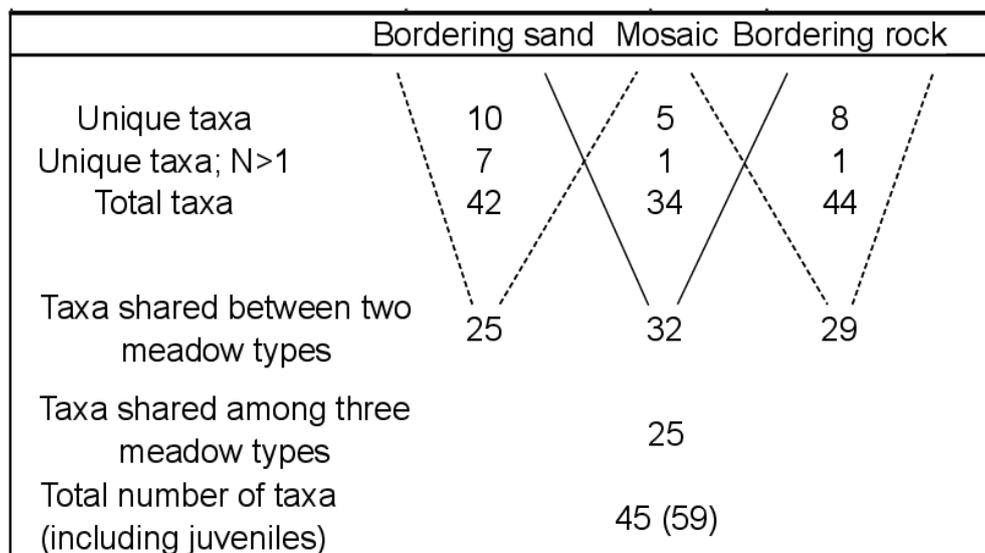
Fig 3. Box plot of abundance per volume unit (m³) of fish in each of the three seascape contexts (bordering sand/ bordering rock/mosaic) of *Posidonia oceanica* meadows. Box plots show the median (line near the center), the first and third quartile (the box), the extreme values whose distance from the box is at most 1.5 times the interquartile range (whiskers) and remaining outliers (black dots)

Table 3. Analysis of variance using ANOVA of fish abundance per m³, across three different seascape contexts of *Posidonia oceanica* meadows in the Adriatic Sea, Croatia (Df – degrees of freedom, SS – Sums of squares, MS – Mean Sums of squares)

Response: abundance (per volume unit; m³)	Df	Ss	Ms	F value	P	
Meadow	2	0.036	0.018	5.128	0.009	**
Residuals	52	0.184	0.004			

*p < .05; **p < .01; ***p < .001

Table 4. Fish taxa observed within *Posidonia oceanica* meadows in the Adriatic Sea, Croatia, their ordination coordinates, deviance values in the analysis of deviance of abundance across different seascape contexts and associated null probability values (taxa with an asterisk sign showed a significant abundance variation across the *P. oceanica* seascape contexts; p < 0.05 shown in bold)

Taxon	NMDS1	NMDS2	deviance value	p
Atherina hepsetus	0.599	-0.801	0.509	0.604
Boops boops	0.96	-0.281	2.362	0.104
Chromis chromis	-0.837	0.546	2.778	0.071
Chromis chromis juvenile	-0.962	-0.273	1.491	0.235
Conger conger	0.972	-0.233	0.509	0.604
Coris julis	-0.867	-0.499	3.104	0.053
Coris julis juvenile	-0.161	-0.987	1.883	0.162
Diplodus annularis*	0.447	0.894	8.657	**0.001**
Diplodus annularis juvenile*	0.33	0.944	5.781	**0.005**
Dicentrarchus labrax	0.761	0.649	1.491	0.235
Diplodus vulgaris	-0.065	0.998	1.907	0.159
Diplodus vulgaris juvenile	0.879	-0.477	0.829	0.442
Gobius sp.	0.998	0.061	1.028	0.365
Gobius sp. juvenile	0.637	0.771	1.539	0.224
Gobius bucchichi/incognitus*	0.682	0.731	3.177	**0.05**
Gobius bucchichi juvenile	-0.768	0.64	1.491	0.235
Gobius cruentatus	0.644	0.765	0.449	0.641
Gobius fallax	0.233	-0.973	0.347	0.709
Gobius geniporus	0.554	0.833	1.95	0.152
Gobius auratus	0.998	0.059	1.491	0.235
Gobius niger	0.841	0.542	0.509	0.604
Gobius vittatus	0.392	-0.92	1.262	0.292
Muraena helena	-0.962	-0.273	1.491	0.235
Mullus surmuletus*	0.009	0.999	20.003	**0**
Oblada melanura	-0.999	-0.024	0.731	0.486

