Predators structure fish communities in *Posidonia oceanica* meadows: meta-analysis of available data across the Mediterranean basin

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ABSTRACT: *Posidonia oceanica* meadows are thought to provide refuge for prey species, which suggests that fish communities are organized according to the abundance and behavior of predators. We collected published research on fish assemblages associated with *P. oceanica* meadows in the Mediterranean Sea and performed a meta-analysis to test hypotheses regarding the drivers of community structure. In 14 studies documenting the relative abundance of fish species, 112 taxa within a depth range of 1–40 m were reported at local *P. oceanica* meadows. Sampling method had the most significant effect on community abundance. Total predator abundance and abundance of resident predators each had a significant effect on the prey fish community. A higher abundance of resident predator species such as *Scorpaena notata* and *Zosterisessor ophiocephalus* was associated with a lower abundance of small *Symphodus* spp., *Chromis chromis*, and Gobiidae, and overall lower prey species richness. Fish communities in *P. oceanica* meadows are, therefore, in part organized in response to the presence and abundance of piscivorous species, which reduces the value of seagrass as a refuge habitat for potential prey species. For more robust estimates of the habitat value of *P. oceanica*, a concerted international, collaborative research effort that applies uniform, non-destructive sampling methods, such as visual census or stereo-videography within and outside meadows, is needed.

KEY WORDS: *Posidonia oceanica* · Seagrass · Fish · Community structure · Predation · Predator–prey interactions

INTRODUCTION

Seagrass meadows worldwide are hypothesized to provide critical habitat for mobile animals, and to be 'biodiversity hotspots' for both invertebrates and fish (Orth et al. 1984, Jenkins et al. 1997, Beck et al. 2001, Pergent 2012). The primary habitat value of seagrass for mobile demersal species is proposed to be the refuge it provides to potential prey individuals by reducing prey visibility and impeding predator movement. The 'seagrass superiority hypothesis' posits that the net risk of predation mortality for a mobile animal is lower within seagrass meadows than within neighboring open habitat (Heck & Orth 1980, Bell & Pollard 1989). Thus, species in seagrass meadows are thought to have increased fitness through protection against predation mortality during vulnerable life history phases such as spawning, larval settlement, and juvenile development. This hypothesis explains the higher abundance and diversity of fish and invertebrates in seagrass relative to adjacent open habitat sometimes reported in Australia and the eastern and southern USA (Bell & Pollard 1989). In those regions, prey are thought to actively search for seagrass habitat in response to perceptual cues that may be associated

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with lower predation effectiveness, such as lower light intensity (Zupo & Nelson 1997).

The seagrass superiority hypothesis, however, fails to explain a negative preference for seagrass habitat in many prey species and the high spatio-temporal variation in fish communities associated with seagrass meadows. It also fails to account for the ability of predators to learn or evolve to see, capture, and feed on the abundant food resource of prey individuals hiding out in seagrass (for a review see Hellman et al. 2009, p. 425–438). For the Mediterranean seagrass *Posidonia oceanica*, for example, many researchers have postulated that the primary habitat value for fish is the refuge from predation provided by the physical structure of vertical shoots and leaves (Bell & Harmelin-Vivien 1982, 1983, Francour 1997, Guidetti, 2000). However, the same researchers have also reported several resident (e.g. *Scorpaena* and *Zosterisessor*) and transient (e.g. families Congridae, Gadidae, Ophiidae) piscivorous predators. The transient piscivorous predators move from rocky reefs to forage within *P. oceanica* at night (Bell & Harmelin-Vivien 1982, 1983). This raises the question: how can *P. oceanica* meadows simultaneously be a critical refuge habitat for fish prey, and a feeding habitat for fish predators?

An alternative hypothesis, the predation mode hypothesis (Schultz et al. 2009), predicts that the relative mortality risk an individual experiences within a seagrass bed is not fixed, but varies greatly depending on the density and behavior of local predator populations. Where large, fast-cruising, transient, chase–capture predators are abundant, the meadow can be a net refuge because its structure restricts the movement and field of vision of these visual hunters (Heck et al. 2003). If alternative structured habitat is not available, then seagrass might be the sole or primary aboveground refuge from these predators, leading to prey aggregations of high abundance and diversity within meadows. On the other hand, any physical structure may help conceal predators, allowing more effective ambushing, stalk–attacking, and wait–chasing than outside structured habitat. If such predators are resident, active, and dominant within seagrass, mortality risks may be far greater within compared with outside the meadow. In this case, seagrass beds are the inverse of a refuge, namely dangerous spaces where populations of prey are effectively regulated by resident predators, and visiting such areas would increase prey mortality (Schultz et al. 2009, Schultz & Kruschel 2010).

