

Seascape context and local predators drive fish community structure of *Posidonia oceanica* meadows

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UNIVERSITY OF SPLIT, UNIVERSITY DEPARTMENT OF MARINE STUDIES
UNIVERSITY OF DUBROVNIK

Postgraduate study of Applied Marine Sciences

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**SEASCAPE CONTEXT AND LOCAL PREDATORS DRIVE FISH
COMMUNITY STRUCTURE OF *POSIDONIA OCEANICA* MEADOWS**

Doctoral thesis

Split, July 2020

This doctoral thesis was performed at the University of Zadar, Department of Ecology, Agronomy, and Aquaculture, under the guidance of Stewart T. Schultz, Ph.D. as a part of the inter-university postgraduate studies of Applied Marine Sciences at the University of Split and University of Dubrovnik.

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“Feeling gratitude and not expressing it is like wrapping a present and not giving it.”

William Arthur Ward

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SEASCAPE CONTEXT AND LOCAL PREDATORS DRIVE FISH COMMUNITY STRUCTURE OF *POSIDONIA OCEANICA* MEADOWS

Ivana Zubak Čižmek

Thesis performed at the University of Zadar

Abstract

Marine underwater habitats dominated by seagrass *Posidonia oceanica* play an important role in the assembly of fish communities, affecting taxonomic and functional diversity, abundance, and fish behavior. In order to identify the relative importance of different seascape contexts of *P. oceanica* meadows as a habitat for fishes, fish communities associated with the seagrass *P. oceanica* were investigated in the Croatian Adriatic Sea, using SCUBA lure-assisted visual census. To test for the effect of predators on fish community structure, existing literature data on fish assemblages associated with *P. oceanica* meadows in the Mediterranean was assembled and a meta-analysis was performed. The results show: I) There is a significant effect of different arrangement of seascape elements on fish community structure -- fragmented mosaic meadows with *P. oceanica* growing directly on and between rocky-algal reefs had significantly higher fish abundances compared to both types of continuous meadows (bordering rock and bordering sand); and II) Total predator abundance and abundance of resident predators had a significant effect on the prey fish community -- a higher abundance of resident predator species was associated with an overall lower number of prey species. This thesis provides evidence that alternative structured habitats within close proximity to seagrass beds may affect the community structure of associated fish assemblages and that the presence of predators reduces the value of *P. oceanica* meadows as a refuge habitat for potential prey species. The dissertation aims at highlighting the need for the consideration of the seascape context of *P. oceanica* meadows in conservation management and experimental design for fish community structure while acknowledging the importance of resident predators when evaluating the relative value of this important seagrass as a habitat for the Mediterranean fish assemblages.

(123 pages, 14 figures, 11 tables, 142 references, 3 appendices, original in English)

Thesis deposited in National and University Library in Zagreb, Split University Library and Library of University of Zadar.

Keywords: Adriatic Sea, community structure, fish, lure assisted visual census, Mediterranean Sea, *Posidonia oceanica*, predation, seagrass, seascape.

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UTJECAJ PROSTORNE ORGANIZACIJE ELEMENATA PODMORSKOG OKOLIŠA I PREDATORA NA STRUKTURU ZAJEDNICA RIBA U NASELJIMA MORSKE CVJETNICE *POSIDONIA OCEANICA*

Ivana Zubak Čižmek

Rad je izrađen na Sveučilištu u Zadru

Sažetak

Naselja morske cvjetnice *Posidonia oceanica* igraju važnu ulogu u strukturiranju zajednica riba te utječu na taksonomsku i funkcionalnu raznolikost, brojnost i ponašanje riba. Nedovoljno je poznato koji sve čimbenici utječu na strukturu zajednice riba povezanih s ovom morskom cvjetnicom. S ciljem utvrđivanja utjecaja različite prostorne organizacije elementa podmorskog okoliša na zajednice riba, proveden je vizualni census uz pomoć mamca u naseljima cvjetnice *P. oceanica* u hrvatskom dijelu Jadranskog mora. Kako bi se ispitao utjecaj predatora na strukturu zajednica riba u naseljima morske cvjetnice *P. oceanica* na razini Sredozemnog mora, provedena je meta-analiza podataka u objavljenim znanstvenim radovima. Utvrđen je značajan utjecaj različite prostorne organizacije elementa 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). Ukupna brojnost predatora i brojnost stalno nastanjenih predatora pokazuje značajan utjecaj na zajednicu riba – povećanje brojnosti predatorskih vrsta dovodi do smanjenja broja vrsta u zajednici plijena. 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 te da prisustvo predatora smanjuje relativnu vrijednost naselja morske cvjetnice *P. oceanica* kao staništa za ribe koje predstavljaju potencijalni plijen. 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. Također je važno razmotriti utjecaj lokalnih, stalno nastanjenih predatora kada se procjenjuje relativni značaj naselja ove važne morske cvjetnice kao staništa za ribe na području Sredozemnog mora.

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Ključne riječi: Jadransko more, morske cvjetnice, podmorski okoliš, *Posidonia oceanica*, predacija, ribe, Sredozemno more, struktura zajednice, vizualni census.

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1. INTRODUCTION

Shallow benthic ecosystems (rocky shores, mangroves, estuaries, seagrass meadows) have many important functions worldwide; they provide high primary and secondary production and support a great diversity of fauna (Orth et al. 1984; Beck et al. 2001; Nagelkerken et al. 2001). Complex habitats offer three-dimensional structure, thus provide habitat and feeding niches, and nursery ground for many commercially and ecologically important fish and invertebrate species (Orth et al. 1984; Jenkins et al. 1997). Both alpha (resource-related) and beta (habitat-related) niches provided by the structured habitats are necessary to maintain high species diversity and richness (Mouillote 2007). Alpha niches or resource-related niches are the results of the variety of prey or food sources, which is, consequently, dependent on the heterogeneity and diversity of habitats. Beta niches or habitat-related niches are present in heterogeneous and diverse habitats with different macrophyte covers and they provide microhabitats and protection from predators (Wilson 1999), as well as cover for ambush predators (Zubak et al. 2017). These goods and services provided by the highly structured habitats should be taken into account when planning strategies for managing fish biodiversity.

Seagrasses represent one of the most productive and diverse marine habitats in shallow coastal waters, mainly because they form extensive and dense meadows of great structural complexity (Duarte & Chiscano 1999). The value of seagrasses goes far beyond simply providing habitat for a diverse fauna; they are important in structuring the entire ecosystem, and are considered to be “ecosystem engineers” because they slow down water movement, stabilize the sediment, protect the coast from erosion, increase sedimentation rate, and are important in the processes of denitrification and serve as carbon storage (Bos et al. 2007; Eyre et al. 2011; McLeod et al. 2011; Mazarrasa et al. 2015). Seagrass habitats play an important role in controlling assembly of fish communities, affecting species diversity, abundance, biomass, and behavior. Their crucial function is to provide habitat for e.g. juveniles, especially in places where there is no other structured habitat available (such as rock or macroalgae). For various marine faunal species, they provide permanent habitat allowing completion of the full life cycle (Deudero et al. 2008), thus play a fundamental role in maintaining their populations. Although seagrasses represent important habitats and are considered to be “biodiversity hotspots”, they are one of the most endangered habitats in the

world (Beck et al. 2001; Pergent 2012) and the lack of knowledge about the significance of this habitat in maintaining fish populations is evident (Unsworth & Cullen 2010; Giakoumi & Kokkoris 2013).

Extensive monospecific meadows of the endemic Mediterranean seagrass *Posidonia oceanica* (L.) Delile, 1813 (Figure 1.1.) are present between the surface and 44 m of depth (e.g. Malta, Corsica; Augier & Boudouresque 1979; den Hartog 1979; Boudouresque et al. 1990; Borg & Schrembi 1995; Procaccini et al. 2003). The recently published data on the distribution of *P. oceanica* shows that the known covered area is approximately 12 200 km², but the lack of information on the distribution along the eastern and southern coast of the Mediterranean basin leads to an underestimation of this value (Telesca et al. 2015). In the Eastern Adriatic Sea, *P. oceanica* occurs at depths ranging from 0 to about 36 meters (Zubak et al. 2020), on mobile sediments, mostly sand, but sometimes also on flat rock and/or rock boulders. The meadows are very diverse and most often occur as dominant habitat in one of the three types of spatial organization of the seascape elements: (i) continuous meadows bordering sand, (ii) continuous meadows bordering rocky-algal reef and (iii) mosaic meadows where *P. oceanica* grows on rocky substrates and between boulders with macro-algae – a special case where seagrasses grow directly in the crevices of rocks and between rocky boulders (Figure 1. 2. and Figure 1. 3.). The meadows of *P. oceanica* are highly sensitive and despite being extremely important, they are threatened by anthropogenic activities (Boudouresque et al. 2000, 2006) and are therefore listed as a priority habitat in Annex I of Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora (Council Directive 92/43/EEC 1992). In the Croatian legislative, *P. oceanica* is considered a strictly protected species (Official Gazette 144/2013).



Figure 1.1. Endemic Mediterranean seagrass *Posidonia oceanica* in the Adriatic Sea, Croatia.
Photo by Ivana Zubak Čižmek (Vir Island; 10 m depth; August 30, 2012).

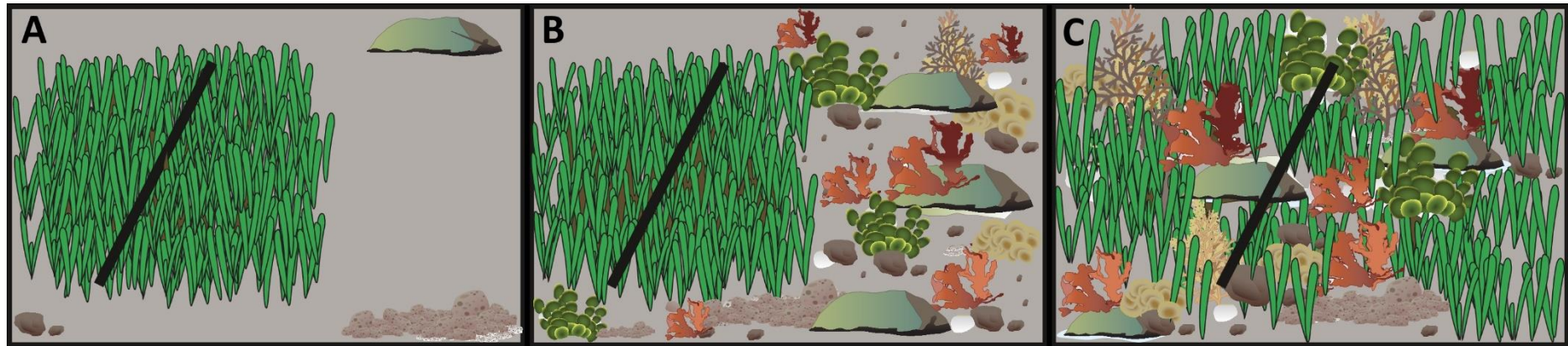


Figure 1.2. Illustration of the three types of the spatial organization of the seascape elements.

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 Čížmek 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).

It is important to understand the different drivers of fish community structure and functioning in order to successfully manage and protect fish communities, as well as to understand the potential impact that various stressors might induce on the marine environment. The structure of the fish community within seagrass meadows, among other factors, can be affected 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. 2006; Pittman et al. 2007; Unsworth et al. 2008). The diversity of species and the abundance of fish in seagrass meadows can be positively influenced by the greater structural complexity of the habitat (Graham & Nash 2013; Henderson et al. 2017), and the importance of habitat structural complexity and its relationship with species richness and abundance is acknowledged, but the mechanisms behind this effect are still not well understood (Kovalenko et al. 2012). The combination of shelter, food resources, and the protection from predators are the major factors that shape fish communities (Connolly & Hindell 2006). The risk of mortality can have a direct impact on the population structure of reef and seagrass associated fish species (Connell 1998). Since predation is the major source of mortality in juvenile and small-bodied individuals, the mortality rates are correlated to the presence and abundance of predator, and resident predators in particular can change the density/abundance and size structure of fishes in a particular habitat (e.g. seagrass meadow) (Connell 1996). In order to understand impacts of predation, different mechanisms through which predators affect the prey communities should be considered (Mukherjee et al. 2014). It is well known that predators can have both consumptive (by reducing density) and non-consumptive (by changing behavior and physiology) risk effects, which are equally important in regulating the remaining (prey) community structure (Preisser et al. 2005). Resident, sit-and-wait ambush predators are more likely to induce non-consumptive risk effects than cruising transient predators (Schmitz 2008), therefore prey might choose to avoid habitats used by resident ambush predators, and concentrate in lower-risk habitats lacking such predators (e.g. neighboring sand) (Schultz & Kruschel 2010). On the other hand, where fast cruising predators are abundant, three-dimensional structured habitats might provide hideout for prey species (Heck & Orth 1980). It was assumed that the primary value of seagrasses for mobile organisms lies precisely in the fact that they represent a prey refuge by reducing visibility and interfering with the movement of predators. The above-mentioned assumption was based on the “Seagrass Superiority

Hypothesis – SSH”, which predicts that seagrasses represent a refuge habitat in which the total risk of mortality is lower than in neighboring “open” habitats (Heck & Orth 1980; Bell & Pollard 1989). Therefore, it was proposed that fish individuals residing in the seagrass meadows might have an increased chance of survival and that the benefits of seagrass habitat are provided through protection against predators during spawning, migration of larvae, and the development of juveniles. What the SSH hypothesis does not explain is the negative preference of many fish species to seagrass habitats and the large differences in the structure of fish communities associated with seagrasses. Also, the SSH hypothesis does not take into account the predators’ ability to learn to find and hunt prey within seagrass canopy (Hellman et al. 2009). To complement the existing knowledge, an alternative hypothesis was proposed, that considers the presence of different types of predators – the Predation Mode Hypothesis predicts that the abundance and behavior of local predator populations affect the relative risk of mortality that an individual may experience within a seagrass meadow, and that individual must respond to a trade-off between food availability and risk of predation, usually by increasing their use of safer but less profitable habitats (e.g. bare sand) (Schultz et al. 2009; Swain et al. 2015).

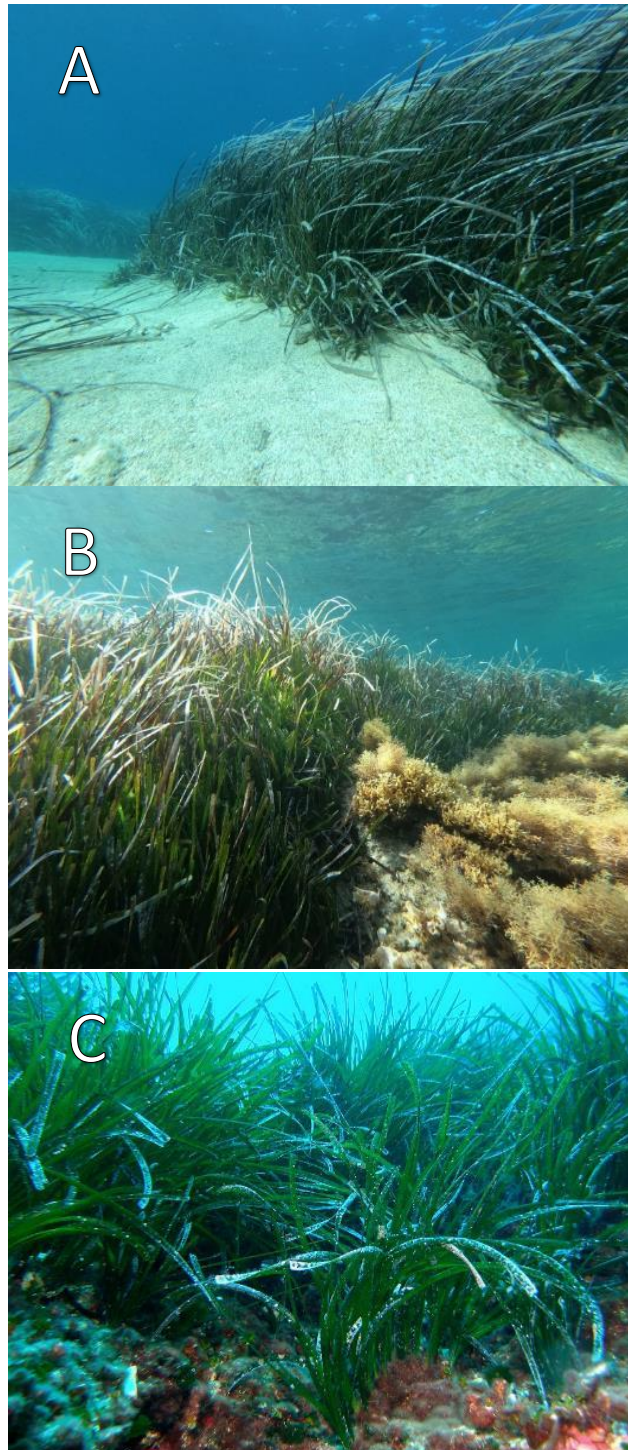


Figure 1.3. Three most common types of the spatial organization of the seascape elements of *Posidonia oceanica* meadows in the Adriatic Sea, Croatia.

A: Continuous meadow bordering sand. B: Continuous meadow bordering rocky-algal reef. C: Mosaic meadow on rocky substrates and between boulders with macro-algae. Photos by Hrvoje Čižmek, A: Korčula Island (10 m depth; May 19, 2012); B: Fulija Island (10.5 m depth; September 28, 2012); C: Galijola (10 m depth; May 31, 2012).

1.1. Aim and goal of the dissertation

This dissertation consists of two parts; one is centered around the main hypothesis that seascape context plays an important role in defining the fish community structure of *Posidonia oceanica* associated species, and the second part focuses on the effect of predators on species richness, abundance and the community structure of *P. oceanica* associated fish. The content regarding the second hypothesis has been published in Zubak et al. (2017). Predators structure fish communities in *Posidonia oceanica* meadows: meta-analysis of available data across the Mediterranean basin. Mar. Ecol. Prog. Ser., 566: 145-157 (<https://doi.org/10.3354/meps12038>), and the Licence to reproduce has been granted by the MEPS and Inter-Research as the copyright holder.

The aim of this dissertation is to provide data and information which can be use to better govern and manage underwater seascapes centered around *P. oceanica* meadows. The information about the potential drivers of fish community structure can be useful to stakeholders and the wider community in the process of making informed decision about the protection, management, and sustainable use of marine resources in Croatia. Therefore, in this dissertation we describe the drivers of community structure of fish associated with *P. oceanica* meadows, and specifically detect:

- a) whether and how the seascape context and the proximity of neighboring three-dimensional habitat affect the fish species richness, fish community structure and abundance, and
- b) what is the effect of predators on the structure of a (prey) fish community.

The specific goals of the dissertation are:

- (1) to detect factors whose variation leads to differences in fish community structure associated with *P. oceanica* meadows, with particular emphasis on documenting the differences that individual fish species will show in their preferences for different types of the spatial organization of *P. oceanica* seascape elements,

- (2) to determine the value of *P. oceanica* meadows as a shelter for fish, which is predicted to be relative and dependent on the presence of different predator species, and

(3) to highlight the need for the consideration of seascape context of *P. oceanica* meadows in conservation management and experimental design for fish community structure.

The null hypotheses proposed in this dissertation are:

H01: There are no differences in fish community structure and abundance of fish assemblages occurring over three different seascape contexts of *P. oceanica* meadows, including the availability of alternative structured neighboring habitat (bordering sand / bordering rocky-algal reef / mosaic).

H02: The differences in species composition and abundance of predators do not affect the fish community structure associated with *P. oceanica* meadows.

2. REVIEW OF FORMER RESEARCH

2.1. The effect of seascape context of seagrass meadows on fish communities

In a classical approach, a landscape can be defined as a mosaic of different arrangements of biotic and abiotic structures (Robbins & Bell 1994) or if we re-state a relatively simple formulation, we might consider the landscape as the area of spatial heterogeneity (Pittman 2017). Analogous term *seascape* was introduced to describe spatial arrangement of habitat structures in the marine context (Pittman et al. 2011). The spatial arrangement of ecosystem elements or **seascape context** changes according to the variations in depth, habitat size, and proximity to other habitats, and is known to alter the diversity of species and the abundance of fish (Olds et al. 2016; Pittman 2017). The migration of organisms, as well as the movement of energy and resources across various seascapes, are affected by habitat heterogeneity, which in turn has an effect on habitat utilization by different marine fish species (Hyndes et al. 2014). Species that move through the space of a certain habitat type are assumed to search for different resources throughout their life (Hanski et al. 2017). Once organisms, such as fish, choose a certain habitat in a given time, their further movements within that area can be affected by various factors, and the most important are the availability of food, predator avoidance and search for a mate (Bond et al. 2012). Most of the evidence for the effect of the seascape context on the faunal communities comes from shallow coral reef and mangrove ecosystems (Kendall et al. 2004; Gilby et al. 2018; Pittman 2017), but it is unclear whether the similar effect can be expected in other ecosystems, especially in the temperate seagrass meadows. The relationship between spatial arrangement of habitat elements and ecological processes that take place at a given habitat is a very important factor in heterogeneous seascape mosaics (Turner 2005), even more so when we aim to better understand the relationship between the observed species and their environment (Fahrig et al. 2011). Seagrass meadows form a seascape mosaic of different patch sizes, patches embedded in different matrix habitats (e.g. sand or rocky reefs), number of edges or different cover (i.e. densities of leaves) (Pages et al. 2014). Worldwide, the migration of animals, especially fish, connects the seagrass meadows to a variety of other habitat types (e.g. mangroves, coral reefs) (Dorenbosch et al. 2004; Mumby et al. 2004; Pittman et al. 2004), and the importance of consideration of the surrounding seascape structure has been

thoroughly described in Pittman et al. (2007). The above mentioned surrounding seascape effect and the effect of predators on animal communities gained attention in recent years because field surveys showed that traditional metrics (e.g. the % of ground cover, patch size, etc.) might not be sufficient to explain variation in community structure of tropical faunal assemblages (Olds et al. 2012; Darling et al. 2017) and it became evident that, for example, coral reef connectivity with adjacent mangroves and seagrass meadows significantly affected the community structure of associated fauna (Olds et al. 2012).

The available scientific information regarding the effect of seascape context on the differences in fish community structure in seagrass meadows predominantly originate from studies conducted in the tropical and subtropical submarine environments of the United States (Adams 1976; Wyda et al. 2002) and Australia (Bell & Pollard 1989). It has long been considered that seagrass meadows represent absolute shelter from predators, and the assumption was due to the fact that such studies were performed in environments where there was no structured habitat available other than the seagrass meadow (Heck & Orth 1980; Bell & Pollard 1989). As the number of research papers began to increase, so did evidence in favor of the assumption that three-dimensional structure in general, rather than the seagrass meadows per se, is the primary value to fish communities: Nakamura & Sano (2004) describe the effect of adjacent coral reefs on fish communities in nearby seagrass meadows (Japan), emphasizing the importance of both habitats for juvenile fish, Gilby et al. (2018) show that it is imperative to observe the overall seascape context in Australian coastal waters, and emphasize that seagrasses significantly affect the fish communities of the different adjacent estuary habitats by increasing the diversity of species and the abundance of individuals. *Posidonia oceanica* is one of the most studied seagrass species with a seascape approach (Abadie et al. 2018) because it builds extensive beds with complex three-dimensional structures. Fish communities in *P. oceanica* meadows in the Mediterranean Sea have been studied extensively (Bell & Harmelin-Vivien 1982; Francour 1997; Moranta et al. 2006; Boudouresque et al. 2012) and very large spatio-temporal differences in the fish community structure have been identified (Guidetti 2000; Deudero et al. 2008; Kalogirou et al. 2010). However, only few published papers document the differences between fish community structure in *P. oceanica* meadows compared to other habitats such as rocky algal reefs or unconsolidated sediments (Jenkins et al. 1997; Mouillote et al. 1999; Guidetti 2000). Moreover, no data are available that account for differences between different types of the spatial organization of *P. oceanica* seascape elements, especially not in the context of composition and

spatial arrangement of resources across the seascape and the availability of alternative structured habitats in close proximity.