Continued

Taxon	NMDS1	NMDS2	deviance value	*p*
Oblada melanura juvenile	0.982	-0.189	0.881	0.42
Parablennius sp.	-0.793	-0.609	2.915	0.063
Pomatoschistus sp.	-0.137	0.991	1.491	0.235
Sarpa salpa	-0.552	0.834	1.491	0.235
Scorpaena notata	-0.883	-0.47	2.701	0.077
Scorpaena porcus	-0.937	-0.35	1.491	0.235
Scorpaena scrofa	0.594	-0.804	0.509	0.604
*Serranus cabrilla**	-0.998	-0.07	15.483	0
Seriola dumerili	-1	0.02	0.509	0.604
Serranus hepatus	0.992	-0.129	1.278	0.287
Serranus hepatus juvenile	0.234	-0.972	0.509	0.604
Serranus scriba	-0.69	0.724	2.515	0.091
Serranus scriba juvenile	-0.999	0.02	0.509	0.604
Sparus aurata	-0.522	0.853	0.926	0.402
*Spondyliosoma cantharus**	-0.858	0.513	7.929	0.001
Spondyliosoma cantharus juvenile*	-0.982	-0.187	3.526	0.037
Spicara maena	-0.054	0.999	0.602	0.551
Spicara smaris	0.378	0.926	0.685	0.509
Spicara smaris juvenile	-0.992	0.13	1.491	0.235
*Symphodus cinereus**	0.985	0.171	6.587	0.003
Symphodus doderleini	0.082	-0.997	1.57	0.218
Symphodus melanocercus	-0.558	-0.83	2.979	0.06
Symphodus mediterraneus	-0.749	0.662	0.072	0.931
*Symphodus melops**	-0.723	0.691	6.428	0.003
Symphodus sp.	0.216	-0.976	0.573	0.567
Symphodus sp. juvenile	0.167	-0.986	1.366	0.264
*Symphodus ocellatus**	0.625	-0.781	9.563	0
Symphodus ocellatus juvenile	-0.967	-0.255	2.772	0.072
*Symphodus roissali**	-0.537	0.844	3.225	0.048
Symphodus rostratus	0.247	0.969	0.226	0.799
Symphodus tinca	-0.591	0.807	2.19	0.122
Thalassoma pavo	-0.516	0.857	1.491	0.235
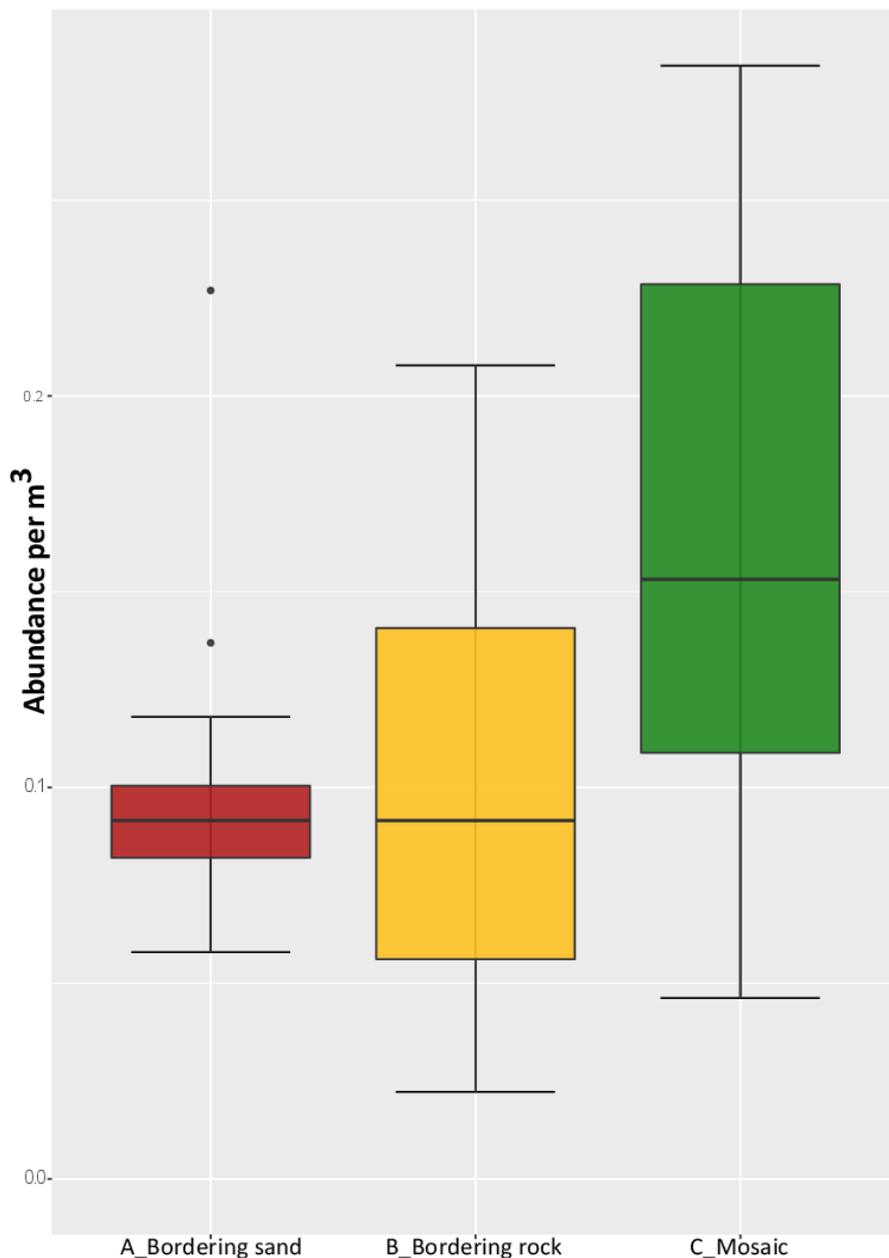
Fig 4. Total, shared and unique fish taxa across three different seascape contexts (bordering sand/bordering rock/ mosaic) of *Posidonia oceanica* meadows in the Adriatic Sea, Croatia

PERMANOVA results indicate a significant individual influence of seascape context, seagrass cover and temperature on fish community structure variation with no interaction between the predictor variables (Table 5). The primary variable of interest, the meadow's seascape context, explained approximately 13% of the fish community structure variability (PERMANOVA $R^2 = 0.13$, $p<0.01$). Although the seagrass cover and temperature showed no significant effect on species richness or abundance, they were included as covariates in the PERMANOVA analysis to control potential interaction with the primary variable of interest.