Testing predictions of the predation mode hypothesis requires substantial spatial or temporal varia-

tion in the fish community. The influence of predators on prey can be complex, e.g. decreasing the abundance of some species and increasing others as a result of trophic cascades or competition. Furthermore, direct predation effects may result in a positive relationship between predator and prey populations if (large, cruising) predators are more mobile and seek out prey aggregations, or a negative relationship if prey are more mobile and can avoid aggregations of (sedentary ambushing) predators. Several studies have reported high variability in the structure of fish assemblages associated with seagrass meadows (Francour 1997, Jackson et al. 2001, Moranta et al. 2006, La Mesa et al. 2011). The predictions of the predation mode hypothesis have been tested in the seagrass *Zostera marina* in Japan (Horinouchi 2007) and Croatia (Schultz et al. 2009, Schultz & Kruschel 2010) where prey abundance was found to be negatively correlated with resident ambushing predator abundance in seagrass beds, resulting in a net lower abundance of prey species in seagrass relative to neighboring habitats. These relationships have not yet been documented in *P. oceanica*, although Moranta et al. (2006) warned that little attention has yet been given to the variability in the fish assemblages associated with *P. oceanica* meadows, and the relative frequency of predation modes.

The endemic *Posidonia oceanica* (L.) Delile is the most abundant seagrass in the Mediterranean Sea, where it forms extensive monospecific meadows between the surface and 44 m depth in the clearest waters (e.g. Malta, Corsica; Augier & Boudouresque 1979, Boudouresque et al. 1990, Borg & Schrembi 1995). The meadows are highly sensitive to human disturbance (Boudouresque et al. 2000, 2006) and are now listed as a priority natural habitat in Annex I of the EC Directive 92/43/EEC on the Conservation of Natural Habitats and of Wild Fauna and Flora (EC 1992).

Bell & Harmelin-Vivien (1982) were the first to point out the scarcity of published information on faunal communities associated with *P. oceanica* in the Mediterranean Sea, and our resulting lack of understanding of the role of one of the most common and important benthic habitats in sustaining productivity and diversity of fish species. In the intervening 30 years, at least 14 studies have been published to fill this knowledge gap in the western Mediterranean, and these now allow an initial assessment of the major drivers of the variability of fish communities associated with *P. oceanica*. We performed a meta-analysis of their datasets to answer the following questions. (1) What are the major drivers of variability in the fish communities associated with *P. ocean-*

ica meadows? (2) What effect does variability in piscivorous predator abundance have on the community of potential prey species? (3) What are the major gaps and barriers to further progress in understanding the role of *P. oceanica* in sustaining fish communities in the Mediterranean Sea?

MATERIALS AND METHODS

Literature search and data selection

A review of the published literature was performed using the ISI Web of Knowledge service (http://scientific.thompson.com/isi/), Scopus (https://www.scopus.com/), and Google Scholar (https://scholar.google.com/) with search terms 'fish', 'seagrass', and '*Posidonia*' to identify studies of the absolute or relative abundance of fish species associated with Mediterranean *Posidonia oceanica* meadows. Studies based on artificial seagrass beds were not included. The search identified more than 100 publications, of which 14 fulfilled the required criteria. The great majority failed to provide abundance estimates for each encountered species at the same place and time, and/or compiled mean values, lists, or overall species richness. Our final database contained 27 recorded transects (fish community datasets) from 14 independent studies published between 1982 and 2010 (Table 1). Surveys covered several combinations of depths, seasons, times of day, and geographical locations. The sampling methods used were: (1) underwater visual census, mostly strip or belt transects ranging from 20 to 150 m in length and several point counts within a radius of 2 to 5 m; (2) beam trawl, 1.8 m wide and 0.8 m high, hauled for 10 to 30 min at a speed of 1.5 to

Table 1. Research papers (1982–2010) dealing with fish community structure associated with *Posidonia oceanica* meadows in the Mediterranean basin