2.2. The effect of predators on fish communities

The close relationship between the fish and structured habitat could be attributed to the combination of increased food availability and refuge from predators, and the effect of predation in regulating community structure has been well studied because predation is one of the most important factors that define faunal communities in marine habitats (Duffy & Hay 2001; Morin 2011). For a given species, depending on its ontogenetic stage, habitat choice can be the result of tradeoff between food availability and predation risk (Dahlgren & Eggleston 2000). When we talk about the effect of predators on the prey (fish) community in seagrass meadows, studies have shown that prey actively seek shelter in seagrass meadows where predator activity is impeded, for example, due to visual disturbance caused by a decrease in light availability (Zupo & Nelson 1997). Similarly, it has been shown that predation could be lower in *Posidonia oceanica* meadows because the long and dense leaf canopy can prevent predators from actively chasing prey (Bell & Harmelin-Vivien 1982, 1983; Francour 1997; Guidetti 2000), but the presence of local resident predators at the same time has been shown to pose a great threat to some prey species (Bell & Harmelin Vivien 1982, 1983). In a study conducted in the Novigrad Sea (Eastern Adriatic), Schultz et al. (2009) showed that the relative risk of mortality was variable and dependent on the abundance and presence of predators, which is consistent with the results presented in 2003 by Heck et al. They show that in places where there is no other shelter, seagrass meadows are a refuge from transient predators, but the habitat structure can also serve as a hiding place for local ambush predators, in which case, the seagrass meadow is not the place where prey will choose to seek shelter. In *Zostera marina* seagrass meadows in Japan (Horinouchi 2007) and Croatia (Schultz et al. 2009, Schultz & Kruschel 2010), prey abundance was negatively correlated with the presence of local ambush predators, and overall lower abundance of fish was recorded in the seagrass meadows than in adjacent, open habitats. However, up to now, there is no information available on how local, permanently resident predators and predators that actively swim and hunt above seagrass canopy affect the community structure fish associated with the *P. oceanica* meadows.

3. MATERIAL AND METHODS

3.1. The effect of seascape context on the fish community structure

3.1.1. Study area and methods used

The Adriatic Sea has a surface of approximately 138 600 km² and represents the northernmost part of the Mediterranean Sea (reaching north as far as 45°47' N, excluding the Black Sea), and spans more than 800 km in length and approximately 200 km in width. Its geomorphology is associated with a formation of tectonic Apulian or Adriatic microplate which caused the east coast, from the Istrian Peninsula to Albania, to be generally high and rocky, with more than 1200 islands offshore (McKinney 2007). The Croatian coast with the mainland coastline of 1 777 km and additional 4 398 km of island coastline is one of the most indented in the Mediterranean (Duplančić Leder et al. 2004) so the spatial heterogeneity of the benthic assemblages and the organization of seascape elements is very high, and can affect the animal (especially fish) benthic communities (Curiel et al. 2012; Ponti et al. 2014). Rocky, calcareous coasts dominate throughout the eastern part of the basin, affecting benthic assemblages: starting from the shore, the seafloor is dominated by photophilic algae and sea urchin barrens, and near rocky shores, especially in shallow bays, seagrass meadows are recorded (Devescovi et al. 2005). Survey of fish assemblages within seagrass meadows of *Posidonia oceanica* was performed during 2011 (June-September) and 2012 (March-September), along the entire eastern coast of the Adriatic Sea, Croatia (Figure 3.1.1.1.).

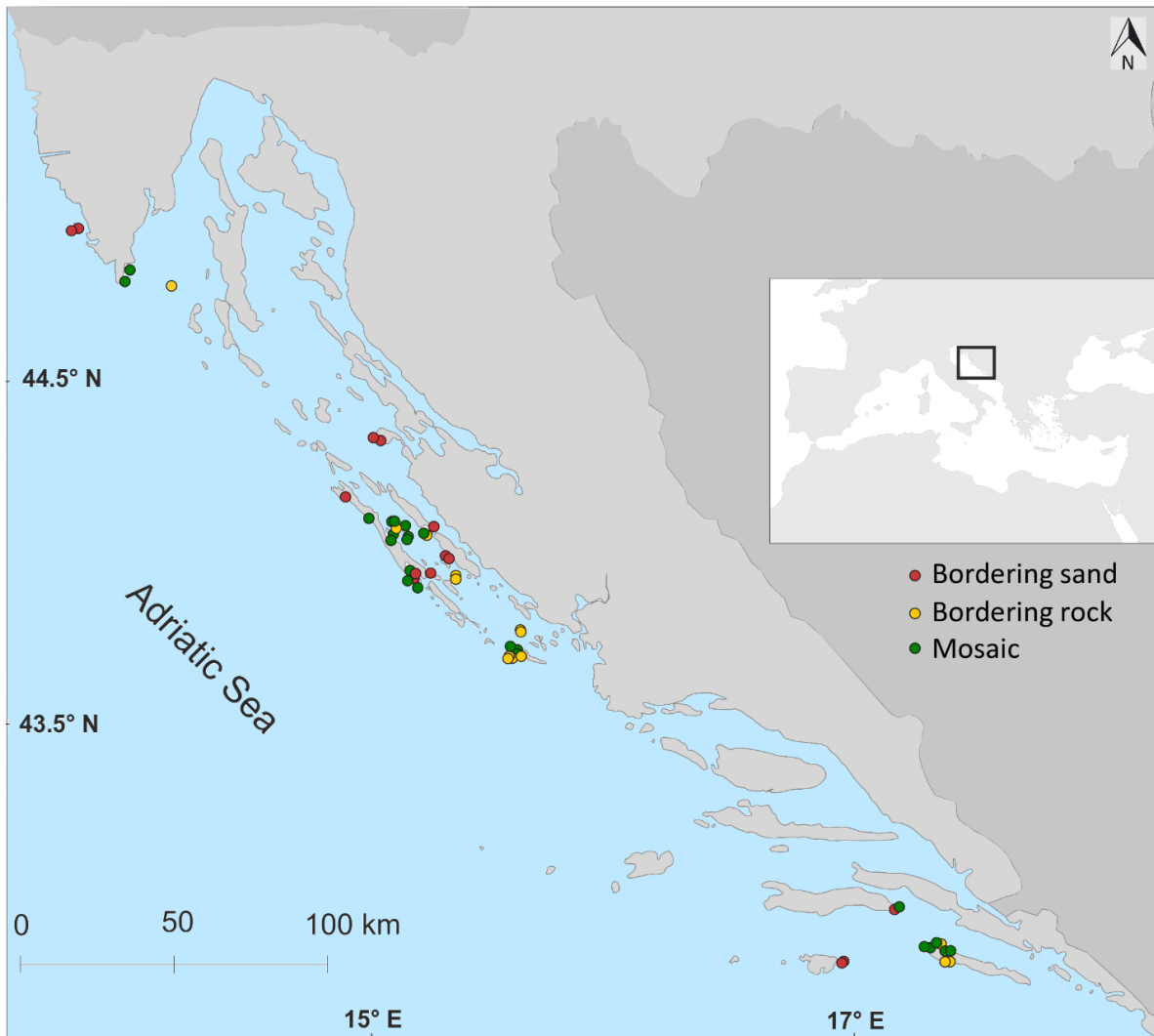


Figure 3.1.1.1. Map of locations of surveyed fish assemblages within seagrass meadows of *Posidonia oceanica* in the Eastern Adriatic Sea, Croatia.

Fifty-five lure assisted visual census belt transects (Table 3.1.1.1.) were performed, using SCUBA diving. The site locations were selected randomly within a study area (Croatian Adriatic coast) making sure that each of the 55 transects represents an independent replicate. Each transect was placed within one of the three seascape contexts (bordering sand / bordering rocky-algal reef / mosaic) of the *P. oceanica* meadows: 14 transects were in the continuous meadows bordering sand, 27 transects were in the continuous meadows bordering rocky-algal reef and 14 transects were in the mosaic meadows. All transects were positioned at 10 meters of depth and at least 10 meters away from the edge of the meadow (excluding the mosaic seascape context). All transects were performed during the daytime,

during calm waters and no wind (0-1 Beaufort). The diver (always the same individual observer, Ivana Zubak Čížmek (IZČ)) moved along each transect, which was georeferenced using a GPS device attached with a thin blue rope to a buoy pulled directly above the diver (Garmin GPSMAP 60CSx Handheld GPS Navigator). The diver observed and recorded all fish appearing within a water column defined by its 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).

The lure assisted visual census method was chosen because it allows to observe fish species that are usually omitted during the standard visual census method (Kruschel & Schultz 2011a, 2012). The method is based on the addition of a lure (small [2x1 cm] piece of lead tied to a fishing line, wrapped around a styrofoam board) to the standard visual census method. The lure was positioned and moved approximately 5 cm above the substrate's surface (Figure 3.1.1.2.), while the diver remained at least 2 m above the lure. 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, and if transects varied in timespan, the error variance in 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. As previously mentioned, 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, etc. (Kruschel & Schultz 2011a, 2012). Along each transect, the diver took the following data on individual fish: 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 & Johnson 2001). If observed individuals were grouping/schooling, individual fish observations were considered non-independent; such groups were defined as 2 or more individuals of the same taxon observed at the same moment - individuals were counted up 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 *Posidonia oceanica* cover ($p_2 < 50\%$, $50\% \leq p_3 \leq 75\%$, $75\% \leq p_4 \leq 100\%$) for each transect. Other predictor

variables, in addition to seascape context and cover, that potentially influence the fish assemblage structure included seawater temperature (°C), the coastline geography (embayment vs. open shore), the distance from the shoreline (m) and the degrees of the slope of the shore (°, calculated from distance from the shore and transect depth) (Table 3.1.1.1.).

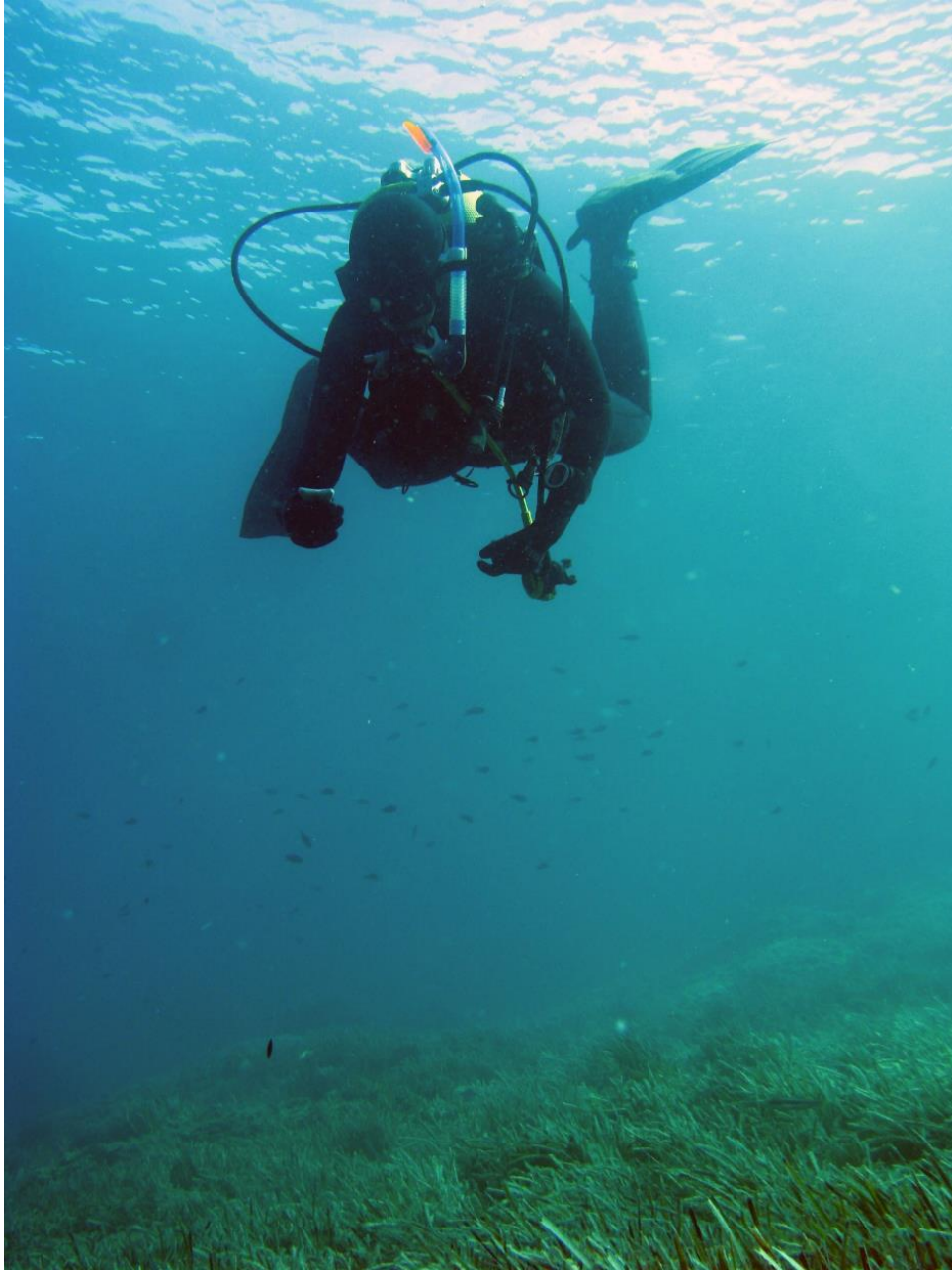


Figure 3.1.1.2. The diver performing lure-assisted visual census of fish communities over a *Posidonia oceanica* meadows in the Adriatic Sea, Croatia. Photo by Hrvoje Čižmek (Dugi otok; 10 m depth; July 11, 2011).

Table 3.1.1.1. 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	<i>P. oceanica</i> 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
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
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

3.1.2. Data analysis

Collected data were organized using the Microsoft Excel 2013. The maps and figures were created and edited using Inkscape 0.92.4. All statistical analyses were conducted using R (R Development Core Team 2017) and RStudio 1.1.383. For statistical analyses, significance level was set at $\alpha = 0.05$.

A number of univariate and multivariate analyses were used to characterize the fish assemblages and to explore the variation in fish community structure between the three seascape context of *Posidonia oceanica* meadows (bordering sand / bordering rock / mosaic).

Fish assemblages were characterized by documenting the total number of individuals (N), species richness (S), Shannon-Weaver diversity index (H) and Pielou's Evenness (J) which were calculated for each transect.

Shannon-Weaver (or Shannon-Wiener) index is defined as

$$H = -\sum p_i \log(b) p_i,$$

where p_i is the proportional abundance of species i and b is the base of the logarithm.

Pielou's measure of species evenness was calculated as

$$J = H' / \ln(S)$$

where H' is Shannon Weiner diversity and S is the total number of species in a sample, across all samples in dataset.

The absolute (the number of individuals found per transect) and relative abundance (the percent abundance of each species relative to the total number of individuals in each transect) of adult and juvenile fish were recorded, and due to the fact that transects varied in length and were time standardized, in the analysis of the effect of seascape context on the fish abundance, the abundance was additionally expressed as abundance per m^3 of each transect;

$$m^3 = volume = length * width * height.$$

In order to test for differences in the selected univariate indices among the three different seascape contexts (bordering sand / bordering rock / mosaic) of *P. oceanica*

meadows, analysis of variance (ANOVA) was done using the aov function (Chambers et al. 2017). The analyses were based on a one-way model and the residuals were checked for normality using the Shapiro-Wilk test.

The Tukey HSD post-hoc test using the TukeyC function and package (Faria et al. 2018) was performed to explore differences in species richness and abundance among all pairs of levels of the selected factor (seascape context).

To compare fish assemblages found associated with the 3 different seascape contexts of *P. oceanica* meadows, we used permutational multivariate analysis of variance PERMANOVA (Anderson 2001; McArdle & Anderson 2001), which is a non-parametric confirmatory statistics method. The predictor variable of interest was the seascape context of the meadow (bordering bare sand, bordering rocky-algal reefs, or mosaic rocky-algal substratum), while *P. oceanica* cover and the response matrix was the matrix of relative fish abundances in each community at each transect, with transect being the statistical sample replicate (N = 55). The fish community matrix was converted to the Bray-Curtis distance matrix prior to analysis. The similarities among communities grouped by the main 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, based on the metaMDS function in the vegan package of R, which is taught to be the most robust unconstrained ordination method in community ecology (Faith et al. 1987; Minchin 1987). Using conventional analysis of variance, we further partitioned abundance variation of each species within and among different seascape contexts of *P. oceanica* meadows, and reported the associated observed F statistic and its probability.

3.2. The effect of predators on the fish community structure

3.2.1. Study area and methods used

Literature search and data selection: As presented in Zubak et al. (2017), the search for the available data on fish communities in *Posidonia oceanica* meadows within the Mediterranean basin, an extensive literature review of ISI Web of Knowledge (<http://scientific.thompson.com/isi/>), Scopus (<https://www.scopus.com/>), and Google Scholar (<https://scholar.google.com/>) database was performed and keywords "fish", "seagrass" and "*Posidonia*" were used to identify research papers containing only the total or relative abundance of all recorded fish species in natural *P. oceanica* meadows. The studies performed over artificial seagrass units were not considered in the analysis. The initial results contained over 100 publications, but only 14 satisfied the required criteria. Most of the papers didn't contain abundance estimates for each encountered species at the same place and time, and/or only the mean or overall species richness values were presented. The final database (Table 3.2.1.1.) contained 27 recorded transects (treated as fish community datasets) from 14 independent studies. The papers presented here were published between 1982 and 2010, and there was great variability in covered combinations of depths, seasons, times of the day and geographical locations. The sampled depth varied from 1 to 40 meters. The studies were conducted during the day (19) and night (8), in warm and cold seasons, and geographical distribution was mainly in the West Mediterranean Sea, from 38.15 to 44.38° N latitude and 0.50 W to 18.48° E longitude (Figure 3.2.1.1.), in Marine Protected Areas (11) and outside (16).

Three distinct sampling methods were used in the reviewed studies:

(1) UVC -- underwater visual census: the length of strip or belt transects varied from 20 to 150 m, point counts were performed within the radius of 2 to 5 m;

(2) 1.8 m wide and 0.8 m high beam trawl: the duration of the hauls varied between 10 and 30 minutes at a speed of 1.5 to 2 knots; and

(3) 1.5 m wide and 0.5 m high skid trawl: the duration of the hauls varied between 40 and 60 minutes at a speed of 1 to 1.5 knots;

Table 3.2.1.1. Research papers (1982-2010) dealing with fish community structure associated with *Posidonia oceanica* meadows in the Mediterranean basin (Zubak et al. 2017).

dataset	reference	method	day / night	season	protection	location	depth (m)
1	Bell & Harmelin-Vivien 1982	skid trawl	day	warm	nonmpa	Plateau des Chevres, France	16.0-18.0
2	Bell & Harmelin-Vivien 1982	skid trawl	night	warm	nonmpa	Plateau des Chevres, France	16.0-18.0
3	Bell & Harmelin-Vivien 1982	skid trawl	day	warm	nonmpa	Carry le Rouet, France	16.0-18.0
4	Bell & Harmelin-Vivien 1982	skid trawl	night	warm	nonmpa	Carry le Rouet, France	16.0-18.0
5	Valle et al. 2001	beam trawl	day	warm	nonmpa	Alicante, Spain	20.0-22.0
6	Valle et al. 2001	beam trawl	night	warm	nonmpa	Alicante, Spain	20.0-22.0
7	Guidetti et al. 1998	visual census	day	all year	nonmpa	Genoa-Quinto, Genoa, Italy	10.0
8	Guidetti et al. 2000	visual census	day	all year	nonmpa	Otranto, Apulian coast, Italy	6.5-8.0
9	Guidetti et al. 2000	visual census	day	warm	nonmpa	S. Domino, Tremiti Islands, Italy	6.5-8.0
10	Valle 2009	visual census	day	all year	mpa	Alicante, Spain	1.0-15.0
11	Valle 2009	visual census	day	all year	nonmpa	Alicante, Spain	1.0-15.0
12	Frau et al. 2003	visual census	day	warm	mpa	Mallorca Island, Spain	10.0-20.0
13	Zupo & Stubing 2010	skid trawl	day	all year	nonmpa	Island of Ischia, Gulf of Naples, Italy	17.0-20.0
14	Reñones et al 1998	visual census	day	all year	nonmpa	Balearic Islands, Spain	30.0

15	Tunesi & Vacchi 1993	visual census	day	warm	mpa	Ligurian Sea, Italy	4.0 - 29.0
16	Guidetti et al. 1996	visual census	day	warm	nonmpa	Noli, Ligurian Sea, Italy	7.0
17	Reñones et al. 1995	beam trawl	day	warm	nonmpa	Mallorca, Balearic Islands, Spain	25.0-30.0
18	Reñones et al. 1995	beam trawl	night	warm	nonmpa	Mallorca, Balearic Islands, Spain	25.0-30.0
19	Harmelin-Vivien 1982	skid trawl	day	warm	mpa	Port-Cross National Park, France	12.0-20.0
20	Harmelin-Vivien 1982	skid trawl	night	warm	mpa	Port-Cross National Park, France	12.0-20.0
21	Harmelin-Vivien 1982	skid trawl	day	cold	mpa	Port-Cross National Park, France	12.0-20.0
22	Harmelin-Vivien 1982	skid trawl	night	cold	mpa	Port-Cross National Park, France	12.0-20.0
23	Harmelin-Vivien 1984	skid trawl	day	warm	mpa	Galeria bay, Regional Natural Park of Corsica, France	18.0 - 40.0
24	Harmelin-Vivien 1984	skid trawl	night	warm	mpa	Galeria bay, Regional Natural Park of Corsica, France	18.0 - 40.0
25	Harmelin-Vivien 1984	skid trawl	day	warm	mpa	Stollo and Calleta, Regional Natural Park of Corsica, France	18.0 - 40.0
26	Harmelin-Vivien 1984	skid trawl	night	warm	mpa	Stollo and Calleta, Regional Natural Park of Corsica, France	18.0 - 40.0
27	Sánchez-Jerez et al. 2002	visual census	day	all year	nonmpa	Alicante, Spain	15.0-17.0

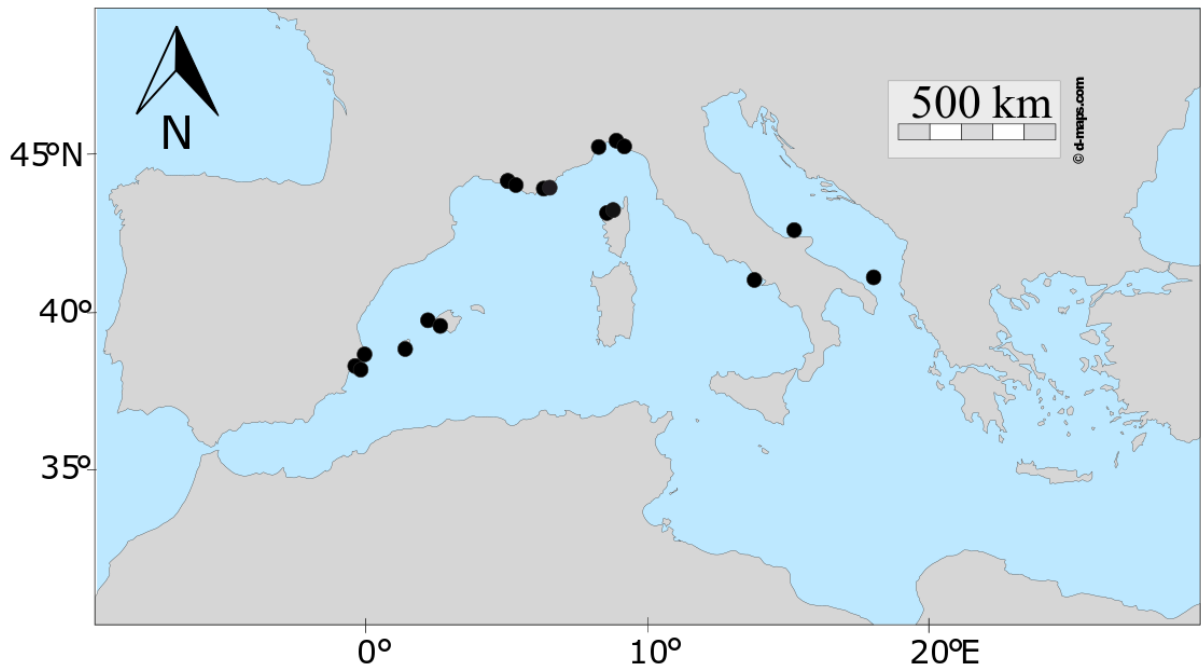


Figure 3.2.1.1. The geographical location of the sampling sites included in the meta-analysis (Zubak et al. 2017).