The relative abundance of each of the 20 selected taxa across different *P. oceanica* meadows' seascape contexts is presented in Fig. 6. Twenty taxa chosen for this analysis either showed a highly significant abundance variation across the three different seascape contexts of *P. oceanica* meadows (11 taxa) or had a high overall abundance (9 taxa).

The proportions of the most abundant species in each of the three different seascape contexts of *P. oceanica* meadows showed that *Coris julis* and *Chromis chromis* are among the four most abundant species in all meadow types (Fig 7).
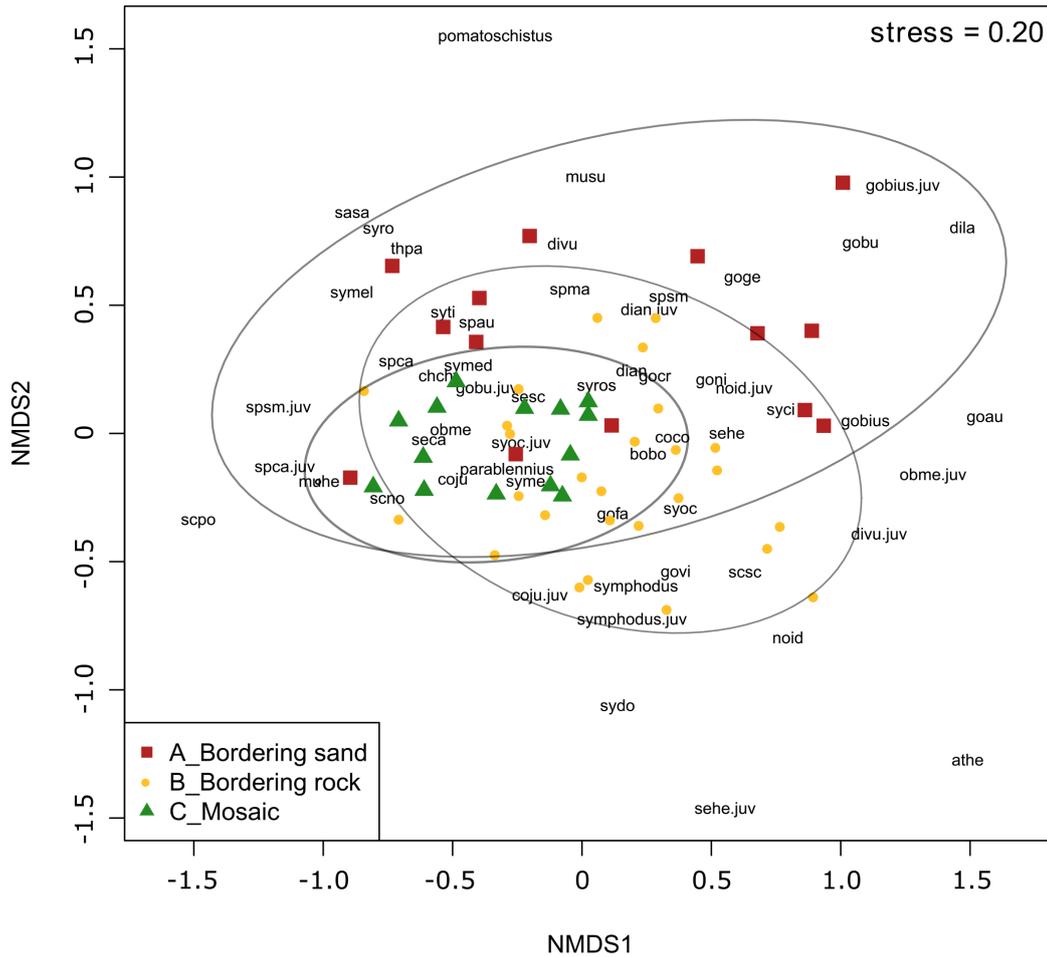
Fig 5. Two-dimensional non-metric multidimensional scaling plots of the fish community across three different seascape contexts (bordering sand/bordering rock/mosaic) of *Posidonia oceanica* meadows in the Adriatic Sea, Croatia. The symbols represent individual transects within the datasets indexed in Table S1. Bray–Curtis distance, final stress = 0.20. Ellipses show 95% confidence limits for the delimitation of each group. For species/taxa abbreviations see Table 1.