| Dataset	Method	Time of day	Season	MPA/non-MPA	Location	Depth (m)	Reference
1	Skid trawl	Day	Warm	Non-MPA	Plateau des Chevres, Marseille, France	16.0–18.0	Bell & Harmelin-Vivien (1982)
2	Skid trawl	Night	Warm	Non-MPA	Plateau des Chevres, Marseille, France	16.0–18.0	Bell & Harmelin-Vivien (1982)
3	Skid trawl	Day	Warm	Non-MPA	Carry le Rouet, Marseille, France	16.0–18.0	Bell & Harmelin-Vivien (1982)
4	Skid trawl	Night	Warm	Non-MPA	Carry le Rouet, Marseille, France	16.0–18.0	Bell & Harmelin-Vivien (1982)
5	Beam trawl	Day	Warm	Non-MPA	Allicante, Spain	20.0–22.0	Valle et al. (2001)
6	Beam trawl	Night	Warm	Non-MPA	Allicante, Spain	20.0–22.0	Valle et al. (2001)
7	Visual census	Day	All year	Non-MPA	Genoa-Quinto, Genoa, Italy	10.0	Guidetti et al. (1998)
8	Visual census	Day	All year	Non-MPA	Otranto, Apulian coast, Italy	6.5–8.0	Guidetti (2000)
9	Visual census	Day	Warm	Non-MPA	S. Domino, Tremiti Islands, Italy	6.5–8.0	Guidetti (2000)
10	Visual census	Day	All year	MPA	Alicante, Spain	1.0–15.0	Valle & Bayle-Sempere (2009)
11	Visual census	Day	All year	Non-MPA	Alicante, Spain	1.0–15.0	Valle & Bayle-Sempere (2009)
12	Visual census	Day	Warm	MPA	Mallorca Island, Balearic Islands, Spain	10.0–20.0	Frau et al. (2003)
13	Skid trawl	Day	All year	Non-MPA	Island of Ischia, Gulf of Naples, Italy	17.0–20.0	Zupo & Stübing (2010)
14	Visual census	Day	All year	Non-MPA	Balearic Islands, Spain	30.0	Reñones et al. (1998)
15	Visual census	Day	Warm	MPA	Ligurian Sea, Italy	4.0–29.0	Tunesi & Vacchi (1993)
16	Visual census	Day	Warm	Non-MPA	Noli, Ligurian Sea, Italy	7.0	Guidetti et al. (1996)
17	Beam trawl	Day	Warm	Non-MPA	Mallorca, Balearic Islands, Spain	25.0–30.0	Reñones et al. (1995)
18	Beam trawl	Night	Warm	Non-MPA	Mallorca, Balearic Islands, Spain	25.0–30.0	Reñones et al. (1995)
19	Skid trawl	Day	Warm	MPA	Port-Cross National Park, France	12.0–20.0	Harmelin-Vivien (1982)
20	Skid trawl	Night	Warm	MPA	Port-Cross National Park, France	12.0–20.0	Harmelin-Vivien (1982)
21	Skid trawl	Day	Cold	MPA	Port-Cross National Park, France	12.0–20.0	Harmelin-Vivien (1982)
22	Skid trawl	Night	Cold	MPA	Port-Cross National Park, France	12.0–20.0	Harmelin-Vivien (1982)
23	Skid trawl	Day	Warm	MPA	Galeria Bay, Regional Natural Park of Corsica, France	18.0–40.0	Harmelin-Vivien (1984)
24	Skid trawl	Night	Warm	MPA	Galeria Bay, Regional Natural Park of Corsica, France	18.0–40.0	Harmelin-Vivien (1984)
25	Skid trawl	Day	Warm	MPA	Stollo and Calleta, Regional Natural Park of Corsica, France	18.0–40.0	Harmelin-Vivien (1984)
26	Skid trawl	Night	Warm	MPA	Stollo and Calleta, Regional Natural Park of Corsica, France	18.0–40.0	Harmelin-Vivien (1984)
27	Visual census	Day	All year	Non-MPA	Alicante, Spain	15.0–17.0	Sánchez-Jerez et al. (2002)
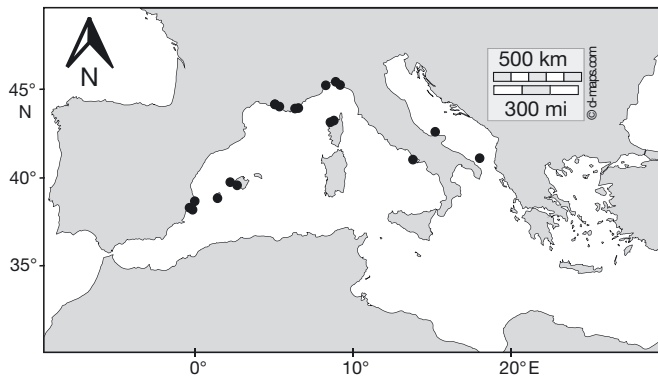
Fig. 1. Geographical location of the *Posidonia oceanica* sampling sites included in the meta-analysis

2.0 knots; and (3) skid trawl, 1.5 m wide and 0.5 m high, hauled for 40 to 60 min at a speed of 1.0 to 1.5 knots—for details of the skid trawl method see Harmelin-Vivien (1981). The sampled depth varied from 1 to 40 m. The studies were conducted during the day (19) and night (8), in warm and cold seasons, from 38.15° to 44.38° N latitude and 0.50° W to 18.48° E longitude (Fig. 1), in locations with different levels of protection (11 in marine protected areas (MPAs) and 16 in non-MPAs).