3.2.2. Data analysis

The details of the analysis of data within this chapter of the dissertation were published in Zubak et al. (2017). The base or vegan libraries of R (R Development Core Team 2016) were used for all statistical analyses.

Each recorded species from the database was assigned to a functional category based on their predatory behavior (Table 3.2.2.1.) which was done because the predation mode hypothesis, adopted in this research, assumes that the risk posed by seagrass resident and transient predators drives fish community structure. The functional categories were defined using the information available in FishBase (www.fishbase.org) on the maximum reported size and trophic level, confirmed by personal observations, and the information contained in several published papers that reported trophic level information on the Mediterranean fish species (Hiatt & Strasburg 1960; Hobson 1968, 1975; Bell & Harmelin-Vivien 1983; Moranta et al. 2006; Elliott et al. 2007; Schultz et al. 2009; Kruschel & Schultz 2012; Pais et al. 2012). Additionally, predators were separated into four categories, based on the modes they use for searching for prey and capturing it. The used categories were: (1) ambush, (2) wait-chase, (3) stalk-attack, and (4) substrate dwelling, and each was further categorized as transient or

resident predator in *Posidonia oceanica* meadows (Table 3.2.2.1). The species that are known to feed on other fish were considered predators and the rest were treated as potential prey. The predation mode hypothesis predicts that differences in predator abundance led to the variation in the structure of the prey community, therefore the community matrix of the relative abundance of each prey species (columns) for each transect (row) as the response matrix for all analyses was used.

The effects of the physical predictor variables (method, time of day, latitude, depth, season) and the abundance of transient and resident predators on the prey fish community were tested using permutational multivariate analysis of variance, PERMANOVA, as this method allows testing the effect of a predictor variable on the entire response community, with no assumptions regarding the direction of the effect on any species or group of species, or regarding normality, dimensions of the response matrix, or definition of community dissimilarity (Anderson 2001; McArdle & Anderson 2001). PERMANOVA was chosen for the predation mode hypothesis testing because the predator can affect the prey in either a positive or negative way, depending, for example, on the mobility of the two species or their ability to migrate between the two habitats, and/or the intensity of competition between different predator or prey species. The prey community matrix was converted to the Bray-Curtis distance matrix, which was then used in the PERMANOVAs with the `vegan` function `adonis`. The first step was to document the effect of predators on the prey community independently of the other physical predictor variables, and the community matrix was separated into three sets corresponding to the three survey methods. Within each of the methods, two-dimensional non-metric multidimensional scaling (NMDS) was used to visually present the correlation structure of the prey community using the ordination plots (Faith et al. 1987; Minchin 1987). The vector showing the direction and impact of the correlation between the predator abundances and the prey ordination was overlain (arrow) in each of these plots (the significance was tested using the permutational procedure in the `envfit` function of `vegan`). The significance of the "top-down" (predator group abundance on the ordination of the remaining prey community) and the "bottom-up" effects (prey abundance on the ordination of the remaining predator community) was tested. Species responsible for the significant `envfit` results were reported ($p < 0.05$ was used as the criterion for statistical significance).

The skid trawl survey method had the largest sample size, thus the relationship between resident predator abundance and the total species richness of the prey community was additionally calculated, and the significance of this relationship was measured using quadratic least squares regression with the *nls* function in R base (R Development Core Team 2016).

Table 3.2.2.1. Fish species associated with *Posidonia oceanica* meadows in the Mediterranean basin, used for the meta-analysis. Each species was assigned to a functional category (Bell & Harmelin-Vivien 1983; Moranta et al. 2006; Elliott et al. 2007; Pais et al. 2012; www.fishbase.org) based on its predatory behavior (RA - resident ambush; RWC - resident wait and chase; RSA - resident stalk and attack; TWC - transient wait and chase; TCC - transient cruise and chase; TSD - transient substrate dweller; prey - potential prey) (Zubak et al. 2017).

Short name	Full name	Family	Functional category
apde	<i>Apletodon dentatus</i>	Gobiesocidae	prey
apim	<i>Apogon imberbis</i>	Apogonidae	TWC
arke	<i>Arnoglossus kessleri</i>	Botidae	RA
arla	<i>Arnoglossus laterna</i>	Bothidae	RA
arth	<i>Arnoglossus thori</i>	Botidae	RA
atbo	<i>Atherina boyeri</i>	Atherinidae	prey
athe	<i>Atherina hepsetus</i>	Atherinidae	prey
atherina sp	<i>Atherina</i> sp.	Atherinidae	prey
blin	<i>Parablennius incognitus</i>	Blenniidae	prey
bloc	<i>Blennius ocellaris</i>	Blenniidae	RA
bobo	<i>Boops boops</i>	Sparidae	prey
bopo	<i>Bothus podas</i>	Bothidae	prey
caac	<i>Carapus acus</i>	Carapidae	prey
cari	<i>Callionymus risso</i>	Callionymidae	prey
chch	<i>Chromis chromis</i>	Pomacentridae	prey
chqu	<i>Chromogobius quadrivittatus</i>	Gobiidae	prey
coco	<i>Conger conger</i>	Congridae	RSA
coju	<i>Coris julis</i>	Labridae	RWC
ctru	<i>Ctenolabrus rupestris</i>	Labridae	prey
deco	<i>Deltentosteus collonianus</i>	Gobiidae	prey
dede	<i>Dentex dentex</i>	Sparidae	TCC

dequ	<i>Deltentosteus quadrimaculatus</i>	Gobiidae	prey
dian	<i>Diplodus annularis</i>	Sparidae	TCC
dibi	<i>Diplecogaster bimaculata</i>	Gobiesocidae	prey
dipu	<i>Diplodus puntazzo</i>	Sparidae	prey
disa	<i>Diplodus sargus</i>	Sparidae	prey
divu	<i>Diplodus vulgaris</i>	Sparidae	prey
epca	<i>Epinephelus caninus</i>	Serranidae	TWC
epco	<i>Epinephelus costae</i>	Serranidae	TCC
epma	<i>Epinephelus marginatus</i>	Serranidae	RWC
game	<i>Gaidropsarus mediterraneus</i>	Lotidae	RSA
gavu	<i>Gaidropsarus vulgaris</i>	Lotidae	RSA
goau	<i>Gobius auratus</i>	Gobiidae	prey
gobius sp	<i>Gobius sp.</i>	Gobiidae	unknown
gobu	<i>Gobius buccichi</i>	Gobiidae	prey
gocr	<i>Gobius cruentatus</i>	Gobiidae	RWC
gofa	<i>Gobius fallax</i>	Gobiidae	prey
goge	<i>Gobius geniporus</i>	Gobiidae	RWC
goni	<i>Gobius niger</i>	Gobiidae	RWC
gopa	<i>Gobius paganelus</i>	Gobiidae	prey
govi	<i>Gobius vittatus</i>	Gobiidae	prey
hihi	<i>Hippocampus hippocampus</i>	Syngnathidae	RA
hira	<i>Hippocampus ramulosus</i>	Syngnathidae	RA
labi	<i>Labrus bimaculatus</i>	Labridae	prey
lame	<i>Labrus merula</i>	Labridae	prey
lavi	<i>Labrus viridis</i>	Labridae	prey
leca	<i>Lepadogaster candolii</i>	Gobiesocidae	prey
lepido	<i>Lepidorhombus sp.</i>	Scophthalmidae	RA
liau	<i>Liza aurata</i>	Mugilidae	prey
limo	<i>Lithognathus mormyrus</i>	Sparidae	prey
lini	<i>Lipophrys nigriceps</i>	Blenniidae	prey
mohi	<i>Monochirus hispidus</i>	Soleidae	prey
muba	<i>Mullus barbatus</i>	Mullidae	prey
mugil sp	<i>Mugil sp.</i>	Mullidae	prey
muhe	<i>Muraena helena</i>	Muraenidae	RSA
musu	<i>Mullus surmuletus</i>	Mullidae	TSD
nema	<i>Nerophis maculatus</i>	Syngnathidae	prey
obme	<i>Oblada melanura</i>	Sparidae	prey
opba	<i>Ophidion barbatum</i>	Ophidiidae	TSD

opgr	<i>Opeatogenys gracilis</i>	Gobiesocidae	prey
opro	<i>Ophidion rochei</i>	Ophidiidae	TSD
paac	<i>Pagellus acarne</i>	Sparidae	prey
paer	<i>Pagellus erythrinus</i>	Sparidae	prey
paga	<i>Parablennius gattorugine</i>	Blennidae	prey
papa	<i>Pagrus pagrus</i>	Sparidae	TCC
paro	<i>Parablennius rouxi</i>	Blennidae	prey
pate	<i>Parablennius tentacularis</i>	Blenniidae	prey
pava	<i>Parophidion vassali</i>	Ophidiidae	prey
pomi	<i>Pomatoschistus minutus</i>	Gobiidae	prey
poqu	<i>Pomatoschistus quagga</i>	Gobiidae	prey
pomato	<i>Pomatoschistus</i> sp.	Gobiidae	prey
sasa	<i>Sarpa salpa</i>	Sparidae	prey
scca	<i>Scyliorhinus canicula</i>	Scyliorhinidae	TCC
scno	<i>Scorpaena notata</i>	Scorpaenidae	RA
scpo	<i>Scorpaena porcus</i>	Scorpaenidae	RA
scsc	<i>Scorpaena scrofa</i>	Scorpaenidae	RA
scum	<i>Sciaena umbra</i>	Sciaenidae	RWC
seca	<i>Serranus cabrilla</i>	Serranidae	RWC
sedu	<i>Seriola dumerili</i>	Carangidae	TCC
sehe	<i>Serranus hepatus</i>	Serranidae	RWC
sesc	<i>Serranus scriba</i>	Serranidae	RWC
sparus	<i>Sparus</i> sp.	Sparidae	TCC
spau	<i>Sparus aurata</i>	Sparidae	TCC
spca	<i>Spondyliosoma cantharus</i>	Sparidae	prey
spch	<i>Spicara chryselis (maena)</i>	Centracanthidae	prey
spma	<i>Spicara maena</i>	Centracanthidae	prey
spsm	<i>Spicara smaris</i>	Centracanthidae	prey
spsp	<i>Sphyaena sphyraena</i>	Sphyraenidae	TCC
syac	<i>Syngnatus acus</i>	Syngnathidae	prey
syçi	<i>Symphodus cinereus</i>	Labridae	prey
sydo	<i>Symphodus doderleini</i>	Labridae	prey
symed	<i>Symphodus mediterraneus</i>	Labridae	prey
symel	<i>Symphodus melanocercus</i>	Labridae	prey
symelo	<i>Symphodus melops</i>	Labridae	prey
syoc	<i>Symphodus ocellatus</i>	Labridae	prey
syroi	<i>Symphodus roissali</i>	Labridae	prey
syros	<i>Symphodus rostratus</i>	Labridae	prey

sysa	<i>Synodus saurus</i>	Synodontidae	RA
syti	<i>Symphodus tinca</i>	Labridae	prey
syty	<i>Syngnatus typhle</i>	Syngnathidae	RA
thpa	<i>Thalassoma pavo</i>	Labridae	prey
trde	<i>Tripterygion delaisi</i>	Tripterygiidae	prey
trdr	<i>Trachinus draco</i>	Trachinidae	RA
trla	<i>Trigloporus lastoviza</i>	Triglidae	prey
trme	<i>Tripterygion melanurus</i>	Tripterygiidae	prey
trra	<i>Trachinus radiatus</i>	Trachinidae	RA
trtr	<i>Tripterygion tripteronotus</i>	Tripterygiidae	prey
ursc	<i>Uranoscopus scaber</i>	Uranoscopidae	RA
vapr	<i>Vanneaugobius pruvoti</i>	Gobiidae	unknown
zefa	<i>Zeus faber</i>	Zeidae	TCC
zoop	<i>Zosterisessor ophiocephalus</i>	Gobiidae	RA

4. RESULTS

4.1. Fish assemblages of *Posidonia oceanica* meadows in the Croatian Adriatic Sea

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, with families Labridae, Gobiidae, and Sparidae being the most diverse with 12, 9, and 7 recorded taxa respectively. In terms of fish abundance, Labridae and Sparidae contained 73% of all observed individuals (Table 4.1.1.).

Table 4.1.1. 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.

Family	N observations	Relative abundance	N taxa
Labridae	1021	0.508	12
Sparidae	393	0.196	7
Serranidae	176	0.088	3
Pomacentridae	155	0.077	1
Centracanthidae	136	0.068	2
Gobiidae	63	0.031	9
Unidentified	39	0.019	1
Mullidae	13	0.006	1
Blennidae	5	0.002	1
Scorpaenidae	4	0.002	3
Atherinidae	1	<0.001	1
Carangidae	1	<0.001	1
Congeridae	1	<0.001	1
Moronidae	1	<0.001	1
Muraenidae	1	<0.001	1
Total	2010		45

The most frequently recorded species in the whole dataset (including juveniles) were *Coris julis* (resident wait and chase predator, 394 observations of 495 individuals), *Symphodus ocellatus* (prey, 364 observations of 778 individuals), *Chromis chromis* (prey, 155 observations of 2740 individuals) and *Diplodus annularis* (transient cruise and chase predator, 117 observations of 129 individuals). Fourteen taxa were observed only on a single occasion: *Dicentrarchus labrax*, *Gobius luteus* and *Scorpaena porcus* in meadows bordering sand; *Atherina hepsetus*, *Conger conger*, *Gobius niger*, *Scorpaena scrofa*, *Seriola dumerili*, *Serranus hepatus* juvenile and *Serranus scriba* juvenile in meadows bordering rock; and *Chromis chromis* juvenile, *Gobius bucchici* juvenile, *Muraena helena* and *Spicara smaris* juvenile in mosaic meadows.

In the continuous meadows bordering sand, the most frequently observed taxa were *Coris julis* (66 observations), *Diplodus annularis* (51 observation), *Symphodus cinereus* (45 observations), *Chromis chromis* (39 observations), *Symphodus ocellatus* (31 observation) *Diplodus vulgaris* (29 observations), and *Spicara maena* (22 observations).

The meadows bordering rocky-algal reef were dominated by *Symphodus ocellatus* (214 observations), *Coris julis* (151 observation), *Spicara smaris* (46 observations), *Diplodus annularis* (42 observations), *Chromis chromis* (42 observations), and *Symphodus melanocercus* (41 observation).

In the mosaic meadows, *Coris julis* (162 observations), *Symphodus ocellatus* (105 observations), *Chromis chromis* (73 observations), *Serranus scriba* (42 observations), *Oblada melanura* (39 observations), and *Serranus cabrilla* (36 observations) were recorded most frequently.

All three seascape contexts of the *P. oceanica* meadows shared a species pool; 25 of 45 taxa (56 % with juveniles considered the same taxon as their conspecific adults), and 25 of 59 (42% when considering juveniles as a separate taxon) co-occurred between the three seascape contexts of *P. oceanica* meadows and the meadows bordering sand had the highest number of unique taxa (Figure 4.1.1., Table 4.1.2.).

	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 seascape contexts	25	32	29
Taxa shared among three seascape contexts		25	
Total number of taxa (including juveniles)		45 (59)	

Figure 4.1.1. 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.

Table 4.1.2. Taxa observed exclusively in one seascape context (bordering sand / bordering rock / mosaic) of *Posidonia oceanica* meadows, observed on more than one occasion, and their abundance shown in parentheses.

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

The mean species richness (S) across all transects was 11.16 ± 3.64 SD. The mosaic meadows had somewhat higher mean species richness (12.36 ± 4.86 SD) compared to the meadows bordering sand and bordering rocky-algal reefs (11.50 ± 2.18 SD and 10.37 ± 3.43 SD, respectively). No statistically significant difference was observed in species richness between the three investigated seascape contexts of *P. oceanica* meadows. The overall highest species richness and abundance were observed in mosaic *P. oceanica* meadows on sites Fulija West (91 observations of 285 individuals belonging to 22 taxa), Zut (53 observations of 256 individuals belonging to 19 taxa) and Galijola (86 observations of 836 individuals belonging to 17 taxa).

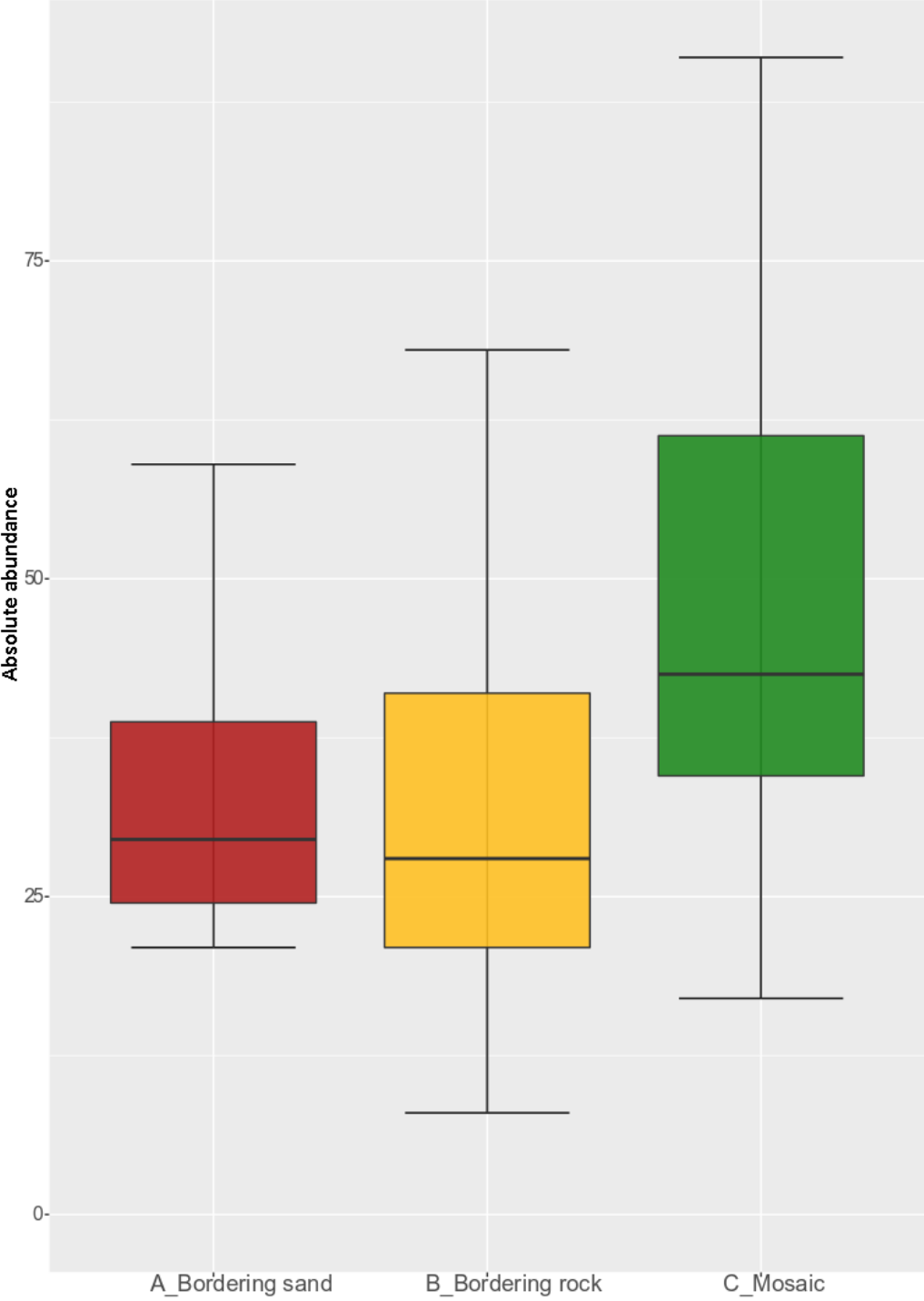
The observed Shannon-Wiener diversity index (H) and Pielou's evenness (J) showed no statistically significant variation between the three meadow types. Meadows bordering rocky-algal reefs had lower mean diversity index (1.95 ± 0.36 SD) compared to meadows bordering sand and mosaic meadows (2.09 ± 0.28 SD and 2.05 ± 0.36 SD, respectively), while mosaic meadows had lower mean evenness between the species (0.84 ± 0.06 SD) compared to meadows bordering sand and meadows bordering rocky-algal reef (0.86 ± 0.08 SD and 0.85 ± 0.08 SD, respectively).

The absolute abundance and the abundance per m³ of recorded fish varied between the three seascape contexts of the *P. oceanica* meadows (Table 4.1.3.) and it was in both cases higher in mosaic meadows than both meadows bordering sand and meadows bordering rocky-algal reef (Figure 4.1.2.). Significant difference in the absolute abundance was found only between mosaic meadows and meadows bordering rocky-algal reef (Tukey $p = 0.034$). Results showed no significant difference in both absolute and relative abundance as well as in the abundance per m³ between meadows bordering sand and meadows bordering rock.