Table 5. Analysis of variance using PERMANOVA of the effect of the temperature, cover, seascape context (SC) and their interactions on the variability in *Posidonia oceanica* fish community structure in the Adriatic Sea, Croatia (Df – degrees of freedom, SS – Sums of squares, MS – Mean Sums of squares)

	Df	SS	MS	F model	R^2	p	
Temperature	1	0.543	0.543	3.333	0.047	0.003	**
Cover	2	1.060	0.530	3.254	0.092	0.001	***
SC	2	1.496	0.748	4.593	0.130	0.001	***
Temperature:cover	2	0.424	0.212	1.302	0.037	0.177	
Temperature:SC	2	0.413	0.206	1.268	0.036	0.195	
Cover:SC	4	0.784	0.196	1.203	0.068	0.184	
Temperature:Cover:SC	3	0.643	0.214	1.317	0.056	0.125	
Residuals	38	6.187	0.163		0.536		
Total	54	11.549			1		

*p < .05; **p < .01; ***p < .001
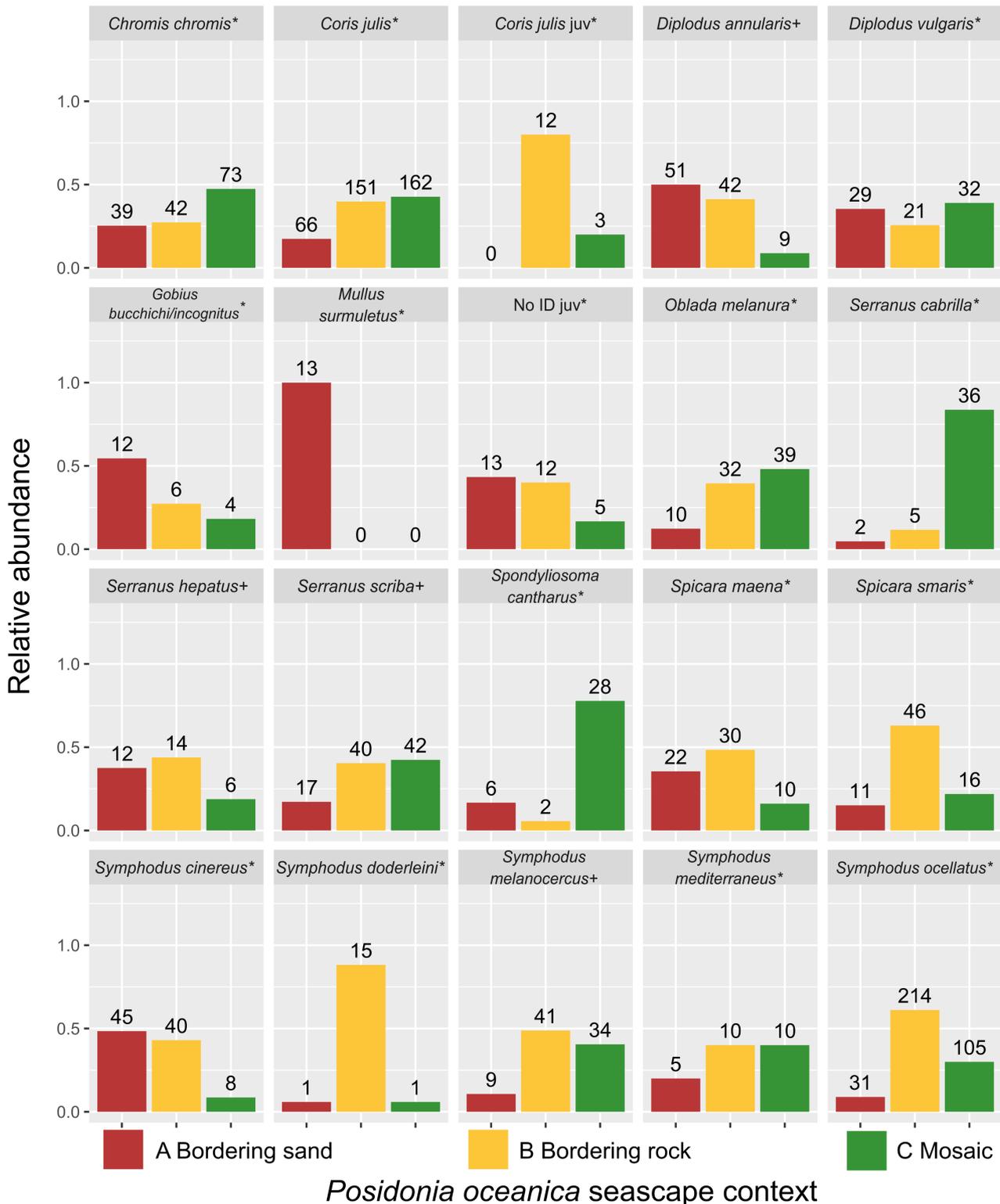
Fig 6. Bar plot showing the relative abundance of twenty selected fish species across different *Posidonia oceanica* seascape contexts (bordering sand/bordering rock/mosaic). Species with an asterisk showed a significant abundance variation across *P. oceanica* seascape contexts, and species with a plus sign were among the most abundant species overall. The numbers above the bars indicate each taxon's absolute abundance in the three *P. oceanica* seascape contexts.
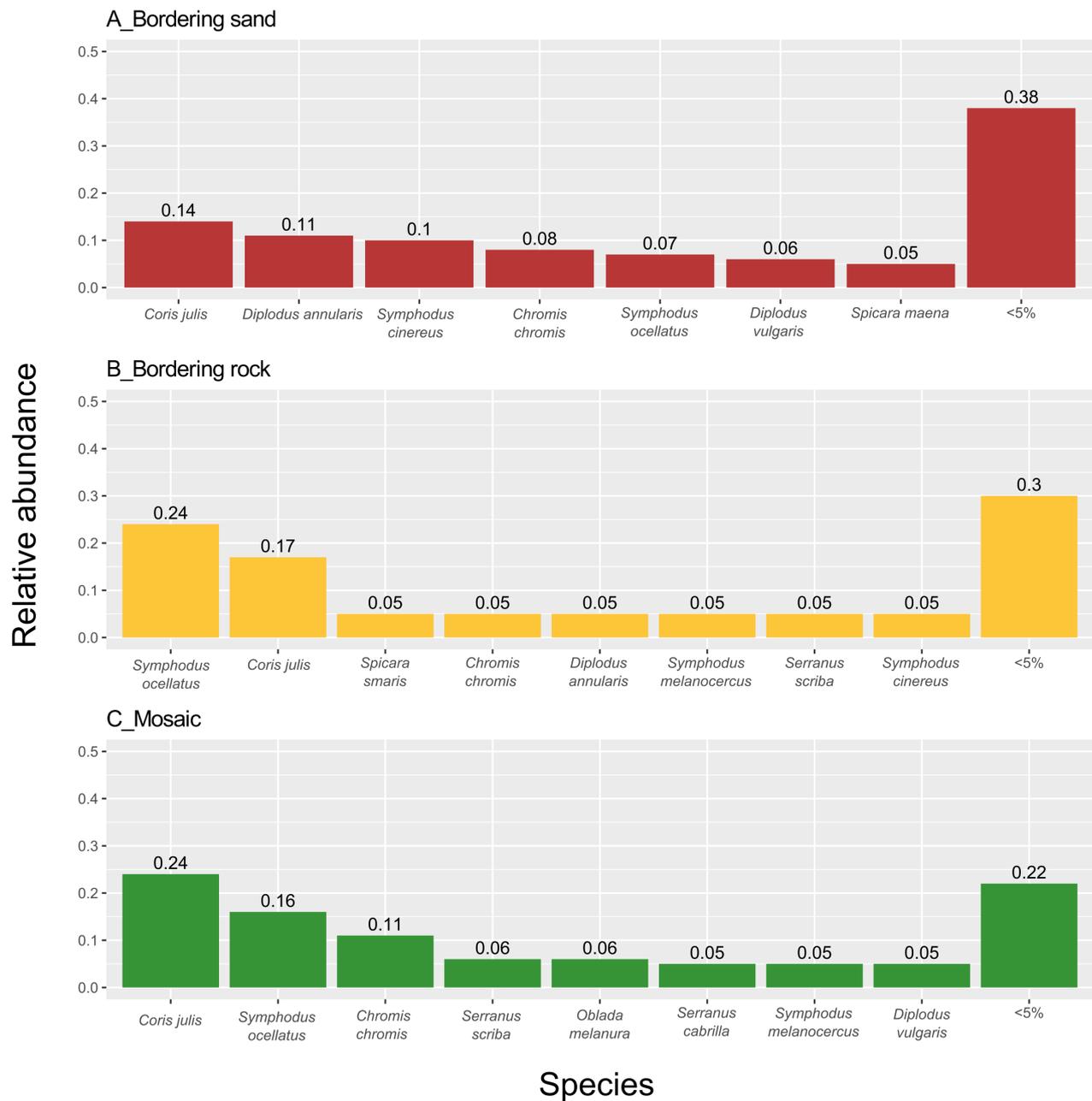
Fig 7. Bar plot showing the proportion of most abundant fish species in each of the three *Posidonia oceanica* seascape contexts (bordering sand/bordering rock/mosaic). The numbers above the bars indicate each taxon's relative abundance in the three seascape contexts. Species whose relative abundances were <5% were pooled.