Table 4.1.3. Analysis of variance using ANOVA of fish abundance across three different seascape contexts of *Posidonia oceanica* meadows in the Adriatic Sea, Croatia; a) absolute abundance and b) abundance per m³.

a)						
Response: abundance	Df	Sum Sqs	Mean Sqs	F value	<i>p</i>	
meadow	2	2403.690	1201.850	370.109	0.031	*
Residuals	52	16885.950	324.730			
b)						
Response: abundance (per volume unit; m³)	Df	Sum Sqs	Mean Sqs	F value	<i>p</i>	
meadow	2	0.036	0.018	51.277	0.009	**
Residuals	52	0.184	0.004			
* <i>p</i> < .05; ** <i>p</i> < .01; *** <i>p</i> < .001						

a) absolute abundance in each meadow type



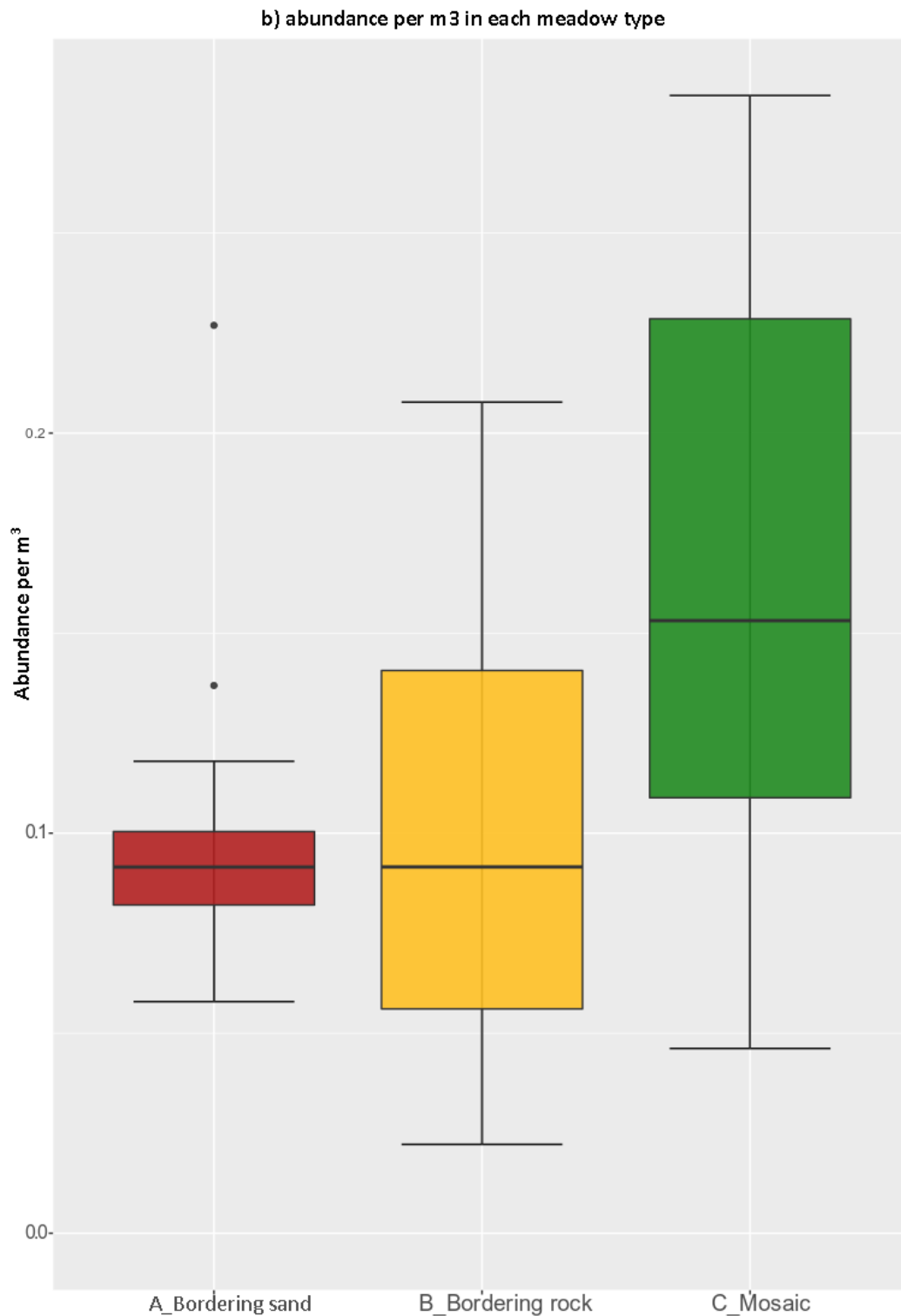


Figure 4.1.2. Box plots of a) absolute abundance and b) abundance per volume unit (m³) of fish in each of the three seascape contexts (bordering sand / bordering rock / mosaic) of the *Posidonia oceanica* meadows. Box plots show the median (line near the center), the first and third quartile (the box), the extreme values whose distance from the box is at most 1.5 times the interquartile range (whiskers), and remaining outliers (black dots).

4.1.1. Fish community structure in different seascape contexts of *Posidonia oceanica* meadows

Analysis of the fish community using nMDS showed the separation based upon differences in fish community structure of three seascape contexts of *Posidonia oceanica* meadows (Figure 4.1.1.1.), with 2D nMDS stress = 0.20 and 3D nMDS stress = 0.14. The overlap of the 95% confidence interval ellipses suggests a relatively unanimous fish assemblage in all three seascape contexts of *P. oceanica* meadows, which is also evident from the number of shared species (Figure 4.1.1.). Further analysis distinguished 11 taxa which showed significant variation in the abundance across different seascape contexts (Table 4.1.1.1.) indicating that these taxa are the most probable candidates causing the variation in the fish community structure. Some of those species are overall very abundant (e.g. *Diplodus annularis* and *Symphodus ocellatus*) and therefore drive the community in a certain direction, while some are observed in only one seascape context but in relatively high numbers (*Mullus surmuletus*) and drive the community structure in a different direction.

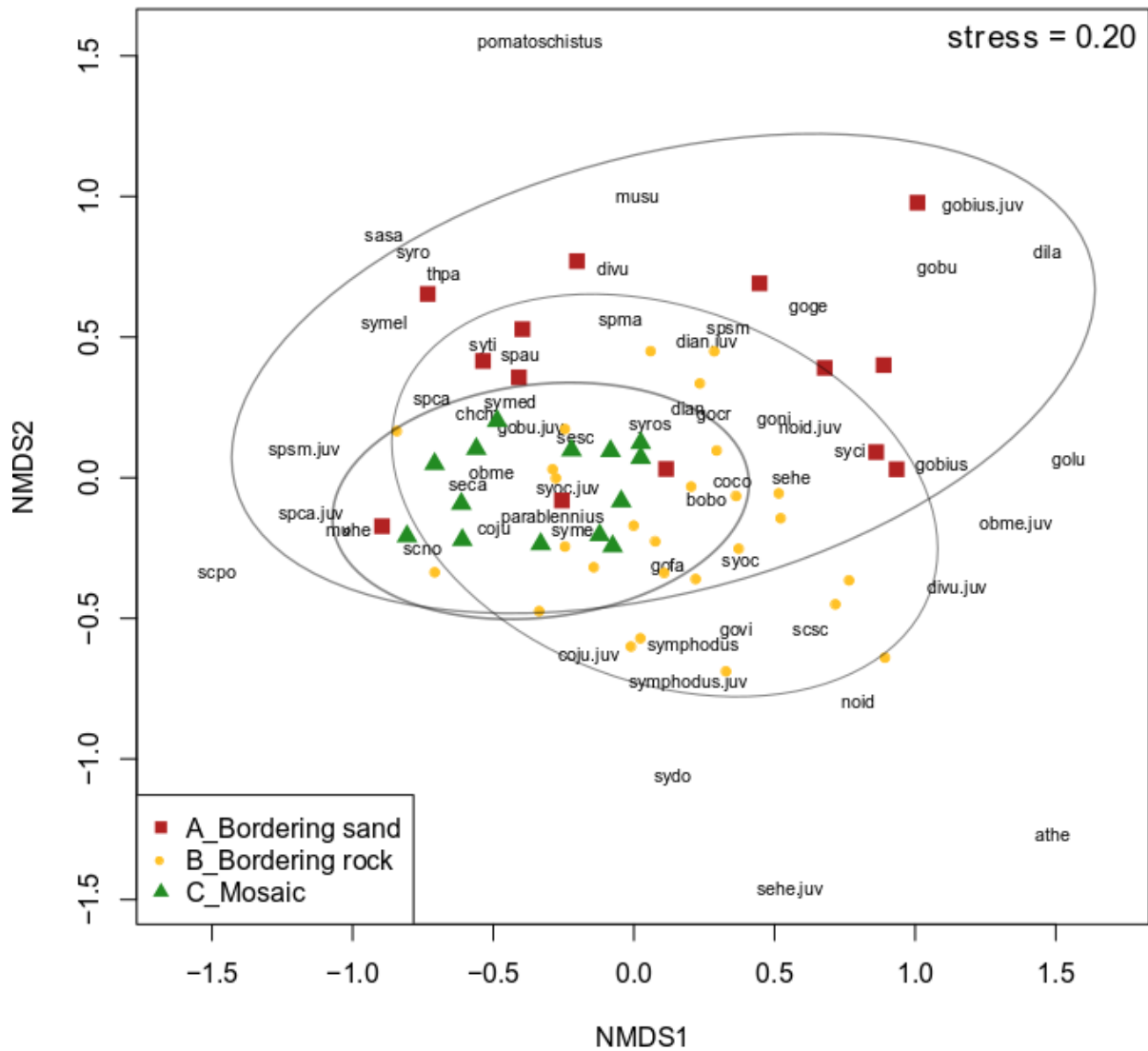


Figure 4.1.1.1. Two-dimensional non-metric multidimensional scaling plots of the fish community across three different seascape contexts (bordering sand / bordering rock / mosaic) of *Posidonia oceanica* meadows in the Adriatic Sea, Croatia. The symbols represent individual transects within the datasets indexed in Table in Appendix 1. Bray–Curtis distance, final stress = 0.20. Ellipses show 95% confidence limits for the delimitation of each group. For species/taxa abbreviations, see Appendix 1.

Table 4.1.1.1. Fish taxa observed within *Posidonia oceanica* meadows in the Adriatic Sea, Croatia, their ordination coordinates, F values in the ANOVA 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	F value	<i>p</i>
<i>Atherina hepsetus</i>	0.599	-0.801	0.509	0.604
<i>Boops boops</i>	0.960	-0.281	2.362	0.104
<i>Chromis chromis</i>	-0.837	0.546	2.778	0.071
<i>Chromis chromis juvenile</i>	-0.962	-0.273	1.491	0.235
<i>Conger conger</i>	0.972	-0.233	0.509	0.604
<i>Coris julis</i>	-0.867	-0.499	3.104	0.053
<i>Coris julis juvenile</i>	-0.161	-0.987	1.883	0.162
<i>Diplodus annularis</i> *	0.447	0.894	8.657	0.001
<i>Diplodus annularis juvenile</i> *	0.330	0.944	5.781	0.005
<i>Dicentrarchus labrax</i>	0.761	0.649	1.491	0.235
<i>Diplodus vulgaris</i>	-0.065	0.998	1.907	0.159
<i>Diplodus vulgaris juvenile</i>	0.879	-0.477	0.829	0.442
<i>Gobius</i> sp.	0.998	0.061	1.028	0.365
<i>Gobius</i> sp. juvenile	0.637	0.771	1.539	0.224
<i>Gobius bucchichi</i> *	0.682	0.731	3.177	0.050
<i>Gobius bucchichi juvenile</i>	-0.768	0.640	1.491	0.235
<i>Gobius cruentatus</i>	0.644	0.765	0.449	0.641
<i>Gobius fallax</i>	0.233	-0.973	0.347	0.709
<i>Gobius geniporus</i>	0.554	0.833	1.950	0.152
<i>Gobius luteus</i>	0.998	0.059	1.491	0.235
<i>Gobius niger</i>	0.841	0.542	0.509	0.604
<i>Gobius vittatus</i>	0.392	-0.920	1.262	0.292
<i>Muraena helena</i>	-0.962	-0.273	1.491	0.235
<i>Mullus surmuletus</i> *	0.009	0.999	20.003	0.000

NoID (unidentified)	0.538	-0.843	2.223	0.118
NoID juvenile	0.920	0.392	1.593	0.213
<i>Oblada melanura</i>	-0.999	-0.024	0.731	0.486
<i>Oblada melanura juvenile</i>	0.982	-0.189	0.881	0.420
<i>Parablennius</i> sp.	-0.793	-0.609	2.915	0.063
<i>Pomatoschistus</i> sp.	-0.137	0.991	1.491	0.235
<i>Sarpa salpa</i>	-0.552	0.834	1.491	0.235
<i>Scorpaena notata</i>	-0.883	-0.470	2.701	0.077
<i>Scorpaena porcus</i>	-0.937	-0.350	1.491	0.235
<i>Scorpaena scrofa</i>	0.594	-0.804	0.509	0.604
<i>Serranus cabrilla</i> *	-0.998	-0.070	15.483	0.000
<i>Seriola dumerili</i>	-1.000	0.020	0.509	0.604
<i>Serranus hepatus</i>	0.992	-0.129	1.278	0.287
<i>Serranus hepatus juvenile</i>	0.234	-0.972	0.509	0.604
<i>Serranus scriba</i>	-0.690	0.724	2.515	0.091
<i>Serranus scriba juvenile</i>	-0.999	0.020	0.509	0.604
<i>Sparus aurata</i>	-0.522	0.853	0.926	0.402
<i>Spondyliosoma cantharus</i> *	-0.858	0.513	7.929	0.001
<i>Spondyliosoma cantharus juvenile</i> *	-0.982	-0.187	3.526	0.037
<i>Spicara maena</i>	-0.054	0.999	0.602	0.551
<i>Spicara smaris</i>	0.378	0.926	0.685	0.509
<i>Spicara smaris juvenile</i>	-0.992	0.130	1.491	0.235
<i>Symphodus cinereus</i> *	0.985	0.171	6.587	0.003
<i>Symphodus doderleini</i>	0.082	-0.997	1.570	0.218
<i>Symphodus melanocercus</i>	-0.558	-0.830	2.979	0.060
<i>Symphodus mediterraneus</i>	-0.749	0.662	0.072	0.931
<i>Symphodus melops</i> *	-0.723	0.691	6.428	0.003
<i>Symphodus</i> sp.	0.216	-0.976	0.573	0.567
<i>Symphodus</i> sp. juvenile	0.167	-0.986	1.366	0.264
<i>Symphodus ocellatus</i> *	0.625	-0.781	9.563	0.000

<i>Symphodus ocellatus</i> juvenile	-0.967	-0.255	2.772	0.072
<i>Symphodus roissali</i> *	-0.537	0.844	3.225	0.048
<i>Symphodus rostratus</i>	0.247	0.969	0.226	0.799
<i>Symphodus tinca</i>	-0.591	0.807	2.190	0.122
<i>Thalassoma pavo</i>	-0.516	0.857	1.491	0.235

The differences in the community structure reflect the differences in absolute and relative abundances among the three seascape contexts of *P. oceanica* meadows. Relative abundances of fish species in each of the three seascape contexts are presented in Figures 4.1.1.2. and 4.1.1.3. Figure 4.1.1.2. refers to the relative abundance of each of the 20 selected species across the 3 different seascape contexts of *P. oceanica* meadows. These selected species showed abundance variation across different seascape contexts and/or had high overall abundance, therefore Figure 4.1.1.2. shows how important each seascape context is for each of the selected species. It is evident that species such as *Chromis chromis*, *Diplodus vulgaris*, and *Symphodus mediterraneus*, use all three seascape contexts, while on the other hand, juvenile *C. julis*, *Mullus surmuletus* (in meadows bordering sand), *Symphodus doderleini* (in meadows bordering rock), and *Serranus cabrilla* (in mosaic meadows) dominantly use only one seascape context and were observed in very low numbers in others. Figure 4.1.1.3. shows the proportion of the most abundant species in each of the three seascape contexts of *P. oceanica* meadows. Results were pooled for species whose abundance made up less than 5% of total observations.

In meadows bordering sand, *C. julis* (14%) was the most abundant taxon, followed by *Diplodus annularis* (11%) and *Symphodus cinereus* (10%). The meadows bordering rocky-algal reefs were dominated by *Symphodus ocellatus* (24%) and *C. julis* (17%), followed by *Spicara smaris*, *C. chromis*, *D. annularis*, *Symphodus melanocercus*, *Serranus scriba*, and *S. cinereus*, all of which were represented by 5% of the total abundance. *Coris julis* was again the most abundant taxon in the mosaic meadows (24%), followed by *Symphodus ocellatus* (16%) and *C. chromis* (11%). *Serranus scriba* and *Oblada melanura* were represented by 6%, while *S. cabrilla*, *S. melanocercus*, and *D. vulgaris* each accounted for 5% of the abundance.

In seascape contexts where alternative structured habitat is available (meadows bordering rocky-algal reefs and mosaic meadows), *C. julis* and *S. ocellatus* constitute 41% and 40% of the total community, respectively.

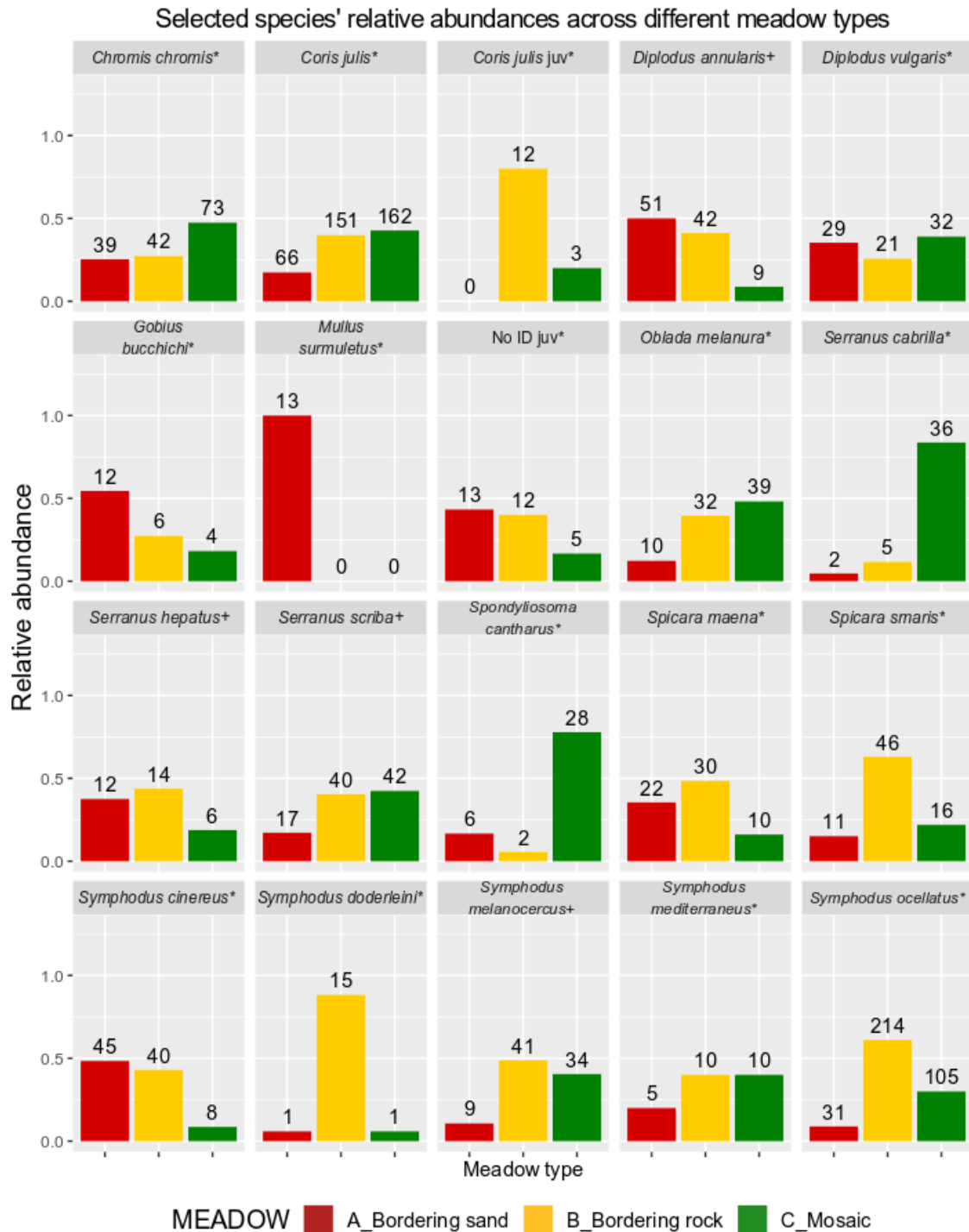


Figure 4.1.1.2. Bar plot showing the relative abundance of 20 selected fish species across different *Posidonia oceanica* seascape contexts (bordering sand / bordering rock / mosaic). Species with an asterisk showed a significant abundance variation across the *P. oceanica*

seascape contexts, and species with a plus sign were among the most abundant species overall. The numbers above the bars indicate the absolute abundance of each taxon in each of the three *P. oceanica* seascape contexts.