DISCUSSION

The fish assemblage of Posidonia oceanica meadows

This research indicates that *Posidonia oceanica* ichthyofauna in all explored seascape contexts is relatively homogeneous and shares a species pool. However, statistically significant differences in fish community structure across the three different seascape contexts of *P. oceanica* meadows were found, and 11 taxa with significant differences in abundance across seagrass structural arrangements were discovered.

The total number of recorded taxa (45) was somewhat higher than previously described in other Mediterranean areas (at similar depth and using visual census): 38 from the Balearic Islands (Frau et al., 2003), 37 from Alicante, Spain (Valle and Bayle-Sempere, 2009), 35 from the Ligurian Sea (Tunesi and Vacchi, 1993) and 34 from Otranto, Apulian coast (Guidetti, 2000). The higher number of recorded taxa is probably because the lure-assisted visual census was used (Kruschel and Schultz, 2012). Visual counts facilitated by a device to lure out fish from their hideout into the view of the diver can significantly improve the probability of detecting small fish hidden within the seagrass canopy, predators that search for and encounter prey from a concealed position (e.g., ambush predators and wait-chase predators) or fast cruising predators which are easily overlooked during their brief appearance in regular transects (Kruschel and Schultz, 2012). A significant difference in abundance was found between complex mosaic meadows and continuous meadows bordering rock/bordering sand. At the same time, the species richness showed no significant difference among the three habitats. The presence of rocky bottom increased abundance, but surprisingly it did not significantly influence species richness despite increased habitat heterogeneity.

Differences in community structure in three different seascape contexts of Posidonia oceanica meadows

The null hypothesis of no differences in community structure of fish occurring over three different seascape contexts of *Posidonia oceanica* meadows was rejected based on nMDS and PERMANOVA results (Fig. 5, Table 5). Significant community differences across habitat arrangements are partly explained by interactions and habitat choice of individual species and their functional roles in the community.

Some of the observed species showed a significant association with one seascape context of *P. oceanica* meadow. For example, *Gobius bucchichi/incognitus* and *Mullus surmuletus* were more abundant in continuous meadows bordering sand. Juveniles of *Coris julis*, *Spicara smaris*, *Symphodus doderleini* and *Symphodus ocellatus* were more abundant in continuous meadows bordering rock, while *Serranus cabrilla* and *Spondyliosoma cantharus* were more abundant in mosaic meadows.

That association may be related to their interactions and choice of habitat components, a very similar observation to Rees et al. (2018) in Australia who detected differences in the abundance of species and families among habitats that contributed to the observed multivariate patterns of fish associated to temperate rocky reefs surrounded by seagrass meadows.

In our study, the most obvious observation is that *Coris julis*, the most abundant species, is common in all three seascape contexts of *Posidonia oceanica* meadows (Fig. 6). However, *C. julis* has higher abundances in mosaic meadows than in continuous meadows bordering sand (on average about 2.5x) and higher abundances in continuous meadows bordering rock vs. sand (on average about 2.3x) (Fig. 6). *C. julis* juveniles are seen more frequently in continuous *P. oceanica* meadows bordering rock and seem to avoid the mosaic arrangement, which could indicate interference competition with conspecific adults or an increased predation risk within the mosaic meadow. Mosaic meadows are characterized by high abundances of *Serranus scriba*, *Serranus cabrilla* and *C. julis*. They share a sit-and-pursue (Schmitz et al., 1997) or wait-chase (Kruschel and Schultz, 2010) predation mode, specifically promoted by mosaic habitat arrangements. Together, they make up 36% of the total abundance in the mosaic meadows (Fig. 7). *S. cabrilla* is thought to be a resident wait-chase predator (Bell and Harmelin-Vivien, 1983) that prefers coralligeneous hard bottoms and rocky reefs (Tunesi and Vacchi, 1993; Seytre et al., 2013), so it might be more abundant in mosaic meadows because it could use the benefit of a structurally more complex habitat for hunting prey (Fernandez et al., 2005). Another aggressive and very abundant (in all three seascape contexts) mesopredator is *Diplodus annularis*. However, it was seen to avoid the mosaic arrangement, perhaps because it cannot compete for food with its cruise-chase predation mode against the overall more abundant wait-chase predators. Active and visual pursuits of prey are less adaptive in highly complex habitats than passive pursuit tactics (Schultz et al., 2009).

The mosaic meadow is further defined by two substrate dwelling labrids (*Symphodus ocellatus* and *Symphodus melanocercus*) and two benthopelagic fish species taxa - adult *Chromis chromis* and adult Oblada melanura. It was interesting to note that the juveniles of *O. melanura* have not been observed within the mosaic arrangement. Adult *C. chromis* are almost twice as abundant in the mosaic arrangement than in the other two seascape contexts. Adult *O. melanura* are four times more abundant in mosaic meadows and 3.2x more abundant in continuous meadows bordering rock than in continuous meadows bordering sand (Fig. 6). The results mentioned above indicate that mosaic meadows' high structural complexity provides various food items and represents a very attractive habitat for such species (Guidetti and Bussotti, 1998). Bonaca and Lipej (2005) found that *C. chromis* avoided continuous seagrass meadows in general, so the

higher abundance of this species in mosaic meadows might indicate that the combination of *P. oceanica* and rocky boulders with macroalgae provided a more favorable habitat.

Overall, the highest fish abundances were recorded on transects placed in mosaic meadows with high habitat complexity where seagrasses and rocky-algal reefs are closely interspersed, constituting more habitat combinations and food niches than areas where one of the components is missing. Mosaic meadows are more heterogeneous and probably also more complex habitats, which may explain the highest fish abundances. The proximity of feeding grounds and shelter may enhance fish abundance and richness in seagrass beds, implying that complexity per se may be an essential factor in habitat choice; a combination of habitat types might have a higher value for fish than any individual component of a habitat (Unsworth et al., 2008).

In continuous meadows bordering rock, species such as *Symphodus doderleini* and *Symphodus ocellatus* were observed in higher abundances than in the other meadow types, probably because they generally inhabit seagrass beds and rocky reefs (Guidetti, 2000; Frau et al., 2003). Even though the mosaic meadows and continuous meadows bordering rock might look similar and are made of the same two structural elements (seagrass and rocky-algal reefs/boulders), it was interesting to see that in continuous *P. oceanica* meadows bordering rich rocky-algal habitat, *C. chromis* are less abundant than in mosaic meadows, and adult *O. melanura* are replaced by *Spicara smaris*, a zooplanktivorous fish (Karachle and Stergiou, 2014). Juveniles, observed to be more common in meadows bordering rock, are *Diplodus vulgaris* and small gobies, which were not observed in the mosaic arrangement.

In continuous meadows bordering sand, the species highly indicative of community structure were *Mullus surmulletus* and *Symphodus melanocercus*, which were exclusively observed in *P. oceanica* bordering sand (13 and 8 times, respectively). *M. surmuletus* is a bottom-dwelling transient predator, frequently found over sand and soft bottoms at depths less than 100 m (Ben-Tuvia, 1990). Although it is considered associated with *P. oceanica* (Stagličić et al., 2011), it was recorded during our research only if the adjacent habitat was unconsolidated sediments (Fig. 6), consistent with results of Fernández et al. (2005) who found that *M. surmuletus* forages along the seagrass boundaries and in sandy corridors. *Gobius bucchichi/incognitus* was more abundant in the continuous sand-bordering than in the rock-bordering *P. oceanica* meadows (Fig. 6), probably because it prefers sandy bottoms combined with structured habitat (*P. oceanica*, in this case) (Francour et al., 2011).