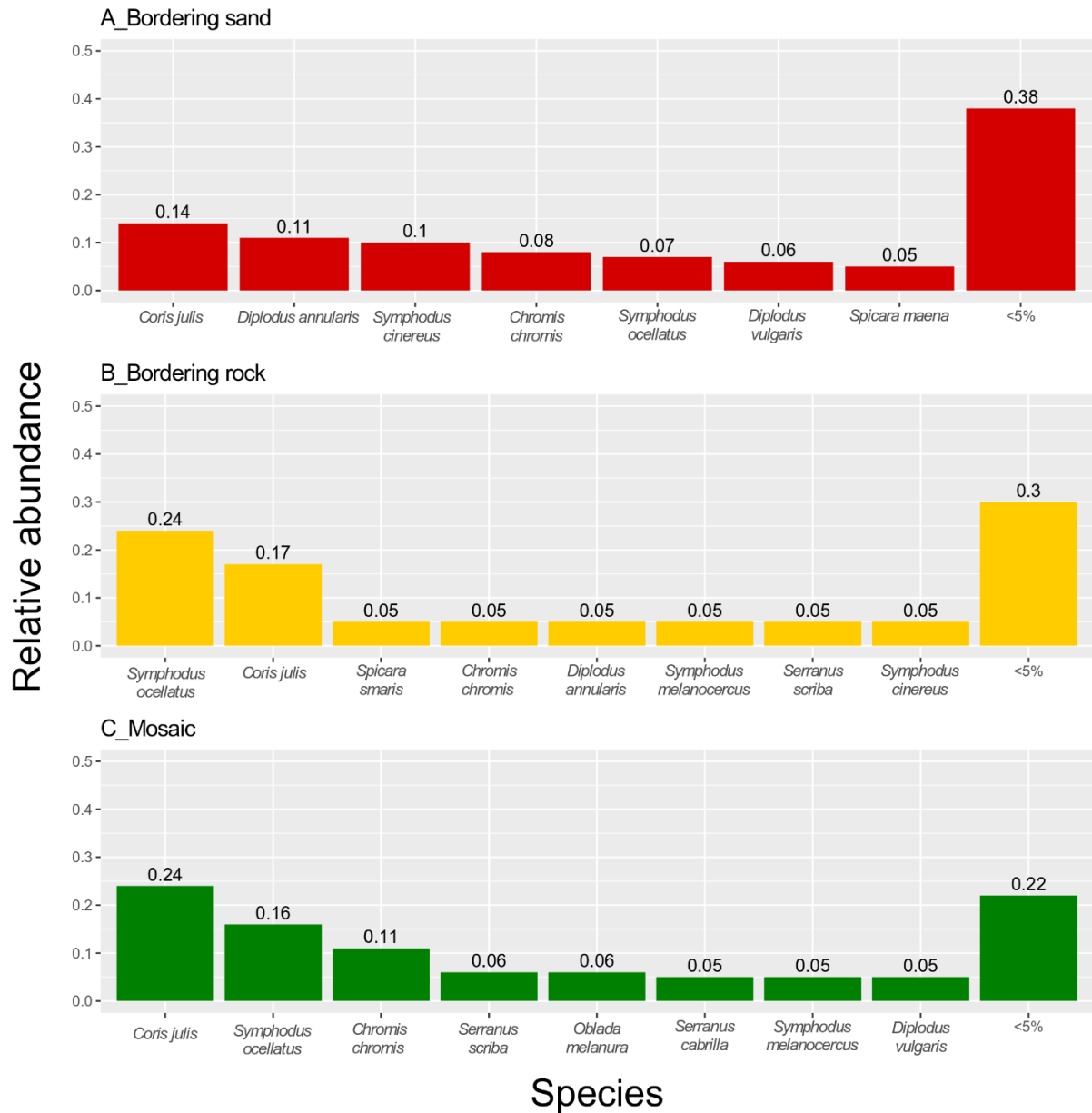


Figure 4.1.1.3. Bar plot showing the proportion of most abundant fish species in each of the three *Posidonia oceanica* seascape contexts (bordering sand / bordering rock / mosaic). The numbers above the bars indicate the relative abundance of each taxon in each of the three seascape contexts. Species whose relative abundances were <5% were pooled.

PERMANOVA results indicate a significant influence of the seascape context, cover, and temperature on variation in fish community structure. There was no interaction between the predictor variables (Table 4.1.1.2.), therefore it was possible to analyse the individual effect of the main predictor variable, the seascape context (SC) on the variability in fish community structure. The results show that there are statistically significant differences in the fish community structure between the observed seascape contexts of *P. oceanica* meadows. The seascape context explained approximately 13% of the variability in fish community structure (PERMANOVA $R^2 = 0.13$, $p < 0.01$). Temperature and cover showed significant effect on the fish community, but the amount of explained variability by these two predictor variables was relatively low (9% and 5%, respectively). These two variables showed no significant effect on species richness or abundance of fish and for that reason they were not further analysed. They were, however used to control for the amount of explained variability of the predictor variable of interest (seascape context - SC).

Table 4.1.1.2. 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	MM	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		

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

4.2. Effect of physical factors and predators on the variability of the fish community structure in the Mediterranean *Posidonia oceanica* meadows

The content of this sub-chapter content has been published in Zubak et al. (2017).

The final database contained 14 papers that were reviewed and from these papers 27 distinct datasets (transects) were analyzed. Analysis showed a total of 112 fish taxa from 33 families that were reported in the Mediterranean *Posidonia oceanica* meadows. Family Gobiidae had the highest number of species (17 species - 15%), followed by Labridae and Sparidae with 15 species each (14%), and Blennidae and Serranidae with 6 species each (5%) (Figure 4.2.1.). Most of the families (17) contained only a single species (Figure 4.2.1.).

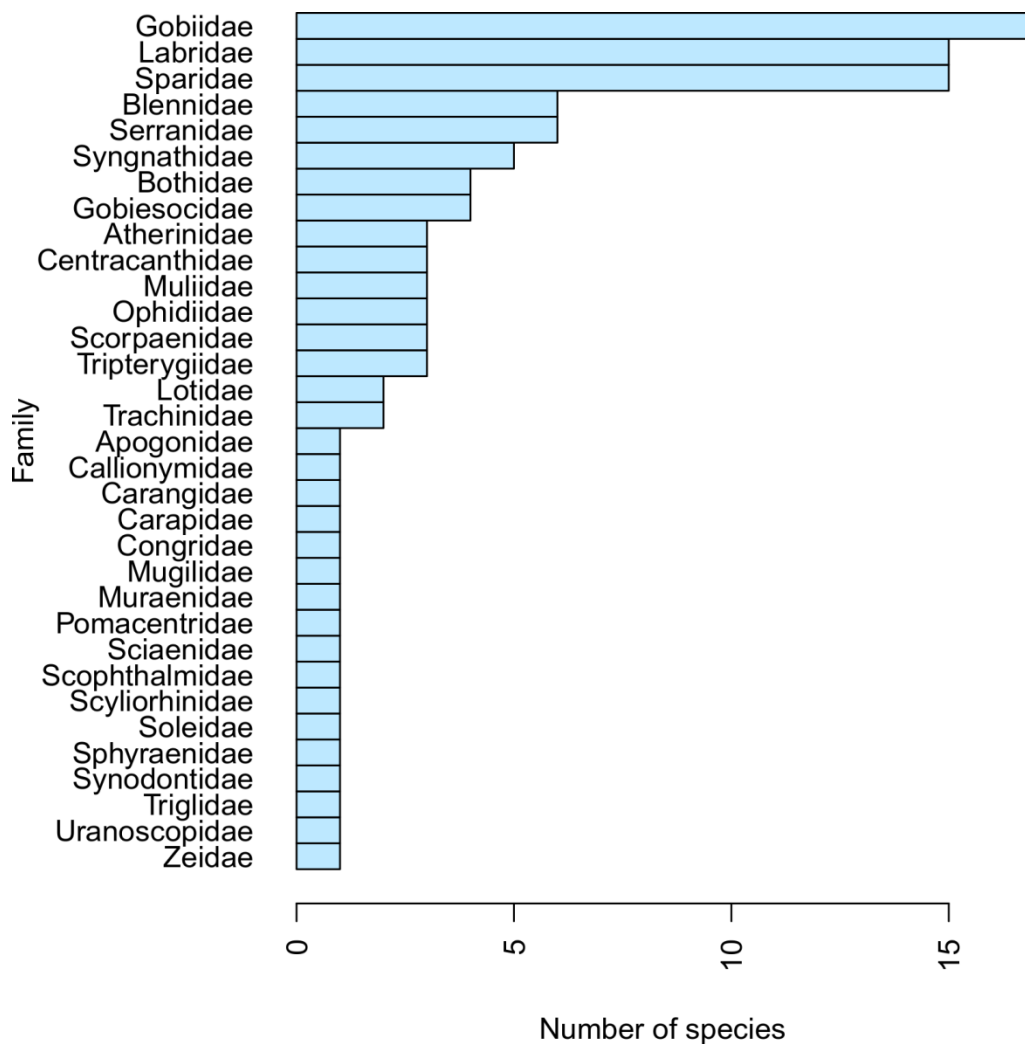


Figure 4.2.1. The total number of fish species associated with *Posidonia oceanica* meadows in the Mediterranean Sea sampled in all studies, ordered by family (Zubak et al. 2017).

Physical predictor variables (survey method, time of day, latitude, depth, season) explained approximately 70% of the variability in the fish community matrix across all transects. In the reviewed datasets, three survey methods were used: a skid trawl (13 datasets - 4 papers), visual census (10 datasets - 8 papers), and beam trawl (4 datasets - 2 papers) (Table 3.2.1.1.). Expectedly, survey method had the most statistically significant effect and explained more than 30% of the variability (PERMANOVA $p < 0.001$). Other physical factors, such as the time of day, season, latitude and sampling depth also individually showed a significant effect ($p = 0.014, 0.002, 0.004, \text{ and } 0.001$ respectively).

Analysis revealed that piscivorous predators have significant effect on fish community. Total predator abundance and total resident predator abundance showed a significant effect on the remaining fish community ($p = 0.005$ and 0.008 respectively, Tables 4.2.1. and 4.2.2., Figure 4.2.2.), even in the case when the other significant physical variables (survey method, latitude and season) were controlled for. Results also showed significant effect in respect to predator-specific behaviour and hunting style with resident wait chase, resident stalk and attack and transient wait chase predators each having a statistically significant effect on the remaining fish community ($p = 0.003, 0.001$ and 0.038 respectively).

Table 4.2.1. Analysis of variance using PERMANOVA of the effect of total predators on prey abundance matrix, controlling for the physical predictor variables (Zubak et al. 2017).

Predictor variables	Effect of total predators on the prey abundance matrix			
	Df	F	r^2	p
Method	2	7.40	0.307	0.001
Latitude	1	4.68	0.097	0.001
Season	2	2.72	0.113	0.002
All predators	1	3.31	0.069	0.005
Residuals	20		0.415	

Table 4.2.2. Analysis of variance using PERMANOVA of the effect of resident predators on prey abundance matrix, controlling for the physical variables (Zubak et al. 2017).

Predictor variables	Effect of the resident predators on the prey abundance matrix			
	Df	F	R ²	<i>p</i>
Method	2	7.35	0.307	0.001
Latitude	1	4.65	0.097	0.001
Season	2	2.71	0.113	0.002
Resident predators	1	3.17	0.066	0.008
Residuals	20		0.417	

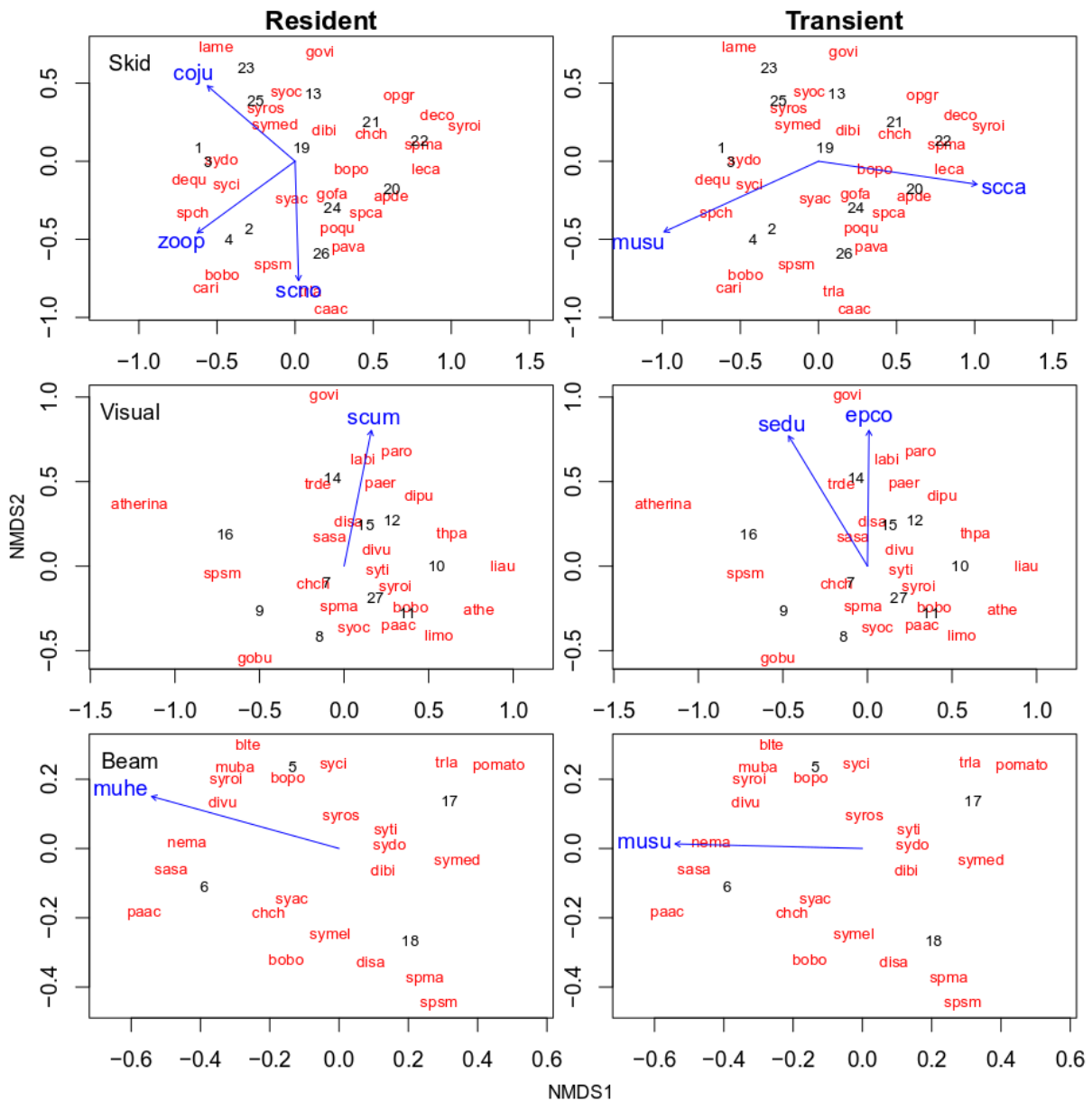


Figure 4.2.2. Non-metric multidimensional scaling plots with vectors indicating direction and magnitude of correlation between ordinations and resident (left) and transient (right) predators within sampling methods skid trawl (top), visual census (middle), and beam trawl (bottom). The numbers within the plots represent individual transects within the datasets indexed in Table 3.2.1.1. For species abbreviations, see Table 3.2.2.1. For probability values of correlations (all $p < 0.1$), see Table 4.3.2.

When analysing predator effect on prey community regarding different sampling method, it was evident that resident ambush predators *Scorpaena notata* and *Zosterisessor ophiocephalus* (skid trawl), transient chase-capture species *Scyliorhinus canicula* (skid trawl) and *Seriola dumerili* (visual census), and finally resident stalk-attack species *Muraena helena*

(beam trawl) were the predator species that showed the strongest negative correlation with the prey community (Table 4.2.3.).

Table 4.2.3. *P* values of correlations between the indicated fish species and the axes of the NMDS ordinations of the prey community or predator community, within each of the three sampling methods. All values < 0.1 are reported (Zubak et al. 2017).

Method	Correlation	Species	<i>P</i> value
Skid trawl	Predators on prey ordination	<i>Scyliorhinus canicula</i>	0.032
		<i>Scorpaena notata</i>	0.033
		<i>Zosterisessor ophiocephalus</i>	0.044
		<i>Coris julis</i>	0.044
		<i>Mullus surmuletus</i>	0.054
	Prey on resident preds ordination	<i>Symphodus doderleini</i>	0.004
		<i>Symphodus cinereus</i>	0.007
		<i>Tripterygion delaisi</i>	0.008
		<i>Diplodus vulgaris</i>	0.020
		<i>Nerophis maculatus</i>	0.020
		<i>Chromis chromis</i>	0.030
		<i>Lepadogaster candolii</i>	0.058
		<i>Gobius vittatus</i>	0.075
		<i>Labrus viridis</i>	0.098
		Prey on transient preds ordination	<i>Lepadogaster candolii</i>
<i>Chromis chromis</i>	0.007		
<i>Symphodus doderleini</i>	0.007		
<i>Parablennius tentacularis</i>	0.015		
<i>Tripterygion delaisi</i>	0.031		
Visual census	Preds on prey ordination	<i>Seriola dumerili</i>	0.030
		<i>Epinephelus costae</i>	0.048
		<i>Sciaena umbra</i>	0.090
	Prey on resident preds ordination	<i>Diplodus puntazzo</i>	0.002
		<i>Chromis chromis</i>	0.036
		<i>Symphodus doderleini</i>	0.060
		<i>Tripterygion delaisi</i>	0.087
		<i>Gobius bucchichi</i>	0.095
	Prey on transient preds ordination	<i>Tripterygion delaisi</i>	0.030
		<i>Gobius auratus</i>	0.081
<i>Gobius vittatus</i>		0.081	
Beam Trawl	Preds on prey ordination	<i>Muraena helena</i>	0.080
		<i>Mullus surmuletus</i>	0.083
		<i>Spicara smaris</i>	0.040

	Prey on resident preds ordination	<i>Diplodus vulgaris</i>	0.080
	Prey on transient preds ordination	<i>Symphodus mediterraneus</i>	0.041
		<i>Spicara maena</i>	0.080
		<i>Deltentosteus quadrimaculatus</i>	0.083

The skid trawl method was the survey method with the largest sample size and thus capable of the most accurate census of seagrass-resident predators. The results of quadratic least squares regression analysis presented in Figure 4.2.3. showed a significant negative effect of total percent abundance of resident predators on the total species richness of the prey community ($p = 0.0067$) documented within the skid trawl method, with 23 prey species recorded in the absence of predators, and only 14 prey species at a predator abundance of 35%.

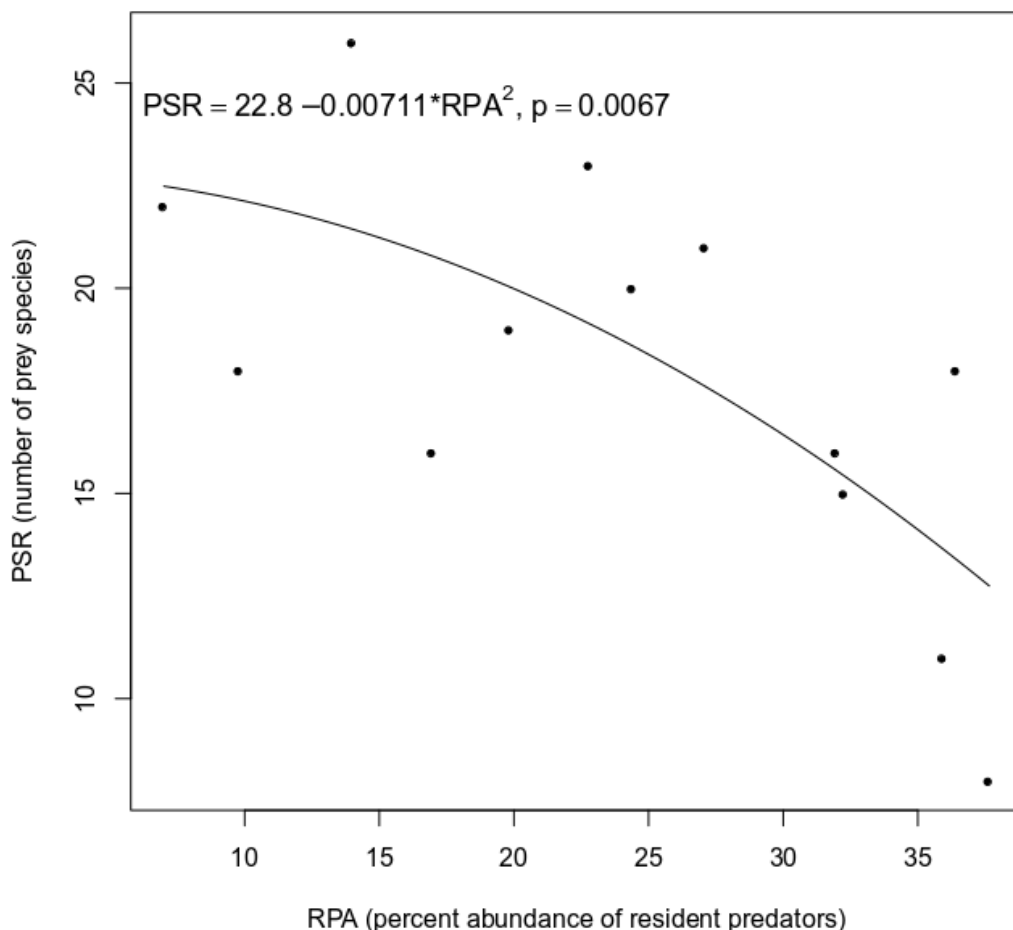


Figure 4.2.3. The significance of the relationship between the total percent abundance of resident predators (RPA) and the total number of prey species (PSR) in skid trawl transects. Regression parameters are 0.007 (SE = 0.002) and 22.8 (SE = 1.8).

5. DISCUSSION

5.1. The seascape context drives fish community structure

Results obtained in this research indicate that *Posidonia oceanica* ichthyofauna in all major arrangements is relatively homogeneous and shares a species pool, however statistically significant differences in fish community structure across the three different seascape contexts (bordering sand / bordering rock / mosaic) of *P. oceanica* meadows were found. Furthermore, several species with significant abundance differences across the different *P. oceanica* structural arrangements were discovered.

The total number of recorded taxa (45 taxa, Table 4.1.1.) was somewhat higher than previously described in other Mediterranean areas at similar depth and also using visual census method: 38 taxa from Balearic Islands (Frau et al. 2003), 37 taxa from Alicante, Spain (Valle & Bayle-Sempere 2009), 35 taxa from Ligurian Sea (Tunesi & Vacchi 1993) and 34 taxa from Otranto, Apulian coast (Guidetti 2000). The higher number of recorded taxa in this research can be attributed to the fact that lure-assisted visual census was used. 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 (Kruschel & Schultz 2012). The lure also increases the likelihood of observing predators that search for and encounter prey from a hidden position (e.g. ambush predators and wait-chase predators) and fast cruising predators which are easily overlooked during their brief appearance in regular transects (Kruschel & Schultz 2012).

We did not find significant differences in abundance and species richness between continuous meadows bordering sand and continuous meadows bordering rocky-algal reef. The lower (but not significant) species richness and abundance of fish in continuous meadows bordering rocky-algal reef compared to complex mosaic meadows was observed and that could be explained by the fact that structured habitats such as rocky-algal reefs/boulders provide greater abundance of physical structures that are attractive to fish (increased reef complexity provides more refuges of different sizes), therefore fish approaching the seagrass – rock border might show a general preference for the mosaic habitat.

5.1.1. Differences in fish community structure in different seascape contexts of *Posidonia oceanica* meadows

The null hypothesis of this thesis proposing no differences in fish community structure and abundance of fish assemblages within three different *Posidonia oceanica* seascape contexts was rejected based on nMDS and PERMANOVA results (Figure 4.1.1.1., Table 4.1.1.2.). Significant community differences found across different habitat arrangements may be in part explained by interactions and habitat choice of individual species and their functional roles in the community. Some of the observed species showed significant association with one of the *P. oceanica* seascape context and strong habitat preference. For example, *Mullus surmuletus* was observed 13 times and only in meadows bordering sand, *Spicara smaris*, *Spicara maena* and *Boops boops* were observed 2-3 times as often in meadows bordering rocky-algal reef as compared to other meadow types, while *Chromis chromis*, *Serranus cabrilla* and *Spondylisoma cantharus* were dominant in mosaic meadows. This association is probably strongly related to their interactions and choice of habitat components, as was observed by 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 in surrounded by seagrass meadows.