What is most interesting about the community within sand-bordering *P. oceanica* meadows, and seems to define it in contrast to the rock-related arrangements, is the presence of exclusively observed species that may

enter the *P. oceanica* meadow from within bare sand habitats in proximity (Jenkins et al., 2015). Examples aside from the above mentioned and relatively abundant *M. surmulletus*, *S. melanocercus* and *G. bucchichi/incognitus* are *Sarpa salpa*, *Symphodus rostratus*, *Thalassoma pavo* and juvenile *Spondyliosoma cantharus*. Juvenile *S. cantharus* choose a completely different habitat from their adult conspecifics. While juveniles are exclusively seen in continuous *P. oceanica* bordering sand, adults are more abundant in mosaic meadows than in continuous meadows bordering rock (14x) and meadows bordering sand (4.7x) (Fig. 6). This situation resembles that of adult and juvenile *C. julis* and might be another example of intraspecific competition and niche partitioning between adults and juveniles (Kimirei et al., 2013).

Species such as *Diplodus annularis* and *Symphodus cinereus* are known to occur on bare soft bottoms in the vicinity of seagrasses (Bell and Harmelin-Vivien, 1983), where they can feed. In our study, bare sand patches were absent from mosaic meadows and relatively rare in meadows bordering rock, which might explain the somewhat higher abundances of *D. annularis* and *S. cinereus* in continuous meadows bordering sand.

"Fishes associated with *Posidonia oceanica*" are often assumed to be uniform communities with local differences in temperature, currents and seafloor characteristics responsible for variation in their structure. However, fish individuals continuously make choices about habitat use as they move through the overall landscape, and their decision to associate with different habitats and habitat arrangements also depends on spatial proximity to habitat relative to their current needs (e.g., food, shelter, mates, predation evasion). Whether suitable structured or unstructured habitat is available in the direct vicinity of seagrass in part determines the community structure of associated fishes. Models of seagrass habitat preference and conservation plans for shallow fish communities in the Adriatic Sea would benefit from a more realistic view of habitat as an intricate mosaic in which seagrass is embedded in many habitat types that influence fish function, movement and preference for seagrass structure.

ACKNOWLEDGMENTS

UTJECAJ PROSTORNE ORGANIZACIJE ELEMENATA PODMORSKOG OKOLIŠA NA STRUKTURU ZAJEDNICA RIBA U NASELJIMA MORSKE CVJETNICE *Posidonia oceanica* U JADRANSKOM MORU

SAŽETAK

Naselja morske cvjetnice *Posidonia oceanica* igraju važnu ulogu u strukturiranju zajednica riba te utječu na taksonomsku i funkcionalnu raznolikost, brojnost i ponašanje riba. Relativna vrijednost naselja morskih cvjetnica ovisi o prostornoj organizaciji elemenata podmorskog okoliša te dostupnosti alternativnih staništa. Međutim, nedovoljno je poznato koji sve čimbenici utječu na strukturu zajednice riba povezanih s ovom morskom cvjetnicom. S ciljem utvrđivanja utjecaja različite prostorne organizacije elemenata podmorskog okoliša na zajednice riba, proveden je vizualni cenzus uz pomoć mamca u naseljima cvjetnice *P. oceanica* u hrvatskom dijelu Jadranskog mora. Utvrđen je značajan utjecaj različite prostorne organizacije elemenata podmorskog okoliša na strukturu zajednice riba – u rascjepkanim mozaičnim naseljima u kojima se *P. oceanica* isprepliće s kamenom podlogom obraslom makro-algama zabilježena je značajno veća brojnost riba u odnosu na kontinuirana cjelovita naselja (uz sediment ili uz kamenitu obalu). U radu su predstavljeni dokazi da dostupnost alternativnih strukturiranih staništa u neposrednoj blizini naselja morske cvjetnice *P. oceanica* utječe na strukturu zajednice riba koje u njoj žive. Neophodno je uzeti u obzir kontekst prostornog rasporeda elemenata podmorskog okoliša kojima dominira morska cvjetnica *P. oceanica* prilikom planiranja znanstvenih istraživanja, ali i kod upravljanja priobalnim područjima.

Ključne riječi: morske cvjetnice, ribe, struktura zajednice, vizualni cenzus uz pomoć mamca

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Table S1. Detailed information on all 55 lure-assisted visual transects performed in *Posidonia oceanica* meadows in the Adriatic Sea, Croatia, with measured variables