In this study, the most obvious observation is that resident wait and chase predator *Coris julis*, the most abundant species, is common in all three seascape contexts of *P. oceanica* meadows (Figure 4.1.1.3.). However, *C. julis* clearly has higher abundances in mosaic meadows than in meadows bordering sand (2.5x) and higher abundances in meadows bordering rocky-algal reef vs. meadows bordering sand (2.3x) (Figure 4.1.1.2.). It therefore strongly contributes to the community differences between the three *P. oceanica* seascape contexts. *Coris julis* juveniles are, in contrast to the adults, only seen in *P. oceanica* meadows bordering rocky-algal reef or positioned on a rock, seemingly avoiding 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 aggressive mesopredators of three species, *Serranus scriba*, *Serranus cabrilla* and *C. julis*, who share a sit-and-pursue (Schmitz et al. 1997) or wait-chase (Kruschel & Schultz 2011b) predation mode specifically promoted by mosaic habitat arrangements. Together, they make up 36% of the

total abundance in the mosaic meadow (Figure 4.1.1.3.). *Serranus cabrilla* is thought to be a resident wait-chase predator (Bell & Harmelin-Vivien 1983) that prefers coralligenous hard bottoms and rocky reefs (Tunesi & Vacchi 1993; Seytre et al. 2013) so it might be more abundant in mosaic meadows because it could use the benefit of structurally more complex habitat for hunting prey as suggested by Fernández et al. (2005). Another aggressive and very abundant mesopredator is *Diplodus annularis*, but it was seen to avoid the mosaic arrangement (Figure 4.1.1.2.), perhaps because it cannot compete for food with its cruise-chase predation mode against the overall more abundant wait-chase predators. Active and visual pursuit of prey is predicted to be 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 by two species of benthopelagic fish taxa (adult *Chromis chromis* and adult *Oblada melanura*), constituting 21 and 17% of the total abundance (Figure 4.1.1.3.). *Chromis chromis* individuals were observed to hover in small groups over the rock-seagrass mosaic canopy rather than looking for food inside complex structures or small gaps. *Oblada melanura* were recorded in small groups, moving throughout the entire heterogeneous space offered by the mosaic. Adults of these species may not be a potential target of the gape-restricted mesopredators, but the juvenile *O. melanura* would be and, fittingly, have not been observed at all within the mosaic arrangement. Adult *C. chromis* is more abundant in the mosaic arrangement than in *P. oceanica* bordering rocky-algal reef (1.7x) or sand (1.9x) (Figure 4.1.1.2.). Adult *O. melanura* is 3.9x as abundant in mosaics meadows and 3.2x as abundant in meadows bordering rocky-algal reef as in meadows bordering sand (Figure 4.1.1.2.). The high structural complexity of mosaic meadows can provide a variety of food items and might represent a very attractive habitat for such species (Guidetti et al. 1998). Bonaca & 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 more favorable habitat. The highest fish abundances overall were recorded on transects placed in mosaic meadows where seagrasses and rocky-algal reefs are closely interspersed, constituting more habitat combinations and also food niches than areas where one of the components is missing. Mosaic meadows are by definition more heterogeneous and probably also more complex habitats, which may explain the highest fish abundances. The close proximity of feeding grounds and shelter may enhance fish abundance

and richness in seagrass beds, implying that complexity per se may be an important factor in habitat choice, and combinations of habitat types might have a higher value for fish than any individual component 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 other seascape contexts (Figure 4.1.1.3.). These species are known to inhabit seagrass beds and rocky reefs (Guidetti 2000; Frau et al. 2003). It is interesting to see that in *P. oceanica* meadows bordering rocky-algal habitat, *C. chromis* is less abundant than in mosaic meadows, probably because it is usually found associated with locations of high habitat complexity (Harmelin-Vivien et al. 2005). In meadows bordering rocky-algal reef as compared to mosaic meadows, adult *O. melanura*, an aggressive opportunistic zooplanktivore (Pallaoro et al. 2003), is replaced by *Spicara smaris*, a fish that shares similar feeding style, but is usually found consuming smaller zooplankton prey (Karachle & Stergiou 2014), and was observed mainly above the *P. oceanica* canopy (Figure 4.1.1.3.). Wait-chase mesopredators were observed less frequently in the continuous meadows bordering rocky-algal reef than in the mosaic arrangement. Juveniles that were observed to be more common in meadows bordering rocky-algal reef are *Diplodus vulgaris* and small gobies, which were not at all observed in the mosaic arrangement.

In continuous meadows bordering sand, the species highly indicative of community structure were predominately species usually found associated with unconsolidated sediments. Except for *Mullus surmuletus* and *S. melanocercus*, which were exclusively observed in *P. oceanica* bordering sand (13 and 8x, respectively), there is also *Gobius bucchichi* that was more abundant in the sand-bordering than in the rock-bordering *P. oceanica* meadows (Figure 4.1.1.2.). *Mullus surmuletus* is a bottom-dwelling transient predator, frequently found over sand and soft bottoms at depths less than 100 m (Ben-Tuvia 1990), and although it is considered associated with *P. oceanica* (Stagličić et al. 2011), it was recorded during this research only if the adjacent habitat was unconsolidated sediments (Figure 4.1.1.2.). This finding is consistent with results of Fernández et al. (2005) who found that *M. surmuletus* forages along the seagrass boundaries and in sandy corridors. *Gobius bucchichi* is also known to prefer sandy bottoms in combination with structured habitat, such as *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 (Figure 4.1.1., Table 4.1.2.). The presence of species predominantly or exclusively found in meadows bordering sand might indicate that some species have specific preferences for the combinations of three-dimensionally structured habitats and unconsolidated soft bottoms, e.g. because they have specific predation modes, predator evasion strategies, or due to differences in available food between unvegetated sediments and *P. oceanica* meadows. These species may enter the *P. oceanica* meadow from within bare sand habitats that are present in relatively close proximity (Jenkins et al. 2015). Examples aside from the quite abundant *M. surmuletus*, *S. melanocercus* and *G. bucchichi* are *Sarpa salpa*, *Symphodus rostratus*, *Thalassoma pavo*, and juvenile *Spondyllosoma cantharus*. Juvenile *S. cantharus* obviously chose a completely different habitat from their adult conspecifics. While juveniles are exclusively seen in *P. oceanica* bordering sand, adults are clearly more abundant in mosaic meadows than in meadows bordering rocky-algal reef (14x) and meadows bordering sand (4.7x) (Figure 4.1.1.2.). This resembles the situation of adult and juvenile *C. julis* and might be another example of intraspecific competition and niche partitioning between adults and juveniles. Species such as *Diplodus annularis* and *Symphodus cinereus* are known to occur on bare soft bottoms in the vicinity of seagrasses (Bell & Harmelin-Vivien 1983) where they can feed. In this study, bare sands were absent from mosaic meadows and relatively rare in meadows bordering rock. This might explain the relatively higher abundances of *D. annularis* and *S. cinereus* in meadows bordering sand (Figures 4.1.1.2. and 4.1.1.3.).

“Fishes associated with *Posidonia oceanica*” are often assumed to be uniform communities with local differences in temperature, currents, seafloor characteristics, etc. responsible for variation in their structure. However, in reality, 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 a 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 a complex mosaic in which

seagrass is embedded in many habitat types that influence fish function, movement, and preference for seagrass structure.

5.2. The effect of predators on the fish community structure

The content of this sub-chapter has been published in Zubak et al. (2017).

The drivers of fish community structure associated with *Posidonia oceanica* meadows in the Mediterranean were analyzed through extensive literature review and meta-data analysis, revealing that a significant variation in sampling methodology and low sample size of published data prevents generalization about the importance of *P. oceanica* as a fish habitat. Nevertheless, the existing data do not confirm the common proposition that seagrass represents a uniform refuge from predation but indicates that the value of *P. oceanica* as a refuge varies greatly in response to the abundance of predators which are resident in seagrass. Each of these points is discussed in the following sections.

5.2.1. The variation in fish community structure caused by the differences in sampling method

The small number of published peer-reviewed studies with high methodological variation characterizes the analyzed dataset. The differences in the sampling methods explain approximately 70% of the variation among communities in the selected studies and lead to different absolute and relative abundances, as has been observed previously in fish community studies (Willis et al. 2000; Pasquaud et al. 2012). Published studies are not comparable with each other, and due to a lack of cross-calibration of different methods used, a single overall ordination could not be constructed. The three sampling methods in the present study resulted in different ordinations of the prey community, and each analyzed community showed a slightly different correlation with key predators. Furthermore, it is evident that the sampling methods differ in their efficiencies to capture fish, which is the result of different gear size, characteristics of the used net (mesh opening, material used), tow speed but also attributable to the differences in the way fish respond to the sampling gear (Pasquaud et al. 2012). Willis et al. (2000, p. 249) state that "methodological standardization across all species is not always appropriate for environmental effects studies and different survey

methods should be considered according to the biology and behavior of the species of interest", which might lead to the conclusion that for total community studies, the only feasible strategy could be using a set of complementary methods (Starr et al. 2010; Oliveira et al. 2014). Multi-method approaches to monitor fish stocks have already been adopted under many state conservation agencies under the EU Water Framework Directive (Council Directive, 2000/60/EC 2000), and also there are recommendations for monitoring Australian reefs by using a combination of non-destructive core methods for fish census, baited remote underwater video (BRUV) and underwater visual census (UVC) (Lowry et al. 2012). It is important to note that BRUV is a useful method that allows high-precision estimates of size of fish which are often frightened by divers when using UVC. The modification of UVC by the addition of lure (Kruschel & Schultz 2012), can improve the detection of sedentary, hidden or otherwise camouflaged fish individuals that could be attracted to or scared away by the lure. The combination of different methods leads to less variation in the collection of data on fish species across different seascape contexts. To better understand the drivers of fish community structure and the relative value of *Posidonia oceanica* as fish habitat in the Mediterranean Sea, we need to acknowledge that complementary sampling and data analysis methods are to be used, and that standard methods, adopted internationally, are needed in order to produce usable datasets of fish communities associated with *P. oceanica* meadows. That way, the value of *P. oceanica* as a faunal refuge habitat, as expressed in legal instruments such as the EU Habitats Directive, will be justified by the scientifically relevant data, which is currently not the case.

5.2.2. The variation in fish community structure caused by the differences in predator/prey relationship

A significant variation in fish communities was detected within each sampling method and that variation can be attributed to the abundance and behavior of piscivorous predators and their prey which is consistent with the predation mode hypothesis and research demonstrating that some fish species actively avoid habitats that conceal predators exhibiting hunting behaviors, and predators that actively seek prey within three-dimensional habitat (Kruschel & Schultz 2011b; Thiriet et al. 2013). In the analysis of the meta-data, a significant effect of resident and transient predators (resident ambushers and transient cruise-chasers)

on the prey fish community was found. Resident predators use the three-dimensional structure offered by *Posidonia oceanica* to improve their foraging efficiency because the seagrass leaves can obstruct prey's vision (Laurel & Brown 2006), and provide hideouts from which predators can attack (Janes 1985). Seagrass canopy can also enable the predator to physically approach the prey without being detected (Horinouchi et al. 2009). The effect of predators on the remaining prey fish community within each of the analyzed methods is discussed in the following paragraphs:

a) Within the skid trawl method, which is efficient at catching seagrass resident species, the resident ambush predators *Scorpaena notata* and *Zosterisessor ophiocephalus* showed significant effects on the *P. oceanica* prey community. These two species are adapted to hunting from within the three-dimensional structure, they ambush prey with one explosive movement, and could be considered the ultimate resident predators (Schultz & Kruschel 2010). The absence of small fish from dense patches of the seagrasses *Zostera marina*, *Zostera noltei*, and *Cymodocea nodosa* was found to be correlated with a higher abundance of *Z. ophiocephalus*, an ambush predator whose gape size can accommodate prey of a wide size range (Kruschel & Schultz 2011b). The same is true for the gape size of *Scorpaena* species, and results of this study show a negative correlation between both predators and potential prey species such as small individuals of *Symphodus* spp. (*S. ocellatus* and *S. roisali*), *Chromis chromis* or small gobies (*Deltentosteus collonianus* and *Gobius vittatus*). The negative correlation of *Coris julis* with most of the prey species might be explained by the fact that this species naturally occurs in high numbers and feeds on juveniles of most of the fish species present in *P. oceanica*. Among the prey, *Symphodus* species and *C. chromis* were most important in structuring the predator communities.

b) A standard method used for fish surveys in shallow seagrass meadows, visual census, (Harmelin-Vivien & Francour 1992) may be successful only at detecting transient and resident predators that are not truly epibenthic (Kruschel & Schultz 2012). Studies without devices that lure fish into view have been shown to be biased against nocturnal and well-camouflaged ambush predators (Harmelin-Vivien & Francour 1992). Meta-analysis data from within the visual census method suggest that large cruising transient predators (e.g. *Seriola dumerili*, *Epinephelus costae*) and resident visual predators (*Sciaena umbra*), which locate prey from above the *P. oceanica* canopy, are negatively correlated with most prey species,

and represent the most important candidates for structuring the prey community. According to the Seagrass Superiority Hypothesis - SSH (Heck & Orth 1980), prey fish should choose to hide in the seagrass in the presence of transient, cruising, visual predators, therefore this result was not expected -- the leaves of *P. oceanica* constitute an effective visual and mechanical barrier to the detection and pursuit of prey only in the presence of predators not physically inside the seagrass canopy. The obtained results of meta-analysis contradict the SSH hypothesis.

c) Beam trawl is biased against transient predators but suitable for detecting cryptic species (Harmelin-Vivien & Francour 1992). The meta-analysis showed that the resident stalk-attack and the substrate-dwelling transient predators are highly correlated with the prey community, and the prey species *Spicara maena* and *Symphodus mediterraneus* are significantly correlated with the resident and transient predator communities.

The small number of published studies using inconsistent methodology has hindered both our understanding of the value of *P. oceanica* as a faunal habitat and the development of scientifically informed strategies for conserving this species and habitat. Both the small number of studies and the fact that they are concentrated in the western and northern Mediterranean prevent easy generalization of the obtained results and understanding of the extent to which they may be mediated by different oceanographic conditions and predator source communities in different basins (Malanotte-Rizzoli et al. 2014).

Review of the literature performed prior to analysis indicates that after 30 years of field research, several critical areas of study are still lacking in regards to the habitat value of *P. oceanica* in the Mediterranean Sea: 1) the comparison of fish community properties (e.g. functional and taxonomic diversity) at *P. oceanica* versus neighboring structured and unstructured habitats (e.g. unconsolidated sediments, other submerged vegetation, and rocky reefs); 2) the value and necessity of *P. oceanica* as a spawning and nursery habitat relative to other structured habitats; 3) before-after control-impact studies of the impact of loss of *P. oceanica* habitat on the local fish community. The results of this study are in disagreement with the common management assumption that seagrass represents an absolute refuge from predators. On the contrary, seagrass is potentially a high-risk habitat due to resident ambush and stalk-attack predators (Schultz et al. 2009). Moreover, the habitat value of seagrass appears to be variable in space and time, depending on the functional and numerical

responses of predators that are highly effective in regulating community structure. Taking these results in local context, centuries of fishing pressure, both commercial and artisanal, has depleted large, cruising apex predators from the Mediterranean Sea (Goni et al. 2000; Lotze et al. 2011), while the density of populations of mesopredators residing in seagrass beds has increased in many areas (Stagličić et al. 2011). These trends suggest that the value of seagrass as a prey refuge has decreased over the last several decades. Furthermore, results indicate that there is an urgent need for research applying uniform and standard, non-destructive and complementary methodologies, such as BRUV and UVC, to monitor fish communities, and investigate the role of predation and predator harvest on fish communities within *P. oceanica* meadows and other structured habitats in the Mediterranean Sea.

6. CONCLUSIONS

This thesis is a result of the two approaches: 1) focusing at a local seascape context and evaluating the extent to which a neighboring habitat affects the fish community structure (performed in the Eastern Adriatic Sea); and 2) focusing on a much broader scale of the whole Mediterranean basin and evaluating the effect of predators on the prey community structure within *Posidonia oceanica* beds. The two approaches are connected by the role of predators: in the first approach the predators (among other factors) are controlling the relative value of *P. oceanica* three dimensional structure within the local seascape context, and in the second approach the predators are causing variation in the relative value of *P. oceanica* as refuge. The final result contributes to a better understanding of the drivers of fish community structure in *P. oceanica* beds. Lure assisted visual census method once again proved to be a successful method used to detect differences in fish community structure in different seascape context of *P. oceanica* meadows. The effect of resident and transient predators on the prey community was also demonstrated but the lack of uniformity in experimental design, methods used and locations sampled prevent us from making general conclusions on the large spatio-temporal scale. The data gathered by this research will help to better govern, protect and monitor fish communities associated with *P. oceanica* meadows.

The conducted research resulted in the following conclusions:

- There are significant differences in fish community structure and abundance of fish assemblages occurring over different seascape contexts of *Posidonia oceanica* meadow in the Eastern Adriatic Sea, Croatia;
- Fish individuals move through the overall seascape and their decision to associate with different habitats and habitat arrangements depends on spatial proximity to habitat relative to their current needs;
- Of the investigated seascape contexts of *Posidonia oceanica* meadow, the mosaic meadows had the highest overall fish abundance;
- Resident and transient predators significantly affect the prey fish community by taking advantage of the three-dimensional structure offered by seagrass;

- Resident ambush predators *Scorpaena notata* and *Zosterisessor ophiocephalus* significantly affect the *Posidonia oceanica* prey fish community;
- Large cruising transient predators *Seriola dumerili* and *Epinephelus costae*, and resident visual predator *Sciaena umbra* have a significantly negative correlation with prey abundance and are responsible for the difference in the structure of the prey fish community;
- Mesopredators such as *Serranus scriba* and *Serranus cabrilla* benefit the most from the three-dimensional habitat offered by the mosaic seascape context of meadows and significantly affect the structure of the prey fish community;
- *Posidonia oceanica* meadows are potentially a high-risk habitat and their value appears to be variable in space and time, depending on the functional and numerical responses of predators.

7. LITERATURE

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8. PROŠIRENI SAŽETAK

UVOD

Morske cvjetnice predstavljaju jedno od najproduktivnijih i najraznolikijih morskih staništa plitkih obalnih voda, uglavnom zbog toga što formiraju prostrana i gusta naselja velike strukturalne složenosti (Duarte & Chiscano 1999), što povećava njihovu vrijednost kao rastilišta/mrjestilišta i hranilišta za mnoge ribe, beskralježnjake i ptice (Orth i sur. 1984; Beck i sur. 2001; Nagelkerken i sur. 2001). Vrijednost morskih cvjetnica nadilazi samo pružanje staništa za raznoliku faunu; one su bitne u strukturiranju cijelog ekosustava jer usporavaju kretanje vode, stabiliziraju sediment, štite obalu od erozije, povećavaju sedimentaciju, a važne su i u procesima denitrifikacije te skladištenja dušika i ugljika (Bos i sur. 2007; Eyre i sur. 2011; McLeod i sur. 2011). Iako naselja morskih cvjetnica u cijelom svijetu predstavljaju važno stanište i smatra se da su „vruće točke bioraznolikosti”, one su jedno od najugroženijih staništa na svijetu (Jenkins i sur. 1997; Beck i sur. 2001; Pergent 2012).

Veća strukturalna složenost staništa može pozitivno utjecati na raznolikost vrsta i brojnost povezane faune u naseljima morskih cvjetnica (Graham & Nash 2013; Henderson i sur. 2017). Dostupnost staništa, osiguravanje prehrambenih resursa i zaštita od predatora su glavni faktori koji oblikuju zajednice riba (Connolly & Hindell 2006). Pretpostavlja se da je primarna vrijednost morskih cvjetnica kao staništa za pokretne organizme upravo činjenica da predstavljaju utočište plijenu na način da smanjuju vidljivost i ometaju kretanje predatora. Jedna od postojećih hipoteza pretpostavlja da su morske cvjetnice superiorno stanište u kojemu je ukupni rizik od smrtnosti niži nego na susjednim “otvorenim” staništima (Heck & Orth 1980; Bell & Pollard 1989). Dugo vremena se smatralo da ribe u livadama morskih cvjetnica imaju povećanu šansu za preživljavanjem koja im je omogućena kroz zaštitu od predatora u najranijim stadijima života (mrijest, migracija ličinki, razvoj mlađi). Međutim, navedena hipoteza ne objašnjava negativnu sklonost mnogih vrsta riba prema naseljima morskih cvjetnica i velike prostorno-vremenske razlike u strukturi zajednica riba povezanih s različitim naseljima morskih cvjetnica. Također, postojeća teorija ne uzima u obzir sposobnost predatora da kroz život uče ili kao vrsta evoluiraju kako bi bolje uočili, uhvatili i konzumirali plijen kojeg u naseljima morskih cvjetnica mogu naći u izobilju (Hellman i sur. 2009). Alternativno, hipoteza o različitim tipovima predatora (Schultz i sur. 2009), predviđa da je

relativni rizik od smrtnosti koji jedinka može doživjeti unutar naselja morske cvjetnice promjenjiv te da se mijenja ovisno o brojnosti i načinu lova tj. ponašanju lokalnih populacija predatora. Unutar naselja morskih cvjetnica, na strukturu zajednice riba utječe i prostorna organizacija različitih elemenata podmorskog okoliša, uključujući dostupnost susjednih alternativnih/strukturiranih staništa (Dorenbosch i sur. 2006; Pittman i sur. 2007; Unsworth i sur. 2008).

Morska cvjetnica *Posidonia oceanica* (L.) Delile endem je Sredozemnog mora, a formira prostrana monospecifična naselja između površine i 44 m dubine u najprozirnijim dijelovima Sredozemnog mora (npr. Malta, Korzika; Augier & Boudouresque 1979; Boudouresque i sur. 1990; Borg & Schrembi 1995) (Slika 1.1.). Naselja morske cvjetnice *P. oceanica* su vrlo osjetljiva i ugrožena antropogenim aktivnostima (Boudouresque i sur. 2000, 2006) te su navedena kao prioritetno stanište u Prilogu I. Direktive EZ 92/43/EEZ o očuvanju prirodnih staništa i divlje faune i flore (Council Directive 92/43/EEC 1992), a sama morska cvjetnica proglašena je strogo zaštićenom vrstom u Hrvatskoj prema Pravilniku o strogo zaštićenim vrstama (Narodne novine, 144/2013). U hrvatskom dijelu Jadranskog mora *P. oceanica* se javlja na dubinama od 0 do oko 36 metara (Zubak i sur. 2020) na pomičnim sedimentnim dnima te na stjenovitoj podlozi u kombinaciji s algama. Naselja su vrlo raznolika i najčešće se javljaju kao dominantno stanište uz sediment ili kamen u jednom od tri osnovna tipa prostorne organizacije elemenata podmorskog okoliša: (i) kontinuirana / cjelovita naselja uz sediment (engl. *bordering sand*), (ii) kontinuirana / cjelovita naselja uz stjenovitu obalu obraslu algama (engl. *bordering rocky-algal reef*) i (iii) fragmentirana mozaična naselja (engl. *mosaic*) koja rastu izravno na stjenovitoj podlozi i kamenim gromadama obraslim makroalgama - poseban slučaj u kojem morska cvjetnica raste izravno u pukotinama stijena i između kamenih gromada (Slike 1.2. i 1.3.).

Svrha i ciljevi istraživanja

U ovoj disertaciji definirani su mehanizmi i čimbenici koji dovode do razlika u strukturnim značajkama zajednica riba povezanih s naseljima morske cvjetnice *Posidonia oceanica*, s posebnim naglaskom na utjecaj različite strukturalne složenosti naselja i dostupnosti alternativnih strukturiranih staništa, te su dokumentirane razlike koje pojedine vrste riba pokazuju u preferenciji prema različitim kontekstima podmorskog okoliša u kojima

dominiraju naselja cvjetnice *P. oceanica*. Na temelju objavljenih podataka o brojnosti pojedinih vrsta riba u Sredozemnom moru, testiran je učinak različitih predatora na zajednice potencijalnog plijena među ribljim vrstama povezanim s naseljima cvjetnice *P. oceanica* kako bi se utvrdila njena relativna vrijednost kao sklonište za ribe.

Cilj ovog istraživanja je utvrditi što utječe na razlike u strukturi zajednica riba povezanih s naseljima morske cvjetnice *Posidonia oceanica* i to pod a) na koji način kontekst podmorskog okoliša i blizina susjednog trodimenzionalnog staništa utječu na strukturu zajednice riba i b) na koji način prisustvo predatora utječe na strukturu zajednice plijena. Ovo istraživanje doprinosi boljem poznavanju čimbenika koji utječu na zajednice riba u različitim tipovima naselja morske cvjetnice *P. oceanica*, a prikupljeni podaci moći će se koristiti za buduće planiranje upravljanja morskim okolišem.

Nul-hipoteze postavljene u ovom istraživanju su sljedeće:

- H01: nema razlike u strukturnim značajkama zajednice riba i brojnosti jedinki između tri različita konteksta podmorskog okoliša kojima dominiraju naselja morske cvjetnice *Posidonia oceanica* (naselja uz sediment / naselja uz kamen s algama / mozaična naselja izmiješana s kamenitim dnom obraslim algama)
- H02: razlike u sastavu vrsta i brojnosti prisutnih predatora nemaju utjecaj na strukturu zajednice riba povezanih s naseljima morske cvjetnice *P. oceanica*.

MATERIJAL I METODE

1. Područje istraživanja

Ova disertacija sastoji se od dvije cjeline:

1.a) Za potrebe utvrđivanja na koji način kontekst podmorskog okoliša i dostupnost susjednog staništa utječu na strukturu zajednice riba u naseljima morske cvjetnice *Posidonia oceanica* provedeno je istraživanje duž istočne obale hrvatskog dijela Jadranskog mora i to od krajnje sjeverne granice prisutnosti naselja cvjetnice *P. oceanica* (NP Brijuni) do južnih otoka Lastova i Mljeta (Slika 3.1.1.1.).

1.b) Istraživanje koje se temelji na meta-analizi dostupnih literaturnih podataka provedeno je analizom dostupne literature, uzevši u obzir podatke o raznolikosti i relativnoj brojnosti vrsta riba u naseljima cvjetnice *P. oceanica* na području cijelog Sredozemnog mora (3.2.1.1.).

2. Metode istraživanja

2.a) S ciljem istraživanja zajednica riba u naseljima morske cvjetnice *Posidonia oceanica* u istočnom dijelu Jadranskog mora korištena je metoda vizualnog cenzusa uz pomoć mamca i autonomne ronilačke opreme (SCUBA). Riba su bilježene duž 55 transekata postavljenih na dubini od 10 metara, u trajanju od 10 minuta, a svaki transekt bio je popraćen ručnim GPS uređajem (Garmin GPSMAP 60CSx Handheld GPS Navigator) kojega je ronionik vukao za sobom. Duž transekta zabilježena je svaka jedinka ribe koja se pojavila unutar vidnog polja ronionika definiranog širinom od po 1 metar sa svake strane transekta i visinom od dna do razine očiju ronionika. Korišteni mamac je komad olova (2x1 cm) privezan za ribolovni najlon omotan oko komada stiropora koji ronionik postavlja i pomiče direktno ispod sebe, otprilike 5 cm iznad površine supstrata (Slika 3.1.1.2). Metoda vizualnog cenzusa uz pomoć mamca opisana je u literaturi kao učinkovita metoda istraživanja zajednica riba u plitkim obalnim područjima (Kruschel & Schultz 2011, 2012), a odabrana je iz razloga što korištenje mamca povećava vjerojatnost opažanja riba koje će se pomaknuti kako bi istražile mamac ili pobjegle od njega. Duž svakog transekta ronionik je bilježio takson (najčešće vrstu) opažene jedinke ribe, razvojni stadij (juvenil ili adult) te broj jedinki iste vrste ako se nalaze u grupi. Ukoliko su opažene jedinke iste vrste u grupi ili plavi, zabilježen je broj jedinki na način da se broji svaka jedinka do 20 jedinki, a zatim se broj procjenjuje u grupama od 10 jedinki do ukupno 100 jedinki te u grupama od 100 jedinki do ukupno 200 ili više jedinki opaženih u isto vrijeme na istom mjestu koje se kreću u istom smjeru. Istovremeno, ronionik je bilježio postotnu pokrivenost morskog dna morskom cvjetnicom *P. oceanica* ($p_2 < 50\%$, $50\% \leq p_3 \leq 75\%$, $75\% \leq p_4 \leq 100\%$). Uz navedeno, zabilježena je temperatura mora, geografija obale, nagib obale i udaljenost od obale za svaki transekt (Tablica 3.1.1.1).

2.b) Utvrđivanje utjecaja predatora na strukturu zajednica riba u naseljima cvjetnice *P. oceanica* provedeno je pretraživanjem dostupnih objavljenih znanstvenih radova koji sadrže podatke o stvarnim (ukupnim) vrijednostima raznolikosti i brojnosti riba zabilježenih u naseljima cvjetnice *P. oceanica* na razini cijelog Sredozemnog mora (Tablica 3.2.1.1.).

Korištene su baze podataka ISI Web of Knowledge, Scopus i Google Scholar i tražene ključne riječi "fish", "seagrass" i "Posidonia" s ciljem pronalaska što više podataka o apsolutnim ili relativnim vrijednostima brojnosti riba u naseljima cvjetnice *P. oceanica*. U obzir su uzete sve istraživane dubine, godišnja doba, doba dana i geografske lokacije te različite metode istraživanja/uzorkovanja. Nisu uzeta u obzir istraživanja provedena na umjetnim morskim cvjetnicama.

3. Statistička obrada podataka

Prikupljeni podaci uneseni su u baze podataka koristeći Microsoft Excel program. Sve statističke analize te obrada i prikaz podataka provedeni su u programima R (R Development Core Team 2016 i 2017) i RStudio.

3.a) S ciljem utvrđivanja razlika u brojnosti jedinki i raznolikosti vrsta između tri različita konteksta podmorskog okoliša kojima dominiraju naselja morske cvjetnice *Posidonia oceanica* korištena je analiza varijance (ANOVA) (Chambers i sur. 2017). Korišten je jednosmjerni model, a za preostalu varijabilnost provjereno je zadovoljava li pretpostavke normalne raspodjele i to korištenjem Shapiro-Wilk testa prije daljnje analize. Tukey HSD post-hoc test proveden je kako bi se istražile razlike u brojnosti jedinki između svih parova razina odabranog faktora (npr. tip naselja). Usporedba strukture zajednica riba povezanih s tri različita tipa naselja morske cvjetnice *P. oceanica*, urađena je korištenjem permutacijske multivarijatne analize varijance PERMANOVA (Anderson 2001; McArdle & Anderson 2001), koja je neparametrijska statistička metoda. Nezavisne varijable koje su uzete u obzir su tip naselja morske cvjetnice *P. oceanica* (cjelovito naselje uz sediment / cjelovito naselje uz kamen s algama / mozaik morske cvjetnice s kamenom obraslim algama) te pokrovnost dna, a matrica koja je korištena u analizi je matrica relativne brojnosti riba u svakoj zajednici na svakom transektu pri čemu svaki individualni transekt predstavlja statističku repliku. Sličnosti između zajednica riba grupiranim po glavnoj varijabli nezavisne varijable (tip naselja) vizualno su prikazane korištenjem nemetričkog višedimenzionalnog skaliranja (nMDS) na temelju Bray-Curtisove udaljenosti i dvostruke Wisconsinove standardizacije, pri čemu je prikazano rješenje s najnižim stresom.

3.b) Na strukturu zajednica riba u naseljima cvjetnice *P. oceanica* može utjecati relativna brojnost predatora, osobito razlika u prisutnosti predatora koji love u prolazu i

predatora koji love iz zasjede. Iz tog razloga, svakoj zabilježenoj vrsti određena je funkcionalna kategorija kojoj pripada s obzirom na način lova. Kategorije su određene prije prikupljanja podataka i to na temelju informacija o načinu prehrane svake vrste u bazi FishBase te na temelju podataka u objavljenim znanstvenim radovima, a dobiveni podaci korigirani su prema potrebi nakon osobnih opažanja za vrijeme istraživanja. Predatori su podijeljeni u 4 kategorije: predatori koji jednim naglim pokretom love iz zasjede, predatori koji vrebaju plijen, a zatim ga aktivno proganjaju i love, predatori koji čekaju plijen i love ga brzim, iznenadnim napadom bez dugotrajnog lova i proganjanja te predatori koji po pomičnoj podlozi traže sitni plijen. Svaka kategorija predatora dodatno je okarakterizirana kao vrsta trajno nastanjena u naselju morske cvjetnice (engl. *resident*) ili vrsta koja dio vremena provodi na nekom drugom staništu, a do naselja cvjetnice *P. oceanica* dolazi aktivno u potrazi za plijenom (engl. *transient*). Sve ostale zabilježene vrste koje se ne hrane ribom smatrane su plijenom. Kako bi se testirao utjecaj fizičkih čimbenika kao što su metoda uzorkovanja, dubina, doba dana, godišnje doba i geografska dužina/širina na razlike u zajednici riba, korištena je permutacijska multivarijatna analiza varijance PERMANOVA (Anderson 2001; McArdle & Anderson 2001). Ista metoda korištena je i za testiranje utjecaja brojnosti različitih kategorija predatora na sastav preostale zajednice riba (plijena).

REZULTATI I RASPRAVA

U ovom istraživanju je tijekom ukupno 2010 opažanja zabilježeno 6842 jedinke riba i 45 različitih taksona (najčešće vrsta) u naseljima morske cvjetnice *Posidonia oceanica* u hrvatskom dijelu Jadranskog mora. Ukupno je zabilježeno 15 različitih porodica riba, pri čemu su porodice Labridae, Gobiidae i Sparidae sadržavale najveći broj različitih vrsta (Tablica 4.1.1). Najčešće zapažene vrste na svim transektima bile su *Coris julis* (394 opažanja s ukupno 495 jedinki), *Symphodus ocellatus* (364 opažanja s ukupno 778 jedinki), *Chromis chromis* (155 opažanja s ukupno 2740 jedinki) te *Diplodus annularis* (117 opažanja s ukupno 129 jedinki). Unutar tri promatrana konteksta prostornog rasporeda elemenata podmorskog okoliša u kojima se pojavljuju naselja cvjetnice *P. oceanica*, zabilježeno je više od 40% zajedničkih vrsta, pri čemu su naselja cvjetnice *P. oceanica* koja graniče sa sedimentom sadržavala najveći broj jedinstvenih vrsta (Slika 4.1.1). Ukupna brojnost riba i brojnost izražena po m³ transeкта značajno je varirala između tri tipa naselja cvjetnice *P. oceanica* (Tablica 4.1.3.). Zabilježena

je veća ukupna brojnost riba i brojnost riba po m³ transekta u mozaičnim naseljima koja rastu izravno na kamenoj podlozi, nego u oba tipa cjelovitih naselja (uz sediment i uz kamen) (Slika 4.1.2.), ali statistički značajna razlika utvrđena je samo u ukupnoj brojnosti između mozaičnih naselja i cjelovitih naselja uz kamen s algama (Tukey $p = 0.034$). Između cjelovitih naselja uz sediment i cjelovitih naselja uz kamen s algama nije bilo statistički značajne razlike u brojnosti riba. Što se tiče razlika u bogatstvu vrsta, indeksima raznolikosti i ujednačenosti, između tri tipa naselja morska cvjetnice *P. oceanica* nije zabilježena statistički značajna razlika. Najveće bogatstvo vrsta kao i najveća ukupna brojnost riba zabilježena je na lokaciji Fulija Zapad (91 opažanja s ukupno 285 jedinki unutar 22 različite vrste). Analiza zajednice istraživanih riba (korištenjem nMDS metode) pokazala je kako se zajednice unutar tri tipa naselja vidljivo razdvajaju na temelju razlika u brojnosti (Slika 4.1.1.1.), a dodatnim analizama pokazano je kako tim razlikama doprinosi upravo značajna varijacija u brojnosti 11 vrsta riba (označenih zvjezdicom u Tablici 4.1.1.1.). Rezultati PERMANOVA analize pokazuju značajan utjecaj tipa naselja, pokrovnosti i temperature na razlike u strukturi zajednice riba (Tablica 4.1.1.2). Između analiziranih faktora nije bilo interakcije, stoga je bilo moguće analizirati utjecaj glavne varijable (tip naselja) pojedinačno, a navedenom varijablom moguće je objasniti oko 13% opažene varijabilnosti. S obzirom da za temperaturu mora i pokrov nije bilo moguće utvrditi statistički značajan utjecaj na raznolikost vrsta, brojnost jedinki, indeks raznolikosti kao niti za indeks ujednačenosti, navedene varijable nisu uzete u obzir u daljnjim analizama.

Za potrebe istraživanja utjecaja predatora na strukturu zajednice riba u naseljima cvjetnice *P. oceanica* u Sredozemnom moru analizirano je ukupno 14 znanstvenih radova koji su sadržavali 27 skupova podataka, a koji su zadovoljavali kriterije pretraživanja i sadržavali podatke o stvarnoj ili relativnoj brojnosti riba (Tablica 3.2.1.1.). Zabilježeno je ukupno 112 taksona (najčešće vrsta) riba unutar 33 različite porodice (Tablica 3.2.2.1.). Porodice Gobiidae, Labridae i Sparidae sadržavale su najveći broj vrsta. Veliki udio varijabilnosti u strukturi zajednice riba uzrokovan je različitim fizičkim čimbenicima, među kojima se kao najznačajnija varijabla istaknula metoda uzorkovanja koja objašnjava više od 30% varijabilnosti ($p < 0.001$). U analiziranim radovima korištene su 3 različite metode uzorkovanja: vizualni cenzus i dvije metode koje koriste povlačnu mrežu koč s gredom (engl. *skid trawl* i *beam trawl*). Daljnja analiza pokazala je značajan utjecaj brojnosti predatora ($p = 0.005$) (Tablica 4.2.1.) i brojnosti stalno nastanjenih predatora ($p = 0.008$) (Tablica 4.2.2.) na preostalu zajednicu riba (plijen).

Vrste *Scorpaena notata*, *Zosterisessor ophiocephalus*, *Scyliorhinus canicula*, *Seriola dumerili* i *Muraena helena* pokazale su najznačajniju korelaciju sa zajednicom riba koje predstavljaju plijen (Tablica 4.2.3.). Naposljetku, za metodu povlačne kočice s gredom (engl. *skid trawl*) pokazan je i statistički značajan negativan utjecaj ukupne brojnosti stalno nastanjenih predatora na ukupno bogatstvo vrsta preostale zajednice riba koje predstavljaju plijen ($p = 0.067$) (Slika 4.2.3.).

Podaci prikupljeni za vrijeme istraživanja zajednica riba u Jadranskom moru ukazuju na dva vrlo bitna aspekta mogućih pokretača varijabilnosti u strukturi zajednice riba povezanih s naseljima morske cvjetnice *P. oceanica*.

Sa stajališta utjecaja prostornog rasporeda elemenata podmorskog okoliša tj. dostupnosti alternativnih susjednih strukturiranih staništa u neposrednoj blizini naselja morske cvjetnice, ovo istraživanje je pokazalo da iako različiti tipovi naselja sadrže vrlo sličan sastav zajednice ribe, i u njima iste vrste u velikom postotku (Slika 4.1.1.), ipak postoji statistički značajna razlika u strukturi zajednice riba. Zapažen manji broj jedinki u cjelovitim naseljima u odnosu na fragmentirana mozaična naselja može se objasniti činjenicom da visoko strukturirana staništa kao što je kamena podloga obrasla makro-algama pružaju veći broj mjesta za skrivanje pa ribe koje se približavaju granici naselja morske cvjetnice i kamene obale s algama radije odabiru kamenito stanište. Zabilježene su vrste čija je brojnost značajno različita u različitim tipovima naselja (Tablica 4.1.1.1.), a preferencija prema jednom od tri osnovna tipa naselja ukazuje da jedinke mogu aktivno birati povoljnije stanište u određenom trenutku. Najbrojnija vrsta u ovom istraživanju, *Coris julis*, ima vidljivo veću brojnost u mozaičnim naseljima u odnosu na dva cjelovita tipa naselja u kojima cvjetnica dominira (Slika 4.1.1.2.) i time značajno doprinosi ukupnoj razlici u strukturi zajednice. Istovremeno, juvenilne jedinke iste vrste izbjegavaju mozaična staništa i njihova brojnost je veća u cjelovitim naseljima uz kamenu podlogu s algama (Slika 4.1.1.2.) što može ukazivati na činjenicu da postoji interferencijska kompeticija između odraslih i juvenilnih jedinki. Mozaična naselja nadalje su definirana velikim brojem agresivnih mezopredatora među kojima dominiraju vrste *Serranus scriba* i *Serranus cabrilla* koje koriste trodimenzionalno stanište za lov iz zasjede (Slika 4.1.1.2.). Zanimljivo je da je u mozaičnim naseljima zabilježena relativno velika brojnost adulta vrste *Oblada melanura* (6% ukupnog broja zabilježenih opažanja, Slika 4.1.1.3.) koje su se kretale kroz cijeli trodimenzionalni prostor ovog staništa, ali istovremeno nije zabilježena niti jedna

juvenilna jedinka što može upućivati na činjenicu da su juvenilni primjerci potencijalni plijen mnogobrojnih mezopredatora koji se hrane malom ribom. Ukupno najveća brojnost svih vrsta zabilježena je na transektima postavljenim u mozaičnim naseljima gdje su cvjetnice i kamena podloga s algama usko isprepletene i stvaraju stanište koje pruža obilje hranidbenih niša. U cjelovitim naseljima uz kamen s algama, vrste *Symphodus doderleini* i *Symphodus ocellatus* opažene su u većem broju nego u druga dva tipa naselja (Slika 4.1.1.2.). Vrsta *Chromis chromis* u cjelovitim naseljima uz kamen je manje brojna nego u mozaičnim naseljima, a također je i vrsta *O. melanura* zabilježena u manjem broju (Slike 4.1.1.2. i 4.1.1.3.), pri čemu je umjesto nje, u povećanoj brojnosti zabilježena vrsta *Spicara smaris* (Slika 4.1.1.2.), inače zooplanktivorna vrsta koja je opažena kako se zadržava u većim plovama izravno iznad naselja cvjetnice. Juvenilni primjerci vrste *Diplodus vulgaris* i mali primjerci glavoča (Gobiidae) zabilježeni su u većem broju u cjelovitim naseljima uz kamen dok u mozaičnim naseljima nisu uopće zabilježeni. U cjelovitim naseljima uz sediment, vrste koje su izrazito indikativne u strukturi zajednice su upravo one vrste koje se i inače mogu opaziti na pješćanim dnima. Osim vrsta *Mullus surmuletus* i *Symphodus melanocercus* koje su zabilježene isključivo u cjelovitim naseljima uz sediment (Tablica 4.1.2.), vrsta *Gobius bucchichi* također je zabilježena u većoj brojnosti nego u cjelovitim naseljima uz kamen (Slika 4.1.1.2.). Ovakav rezultat bio je očekivan jer navedene vrste imaju izraženu potrebu za sedimentnim dnom koje koriste za traženje plijena zakopanog u sediment. Ono što najviše karakterizira cjelovita naselja uz sediment je veliki broj vrsta koje su opažene isključivo u takvom tipu naselja (Slika 4.1.1.), a što ukazuje da pojedine vrste trebaju vrlo specifična staništa u kojima trodimenzionalno naselje morske cvjetnice graniči s područjem čistog sedimenta bez pokrova. Takva kombinacija staništa omogućava im hranjenje, ali i izbjegavanje predatora. Ovdje je bitno spomenuti vrstu *Spondyllosoma cantharus*, koja slično kao i vrsta *C. julis* pokazuje različit prostorni raspored adultnih (koje preferiraju mozaična naselja) i juvenilnih jedinki (koje preferiraju cjelovita naselja uz sediment) i pokazuju još jedan primjer intraspecijske kompeticije između adultnih i juvenilnih jedinki. Iako su zajednice riba u naseljima morske cvjetnice *P. oceanica* tradicionalno smatrane vrlo jednolikima, vidljivo je kako pojedine jedinke aktivno biraju stanište s obzirom na dostupnost alternativnih staništa u blizini.

Kada razmatramo utjecaj predatora na strukturu zajednice riba, analizom postojećih dostupnih podataka o prisutnim vrstama i njihovoj brojnosti na razini Sredozemnog mora,

možemo primijetiti kako inače uvriježena pretpostavka o naselju morske cvjetnice kao apsolutnom skloništu i mjestu u kojem je rizik minimalan, nije uvijek održiva. Velika razlika u metodologiji uzorkovanja između različitih znanstvenih radova onemogućava donošenje općenitih zaključaka, ali unutar svake od metode uzorkovanja ipak je moguće opaziti kako predatori imaju značajan utjecaj na zajednicu plijena (Tablice 4.2.1. i 4.2.2.). Statistički značajna varijacija u strukturi zajednice riba uzrokovana razlikama u brojnosti i ponašanju predatora konzistentna je s hipotezom o različitim tipovima predatora i pokazuje kako neke vrste aktivno izbjegavaju staništa u kojima je povećan rizik od skrivenih, kamufliranih, trajno nastanjenih predatora koji trodimenzionalno stanište koriste kao skrovište iz kojega vrebaju plijen. U naseljima morske cvjetnice *P. oceanica*, predatori pronalaze skrovište jer struktura listova plijenu smanjuje vidljivost, istovremeno omogućavajući predatorima da se neopaženo približe plijenu. Rezultati pokazuju kako predatorske vrste *Scorpaena scrofa* i *Zosterisessor ophiocephalus* koriste upravo takvu taktiku lova što ima značajan utjecaj na zajednicu plijena (Tablica 4.2.3.). Dobiveni rezultati upućuju da naselja morske cvjetnice *P. oceanica* potencijalno predstavljaju stanište u kojemu je relativni rizik od predatora visok jer u njima nalazimo trajno nastanjenje predatore koji love iz zasjede. Promatrajući Sliku 4.2.3. možemo potvrditi prethodno navedena opažanja o relativnoj vrijednosti naselja *P. oceanica* koja je promijenjiva i ovisi o brojnosti i funkcionalnoj kategoriji prisutnih predatora koji reguliraju sastav odnosno brojnost vrsta preostalih vrsta u zajednici.