Transect	Site	Longitude (°E)	Latitude (°N)	Seascape context	*P. oceanica* Cover %	Seawater temperature (°c)	Coastline geography	Distance (m)	Slope (°)
3	Kudica 1	15.105950	44.030900	Bordering rock	P3	21	Open	67	8.5
4	Kudica 2	15.105900	44.030530	Bordering rock	P3	21	Open	60	9.5
5	Karantunic west	15.238048	44.007755	Mosaic	P3	20	Open	25	21.8
6	Karantunic north 1	15.238940	44.009221	Bordering rock	P4	20	Open	55	10.3
7	Karantunic north 2	15.238922	44.009219	Bordering rock	P4	20	Open	55	10.3
8	Pasman 1	15.267011	43.996777	Bordering sand	P3	20	Open	57	10.0
9	Pasman 2	15.266466	43.997343	Bordering sand	P3	20	Open	50	11.3
11	Kukljica	15.244669	44.045738	Bordering sand	P4	20	Open	60	9.5
12	Vir 1	15.026624	44.299919	Bordering sand	P3	19	Open	220	2.6
13	Vir 2	15.025384	44.300499	Bordering sand	P4	19	Open	240	2.4
14	Zut 1	15.334683	43.879622	Mosaic	P3	18	Open	25	21.8
15	Zut 2	15.334170	43.879167	Mosaic	P3	18	Open	30	18.4
16	Fulija east 1	15.113981	44.018591	Bordering rock	P2	16	Open	75	7.6
17	Fulija east 2	15.114600	44.018908	Bordering rock	P3	16	Open	65	8.8
18	Luski 1	15.085862	43.998301	Bordering rock	P4	17	Open	35	16.0
19	Luski 2	15.085387	43.998743	Bordering rock	P4	17	Open	35	16.0
20	Fulija west 1	15.111995	44.017619	Mosaic	P3	17	Open	45	12.5
21	Fulija west 2	15.113311	44.018246	Bordering rock	P2	18	Open	33	16.9
22	Iski Mrtovnjak 1	15.176230	44.011649	Bordering rock	P3	18	Open	33	16.9
23	Iski Mrtovnjak 2	15.175929	44.012069	Bordering rock	P3	18	Open	33	16.9
24	Plic Ljuta 1	15.604806	43.665246	Mosaic	P4	19	Open	56	10.1
25	Plic Ljuta 2	15.605404	43.665475	Mosaic	P4	19	Open	55	10.3

Continued.

Transect	Site	Longitude (°E)	Latitude (°N)	Seascape context	*P. oceanica* Cover %	Seawater temperature (°c)	Coastline geography	Distance (m)	Slope (°)
26	Mala Nozdra 1	15.605914	43.668676	Bordering rock	P3	19	Embayment	42	13.4
27	Plic Grmeni	15.623158	43.620602	Mosaic	P3	18	Open	1	84.3
28	Hrid Balkun 1	15.599330	43.633053	Mosaic	P4	18	Open	40	14.0
29	Hrid Balkun 2	15.599628	43.633440	Mosaic	P4	18	Open	43	13.1
32	Rt Buhanj	15.172067	43.895204	Bordering rock	P2	14	Embayment	85	6.7
33	Cuscica	15.218052	43.898339	Bordering sand	P2	14	Embayment	100	5.7
34	Kobiljak	15.196692	43.868956	Bordering rock	P3	14	Embayment	55	10.3
35	Saharun	14.875875	44.131139	Bordering sand	P4	15	Embayment	220	2.6
36	Brbinjscica	14.991271	44.055451	Bordering rock	P3	14	Embayment	30	18.4
37	Kablinac Kakan	15.608700	43.715474	Mosaic	P3	14	Open	40	14.0
38	Mljet Sij 1	17.322754	42.788030	Bordering rock	P4	15	Open	32	17.4
39	Mljet Sij 2	17.323113	42.788133	Bordering rock	P3	16	Open	42	13.4
40	Mljet Sparozni rat 1	17.329015	42.788957	Bordering rock	P2	16	Embayment	55	10.3
41	Mljet Sparozni rat 2	17.330242	42.789078	Mosaic	P3	16	Embayment	35	16.0
42	Mljet Lokva west 1	17.330833	42.786803	Bordering rock	P2	16	Embayment	45	12.5
43	Mljet Lokva west 2	17.330524	42.786173	Bordering rock	P2	16	Embayment	38	14.7
44	Mljet Lokva east 1	17.332956	42.785474	Bordering rock	P4	16	Embayment	35	16.0
45	Mljet Lokva east 2	17.332571	42.784723	Bordering rock	P3	17	Embayment	44	12.8
46	Mljet Luka Gonoturska 1	17.391375	42.766292	Mosaic	P3	15	Open	35	16.0
47	Mljet Luka Gonoturska 2	17.392726	42.766016	Mosaic	P4	15	Open	40	14.0
48	Lumbarda Przina	17.186266	42.913910	Bordering sand	P4	17	Embayment	78	7.3
49	Lumbarda rt Raznjic	17.200940	42.919044	Bordering rock	P3	16	Open	90	6.3

Continued.

Transect	Site	Longitude (°E)	Latitude (°N)	Seascape context	*P. oceanica* Cover %	Seawater temperature (°c)	Coastline geography	Distance (m)	Slope (°)
50	Kamenjak Fenoliga	13.898255	44.763837	Bordering rock	P3	16	Open	317	1.8
51	Kamenjak Sekovac	13.925496	44.779630	Bordering rock	P2	17	Open	80	7.1
52	Galijola	14.177328	44.725465	Mosaic	P2	17	Open	320	1.8
53	Brijuni Vrbanj	13.735631	44.920838	Bordering sand	P2	16	Open	205	2.8
54	Brijuni Javorika	13.763883	44.905354	Bordering sand	P2	18	Embayment	100	2.9
55	Vela Nozdra 1	15.603839	43.672415	Bordering rock	P4	22	Embayment	64	8.9
56	Vela Nozdra 2	15.604806	43.672308	Bordering rock	P4	22	Embayment	60	9.5
57	Cesminica 1	16.979062	42.767688	Bordering sand	P4	24	Open	75	7.6
58	Cesminica 2	16.978286	42.768253	Bordering sand	P4	24	Open	75	7.6
59	Telascica 1	15.177041	43.877326	Bordering sand	P4	24	Open	75	7.6
60	Telascica 2	15.177367	43.876364	Bordering sand	P4	24	Open	120	4.8