ZAKLJUČCI

Ova disertacija doprinosi boljem razumijevanju čimbenika koji dovode do razlika u strukturi zajednice riba u naseljima morske cvjetnice *Posidonia oceanica*. Problem je sagledan s dva različita aspekta. U prvom dijelu razmotren je i istražen utjecaj karakteristika staništa tj. prostornog rasporeda elemenata podmorskog okoliša (engl. *seascape context*), dok je u drugom dijelu istražen utjecaj predatora na varijabilnost u strukturi zajednice riba. Vizualni census uz pomoć mamca još se jednom pokazao kao učinkovita metoda koja omogućava detektiranje razlika u strukturi zajednice riba u različitim kontekstima podmorskog okoliša (između različitih tipova naselja cvjetnice *P. oceanica*). Statistički značajan utjecaj rezidentnih predatora i predatora općenito je također prikazan, ali velike razlike u dizajnu eksperimenta, korištenim metodama uzorkovanja i geografskoj distribuciji lokacija unutar obrađenih

podataka onemogućavaju donošenje općenitih zaključaka za područje cijelog Sredozemnog mora. Unatoč tome, unutar svake analizirane metode uzorkovanja pokazan je značajan utjecaj predatora, a dobiveni rezultati doprinose boljem upravljanju, zaštiti i praćenju stanja zajednica riba povezanih s naseljima morske cvjetnice *P. oceanica*.

Provedeno istraživanje rezultiralo je sljedećim zaključcima:

- Postoje značajne razlike u u strukturnim značajkama zajednica riba i njihovoj brojnosti između tri različita konteksta podmorskog okoliša kojima dominiraju naselja morske cvjetnice *Posidonia oceanica* (naselja uz sediment / naselja uz kamen / mozaična naselja) u hrvatskom dijelu Jadranskog mora;
- Jedinke riba kreću se kroz podmorski okoliš i pri tome odabiru stanište u kojem će se zadržavati, a njihova odluka ovisi o tome koja alternativna staništa imaju na raspolaganju - zbog toga je važno sagledati ukupni kontekst prostornog rasporeda elemenata podmorskog okoliša kojima dominira cvjetnica *Posidonia oceanica*;
- Vrlo strukturirana trodimenzionalna staništa u kojima se naselja morske cvjetnice *Posidonia oceanica* isprepliću s kamenitom podlogom obraslom algama (mozaična naselja) osiguravaju veliki broj mjesta za skrivanje zbog čega u njima nalazimo veću brojnost jedinki nego u cjelovitim naseljima morske cvjetnice;
- Trajno nastanjeni predatori i predatori u prolazu značajno utječu na zajednicu riba koje predstavljaju plijen, pri čemu koriste trodimenzionalnu strukturu naselja za skrivanje i lov iz zasjede;
- Trajno nastanjeni predatori koji love iz zasjede (engl. *resident ambush predators*), *Scorpaena notata* i *Zosterisessor ophiocephalus*, značajno utječu na strukturne značajke zajednice riba koje čine plijen;
- Predatori koji love u prolazu i progone plijen (engl. *transient cruise and chase predators*) *Seriola dumerili* i *Epinephelus costae*, te trajno nastanjeni predator koji progoni plijen (engl. *resident wait chase predator*) *Sciaena umbra*, značajno utječu na strukturne značajke zajednice riba koje čine plijen;
- Mezopredatori kao što su vrste *Serranus scriba* i *Serranus cabrilla* imaju najviše koristi od trodimenzionalnog staništa u mozaičnim naseljima cvjetnice *Posidonia oceanica* te značajno utječu na strukturu zajednice riba;

- Naselja morske cvjetnice *Posidonia oceanica* su stanište u kojemu je potencijalni rizik od predatora visok, a njihova vrijednost kao staništa za ribe mijenja se u prostoru i vremenu, ovisno o funkcionalnom i brojčanom sastavu prisutnih predatora.

9. APPENDICES

Appendix 1. Abbreviations and full names for all recorded fish taxa recorded at *Posidonia oceanica* meadows in the Adriatic Sea, Croatia.

Short name	Full name	Family
athe	<i>Atherina hepsetus</i>	Atherinidae
bobo	<i>Boops boops</i>	Sparidae
chch	<i>Chromis chromis</i>	Pomacentridae
coco	<i>Conger conger</i>	Congeridae
coju	<i>Coris julis</i>	Labridae
dian	<i>Diplodus annularis</i>	Sparidae
dila	<i>Dicentrarchus labrax</i>	Moronidae
divu	<i>Diplodus vulgaris</i>	Sparidae
gobius	<i>Gobius</i> sp.	Gobiidae
gobu	<i>Gobius bucchichi</i>	Gobiidae
gocr	<i>Gobius cruentatus</i>	Gobiidae
gofa	<i>Gobius fallax</i>	Gobiidae
goge	<i>Gobius geniporus</i>	Gobiidae
golu	<i>Gobius luteus</i>	Gobiidae
goni	<i>Gobius niger</i>	Gobiidae
govi	<i>Gobius vittatus</i>	Gobiidae
muhe	<i>Muraena helena</i>	Muraenidae
musu	<i>Mullus surmuletus</i>	Mullidae
obme	<i>Oblada melanura</i>	Sparidae
parablennius	<i>Parablennius</i> sp.	Blennidae
pomatoschistus	<i>Pomatoschistus</i> sp.	Gobiidae
sasa	<i>Sarpa salpa</i>	Sparidae
scno	<i>Scorpaena notata</i>	Scorpaenidae
scpo	<i>Scorpaena porcus</i>	Scorpaenidae
scsc	<i>Scorpaena scrofa</i>	Scorpaenidae

seca	<i>Serranus cabrilla</i>	Serranidae
sedu	<i>Seriola dumerili</i>	Carangidae
sehe	<i>Serranus hepatus</i>	Serranidae
sesc	<i>Serranus scriba</i>	Serranidae
spau	<i>Sparus aurata</i>	Sparidae
spca	<i>Spondyliosoma cantharus</i>	Sparidae
spma	<i>Spicara maena</i>	Centracanthidae
spsm	<i>Spicara smaris</i>	Centracanthidae
syct	<i>Symphodus cinereus</i>	Labridae
sydo	<i>Symphodus doderleini</i>	Labridae
syne	<i>Symphodus melanocercus</i>	Labridae
synd	<i>Symphodus mediterraneus</i>	Labridae
symel	<i>Symphodus melops</i>	Labridae
symphodus	<i>Symphodus sp.</i>	Labridae
syoc	<i>Symphodus ocellatus</i>	Labridae
syro	<i>Symphodus roissali</i>	Labridae
syros	<i>Symphodus rostratus</i>	Labridae
syti	<i>Symphodus tinca</i>	Labridae
thpa	<i>Thalassoma pavo</i>	Labridae
NoID	<i>Unidentified</i>	

Appendix 2. Complete dataset of fish assemblages (relative abundances in each dataset, i.e. transect) recorded over *Posidonia oceanica* meadows in the Mediterranean Sea, used for the meta-analysis of the effect of predators on prey community structure.

	<i>dataset</i>													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
apde	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
apim	0.00	0.00	0.00	0.00	0.00	1.79	0.00	0.00	0.00	0.00	0.00	19.23	0.43	1.70
arke	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.65	0.00
arla	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
arth	0.00	0.00	0.00	0.40	0.56	0.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
atbo	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
athe	0.00	0.10	0.00	0.10	0.00	0.00	0.00	0.00	0.00	24.36	16.72	0.00	0.00	0.00
atherina	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
blin	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
bloc	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
blte	0.10	0.00	0.40	0.60	0.44	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
bobo	0.10	18.80	0.20	11.40	0.00	2.89	3.77	1.99	0.00	19.54	19.00	0.00	0.00	0.00
bopo	0.10	0.10	0.00	0.00	0.82	0.60	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.00
caac	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
cari	0.00	0.00	0.00	0.20	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

mugil	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	1.77	0.00	0.00
muhe	0.00	0.00	0.00	0.00	0.12	0.16	0.02	0.04	0.00	0.01	0.00	0.37	0.00	0.12
musu	0.90	0.70	3.70	2.80	1.19	2.13	0.12	0.26	0.20	1.76	1.33	3.10	0.32	0.22
nema	0.00	0.00	0.00	0.00	0.02	0.07	0.00	0.00	0.00	0.00	0.00	0.00	1.84	0.00
obme	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	4.00	2.13	2.08	0.00	0.00

	<i>dataset</i>													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
opba	0.00	0.00	0.00	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
opgr	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
opro	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
paac	0.00	0.00	0.00	0.00	0.00	0.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
paer	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
paga	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
papa	0.00	0.00	0.00	0.00	0.00	0.07	0.07	0.00	0.00	0.09	0.02	0.00	0.00	0.00
paro	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.61	0.00	0.35
pava	0.00	0.40	0.00	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
pomi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
pomatoschistus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
poqu	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sasa	0.00	0.00	0.00	0.00	0.07	0.47	0.00	1.13	0.00	4.14	1.73	11.61	0.00	0.00

scca	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
scno	1.10	1.30	1.40	10.80	2.78	4.45	0.00	0.00	0.00	0.00	0.00	0.07	0.54	0.00
scpo	1.80	1.90	1.20	1.60	3.86	3.47	0.02	0.04	0.00	0.00	0.01	0.69	7.45	0.01
scsc	0.00	0.00	0.00	0.60	0.21	0.31	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.23
scum	0.00	0.00	0.00	0.00	0.05	0.09	0.00	0.00	0.00	0.03	0.01	0.34	0.00	0.35
seca	0.00	0.10	1.20	1.00	2.27	2.48	0.96	1.00	0.35	0.07	0.15	0.08	0.22	0.92
sedu	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	5.97
sehe	0.00	0.00	0.00	0.80	0.63	1.34	0.00	0.00	0.00	0.00	0.00	0.00	1.30	0.00
sesc	0.00	0.00	0.00	0.00	14.68	15.62	0.25	0.48	0.41	0.96	1.52	3.11	4.54	0.76
sparus	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
spau	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00
spca	0.00	0.10	0.00	0.00	0.00	0.00	0.37	1.08	2.19	0.00	0.00	0.31	0.00	0.47
spch	14.30	8.70	4.30	11.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
spma	0.00	0.10	0.00	0.00	0.12	1.95	10.34	14.40	0.00	1.13	0.02	0.00	0.11	2.14
spsm	0.00	19.10	0.00	15.80	0.00	0.69	15.43	3.47	45.10	1.37	0.00	0.00	0.00	5.55
spsp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00
syac	0.00	2.60	0.20	3.10	0.42	4.63	0.00	0.00	0.00	0.00	0.00	0.00	0.86	0.00
syaci	26.60	16.80	22.70	9.30	11.57	3.80	0.12	0.00	0.10	0.00	0.18	0.04	0.65	0.00
sydo	4.60	2.00	7.20	3.80	0.75	0.49	0.13	0.00	0.06	0.00	0.00	0.45	0.11	0.32

dataset

NoID	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Total %	100	100	100	100	100	100	100	100	100	100	100	100	100	100

98

	dataset													
	15	16	17	18	19	20	21	22	23	24	25	26	27	
apde	0.00	0.00	0.00	0.00	0.00	0.58	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
apim	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
arke	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
arla	0.00	0.00	0.00	0.00	0.31	0.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
arth	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.62	0.97	0.00	
atbo	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	
athe	0.00	0.00	0.00	0.43	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	
atherina	0.00	19.34	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
blin	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
bloc	0.00	0.00	0.00	0.00	0.31	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
blte	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
bobo	5.34	0.00	0.00	1.36	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.69	
bopo	0.00	0.00	0.22	0.07	0.00	0.15	0.35	0.08	0.00	0.52	0.00	0.00	0.00	
caac	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.94	0.00	
cari	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
chch	44.81	7.19	0.44	1.08	5.33	46.78	20.74	40.65	0.78	11.34	0.00	1.46	9.11	

muhe	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	
musu	0.29	0.00	0.00	0.14	0.00	0.00	0.18	0.08	0.78	0.00	0.00	0.49	5.66	
nema	0.00	0.00	0.00	0.00	0.31	0.88	0.18	0.24	0.00	1.55	0.00	0.00	0.00	
obme	2.02	2.65	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.38	
opba	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
opgr	0.00	0.00	0.00	0.00	0.00	0.00	0.18	0.00	0.00	0.00	0.00	0.00	0.00	
opro	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
paac	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.42	
paer	0.43	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	

	dataset													
	15	16	17	18	19	20	21	22	23	24	25	26	27	
paga	0.00	0.00	0.00	0.00	0.31	0.29	0.00	0.00	0.00	0.00	0.00	0.49	0.00	
papa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
paro	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
pava	0.00	0.00	0.00	0.00	0.00	2.05	0.00	0.12	0.00	12.37	0.00	5.34	0.00	
pomi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	
pomatoschistus	0.00	0.00	3.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
poqu	0.00	0.00	0.00	0.00	0.00	0.00	0.35	0.00	0.00	0.00	0.00	0.97	0.00	
sasa	6.93	6.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	
scca	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.08	0.00	0.00	0.00	0.00	0.00	

syoc	0.87	0.00	7.51	6.09	26.96	5.26	17.73	2.73	25.00	2.58	20.37	7.77	4.00	
syroi	0.36	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	

	dataset													
	15	16	17	18	19	20	21	22	23	24	25	26	27	
syros	0.22	0.11	8.28	8.10	11.91	3.36	15.43	4.98	25.00	6.70	25.31	9.71	1.93	
sysa	0.00	0.00	0.22	0.00	0.00	0.00	0.35	0.04	0.00	0.00	0.00	0.00	0.00	
syti	1.95	0.08	1.10	0.50	0.63	1.17	1.24	2.08	1.56	0.00	0.62	0.49	6.90	
syty	0.00	0.00	0.99	0.43	0.63	0.00	0.89	0.33	0.78	0.52	0.00	0.49	0.00	
thpa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
trde	0.00	0.00	0.00	0.00	1.88	1.75	2.30	1.47	0.00	0.00	0.00	0.00	0.00	
trdr	0.00	0.00	0.55	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.49	0.00	
trla	0.00	0.00	0.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.94	0.00	
trme	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
trra	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.49	0.00	
trtr	0.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
ursc	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
vapr	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
zefa	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.49	0.00	
zoop	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
NoID	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.78	0.00	0.00	0.00	0.00	

Appendix 3. Complete dataset of fish assemblages (relative abundances of each taxon in each transect, N=55) recorded over *Posidonia oceanica* meadows in the Adriatic Sea, Croatia. For abbreviated names of fish taxa (in the first column) see Appendix 1.

	transect													
	3	4	5	6	7	8	9	11	12	13	14	15	16	17
athe	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
bobo	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.04	0.07	0.02	0.00	0.13	0.04
chch	0.00	0.00	0.18	0.07	0.18	0.00	0.00	0.00	0.04	0.00	0.08	0.03	0.00	0.00
chch.juv	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
coco	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
coju	0.46	0.16	0.26	0.05	0.04	0.04	0.23	0.00	0.21	0.03	0.09	0.15	0.08	0.11
coju.juv	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
dian	0.00	0.00	0.03	0.07	0.04	0.38	0.10	0.00	0.04	0.07	0.00	0.00	0.00	0.00
dian.juv	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.08	0.00	0.03	0.00	0.00	0.00	0.00
dila	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00
divu	0.00	0.00	0.15	0.02	0.18	0.04	0.07	0.12	0.33	0.17	0.04	0.00	0.00	0.00
divu.juv	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00
gobius	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
gobius.juv	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00
gobu	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.07

symphodus.juv	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
syoc	0.20	0.48	0.15	0.48	0.18	0.12	0.17	0.12	0.04	0.07	0.25	0.15	0.25	0.25
syoc.juv	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00
syro	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
syros	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.04	0.00	0.00	0.00
syti	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
thpa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Total %	100	100	100	100	100	100	100	100	100	100	100	100	100	100

transect														
	18	19	20	21	22	23	24	25	26	27	28	29	32	33
athe	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
bobo	0.02	0.10	0.03	0.03	0.08	0.03	0.00	0.02	0.00	0.00	0.03	0.04	0.06	0.05
chch	0.00	0.05	0.08	0.00	0.00	0.00	0.17	0.12	0.12	0.05	0.08	0.04	0.00	0.00
chch.juv	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00
coco	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
coju	0.10	0.03	0.21	0.10	0.35	0.28	0.32	0.17	0.12	0.22	0.36	0.20	0.09	0.00
coju.juv	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.08	0.00	0.00	0.00	0.03	0.00
dian	0.06	0.12	0.01	0.03	0.00	0.00	0.00	0.04	0.08	0.00	0.00	0.00	0.00	0.00
dian.juv	0.00	0.00	0.01	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00

pomatoschistus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sasa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
scno	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
scpo	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
scsc	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

transect														
	18	19	20	21	22	23	24	25	26	27	28	29	32	33
seca	0.00	0.00	0.02	0.03	0.04	0.03	0.04	0.08	0.08	0.16	0.11	0.09	0.00	0.00
sedu	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sehe	0.00	0.00	0.03	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00
sehe.juv	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00
sesc	0.04	0.03	0.04	0.10	0.00	0.08	0.01	0.02	0.12	0.09	0.00	0.07	0.00	0.00
sesc.juv	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
spau	0.02	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00
spca	0.00	0.00	0.01	0.00	0.00	0.00	0.04	0.06	0.00	0.05	0.08	0.20	0.00	0.00
spca.juv	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
spma	0.16	0.10	0.02	0.03	0.00	0.00	0.01	0.00	0.00	0.00	0.06	0.04	0.03	0.00
spsm	0.20	0.25	0.13	0.03	0.08	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05
spsm.juv	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00

syçi	0.02	0.00	0.03	0.16	0.04	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.14
sydo	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.13	0.00
syne	0.02	0.02	0.01	0.06	0.08	0.03	0.01	0.04	0.12	0.06	0.06	0.17	0.03	0.00
syne	0.00	0.00	0.00	0.03	0.04	0.00	0.05	0.00	0.04	0.00	0.06	0.00	0.00	0.00
syne	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
syne	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00
syne	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.09	0.00
syoc	0.20	0.19	0.20	0.19	0.19	0.28	0.03	0.06	0.12	0.31	0.06	0.04	0.09	0.00
syoc	0.02	0.02	0.01	0.03	0.08	0.00	0.01	0.06	0.00	0.02	0.00	0.00	0.00	0.00
syro	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
syros	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00
syti	0.00	0.00	0.01	0.03	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.02	0.00	0.00
thpa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Total %	100	100	100	100	100	100	100	100	100	100	100	100	100	100

transect														
	34	35	36	37	38	39	40	41	42	43	44	45	46	47
athe	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00
bobo	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00
chch	0.00	0.04	0.00	0.00	0.08	0.08	0.05	0.23	0.07	0.05	0.00	0.00	0.21	0.28

gofa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
goge	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
golu	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00
goni	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
govi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
muhe	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
musu	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.03	0.08
noid	0.00	0.04	0.00	0.13	0.01	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00
noid.juv	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00
obme	0.02	0.08	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.10	0.00	0.00
obme.juv	0.00	0.00	0.01	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00
parablennius	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
pomatoschistus	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sasa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05
scno	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
scpo	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00
scsc	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
seca	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.03	0.02	0.00	0.00
sedu	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00
sehe	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.02	0.01	0.00	0.00	0.00	0.00

syti	0.02	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.03	0.02	0.00	0.00
thpa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00
Total %	100	100	100	100	100	100	100	100	100	100	100	100	100

10. BIOGRAFIJA

Ivana Zubak Čižmek rođena je 5. srpnja 1984. godine u Doboju, u Bosni i Hercegovini. 1992. godine dolazi s obitelji u Zadar gdje je završila osnovnu školu Šimuna Kožičića Benje i Gimnaziju Jurja Barakovića. Akademske godine 2003./2004. upisuje dodiplomski studij Biološkog odsjeka Prirodoslovno-matematičkog fakulteta Sveučilišta u Zagrebu gdje završava smjer Inženjer biologije - smjer ekologija među 10% najuspješnijih studenta na godini i smjeru. Diplomski rad na temu „Kartiranje bentoskih zajednica u tjesnacu Mali Ždrelac, zadarsko otočje“, pod vodstvom dr. sc. Tatjane Bakran-Petricioli, obranila je u rujnu 2008. godine. Od veljače 2009. do lipnja 2011. radi kao stručni suradnik edukator u Javnoj ustanovi PP Vransko jezero. U srpnju 2011. godine zaposlena je na MZOS projektu „Ekologija i praćenje stanja bentoskih životnih zajednica hrvatskoga Jadrana“ kao znanstvena novakinja na Pomorskom odjelu Sveučilišta u Zadru, a od listopada 2014. radi na Odjelu za ekologiju, agronomiju i akvakulturu Sveučilišta u Zadru. Međusveučilišni poslijediplomski doktorski studij „Primijenjene znanosti o moru“ pri Sveučilištu u Splitu i Sveučilištu u Dubrovniku upisuje u akademskoj godini 2014./2015. te pod vodstvom prof. dr. sc. Stewarta Schultza sa Sveučilišta u Zadru izrađuje ovu doktorsku disertaciju.

Sudjelovala je na projektu Hrvatske zaklade za znanost „Conditions, resources, enemies and biodiversity: Forces structuring marine communities of the shallow Adriatic Sea – COREBIO“. Na Sveučilištu u Zadru sudjeluje u izvođenju nastave iz kolegija: „Biologija mora“, „Ekologija mora“, „Primijenjena ekologija vodenih ekosustava“, „Oceanologija i limnologija“ te „Statistika i znanstvene metode“.

Tijekom poslijediplomskog studija provela je tjedan dana na Sveučilištu u Nici u Francuskoj u laboratoriju ECOMERS (prof. dr. sc. Patrice Francour) gdje je stjecala znanja i iskustvo potrebno za provođenje nove metode vizualnog cenzusa riba pod nazivom FAST-Fish Assemblage Survey Technique.

Koautor je 6 znanstvenih radova u časopisima indeksiranim u ISI Web of Science Core Collection bazi, jednog rada u časopisu indeksiranom u BIOSIS Citation Indeks bazi, tri rada u ostalim časopisima te dva rada koja su trenutno u postupku recenzije. Sudjelovala je u nekoliko domaćih i međunarodnih znanstvenih i stručnih skupova s ukupno 10 sažetaka.

Osim navedenog, često organizira i provodi aktivnosti popularizacije znanosti kroz razne radionice namijenjene djeci i mladima od vrtićke do srednjoškolske dobi čime doprinosi provođenju edukacije iz područja znanosti o moru. Član je European Marine Science Educators Association (EMSEA) koja promiče znanje o moru (engl. *ocean literacy*) te je predsjednica Udruge za očuvanje bioraznolikosti Aurelia i član UO Društva istraživača mora - 20000 milja gdje također osmišljava, organizira i provodi brojne aktivnosti popularizacije znanosti i edukacije.

Popis radova

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“People ask: Why should I care about the ocean? Because the ocean is the cornerstone of earth's life support system, it shapes climate and weather. It holds most of life on earth. 97% of earth's water is there. It's the blue heart of the planet — we should take care of our heart. It's what makes life possible for us. We still have a really good chance to make things better than they are. They won't get better unless we take the action and inspire others to do the same thing. No one is without power. Everybody has the capacity to do something.

*No water, no life.
No blue, no green!”*

Sylvia A. Earle