Statistical analyses

All statistical analyses were performed using R (R Core Team 2016), using the base or vegan libraries. Because the predation mode hypothesis predicts that fish community structure is driven by the risk posed by seagrass resident and transient predators, each recorded species from the database was assigned to a functional category based on their predatory behavior (Table 2). The categories were determined from information on the maximum reported size and trophic level in FishBase (www.fishbase.org), personal observations, and published papers (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). Based on modes of prey search and/or capture, predators were separated into 4 categories: ambush, wait-chase, stalk-attack, and substrate dwelling, and each was further categorized as transient or residents of seagrass meadows. Only species that were found to feed on other fish, regardless of their size, were considered fish predators; the rest were treated as non-piscivores and potential prey. Because the predation mode hypothesis predicts that variation in

predator abundance has an effect on variation across the entire prey community, we used the community matrix of the abundance of each prey species (columns) for each transect (row) as the response matrix for all analyses.

We used permutational multivariate analysis of variance (PERMANOVA; Anderson 2001, McArdle & Anderson 2001) to test 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 (minus the predators). PERMANOVA allows the effect of a predictor variable on the entire community response to be tested, 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. This method is appropriate for the predation mode hypothesis applied to these datasets because the impact of any predator on any prey could be positive or negative depending on the ecological context such as, for example, the relative mobility of the 2 species, their ability to migrate in and out of the habitat, and the intensity of local competition with other prey species affected by the predator. Furthermore, abundance distributions of species are clearly non-normal with many zeroes, and the total species number is greater than the total site number. The prey community matrix was converted to the Bray-Curtis distance matrix, which was then used in the PERMANOVAs with the vegan function adonis. All analyses were performed twice: first on the real data, and second using a randomly generated null dataset with the same number of predator and prey species as in the real data, but the null abundances chosen as random Poisson variates. The second analysis allowed construction of an empirical cumulative distribution function that provided the null probability of the F value obtained in the PERMANOVA of the real data. In all analyses, the 2 estimated null probabilities were equal to within the reported number of significant digits.

After documenting the effect of transient and resident predators on the prey community independently of the other physical predictor variables, we separated the community data into 3 sets corresponding to the 3 survey methods, and within each method we used non-metric multidimensional scaling (NMDS, the metaMDS function in R; Faith et al. 1987, Minchin 1987) to visualize the correlation structure of the prey community (minus the predators) in 2D NMDS ordination plots. In each of these plots, we overlaid the vector corresponding to the direction and magnitude of the correlation between the resident and transient

predator abundance(s) and the axes of the prey ordination, and tested the significance of this correlation using the permutational procedure in the envfit function of vegan. We tested both the significance of the predator group abundance on the ordination of the remaining prey community ('top-down' effects), and the prey abundance on the ordination of the remaining predator community ('bottom-up' effects). We also reported those species responsible for the significant envfit results and reported all probability values less than 0.1, while still using $p < 0.05$ as the criterion for statistical significance.

Finally, for the survey method with the largest sample size and capable of the most accurate census of seagrass-resident predators, the skid trawl, we computed the relationship between resident predator abundance and the total species richness of the prey community, and tested the significance of this relationship using quadratic least squares regression with the nls function in R base, which uses a Gauss-Newton maximization algorithm (R Core Team 2016).

RESULTS

The 14 papers contained 27 distinct datasets and reported a combined total of 112 fish taxa from 33 families. Gobiidae were the most species-rich family recorded at *Posidonia oceanica* meadows in the Mediterranean Sea, represented by 17 species (15%); Labridae and Sparidae were represented by 15 species (14%); Blennidae and Serranidae by 6 species (5%). Seventeen families were represented by a single species (Fig. 2).

Effect of physical factors on the variability of the fish community matrix

Three methods were used to census for fish species. A skid trawl, visual census, and beam trawl were used in 13 datasets (4 papers), 10 datasets (8 papers), and 4 datasets (2 papers), respectively (Table 1). Physical factors explained about 70% of

Table 2. 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

Short name	Full name	Family	Functional category
apde	*Apletodon dentatus*	Gobiesocidae	Prey
apim	*Apogon imberbis*	Apogonidae	TWC
arke	*Arnoglossus kessleri*	Botidae	RA
arla	*Arnoglossus laterna*	Bothidae	RA
arth	*Arnoglossus thori*	Botidae	RA
atbo	*Atherina boyeri*	Atherinidae	Prey
athe	*Atherina hepsetus*	Atherinidae	Prey
atherina sp	*Atherina* sp.	Atherinidae	Prey
blin	*Parablennius incognitus*	Blenniidae	Prey
bloc	*Blennius ocellaris*	Blenniidae	RA
bobo	*Boops boops*	Sparidae	Prey
bopo	*Bothus podas*	Bothidae	Prey
caac	*Carapus acus*	Carapidae	Prey
cari	*Callionymus risso*	Callionymidae	Prey
chch	*Chromis chromis*	Pomacentridae	Prey
chqu	*Chromogobius quadrivittatus*	Gobiidae	Prey
coco	*Conger conger*	Congridae	RSA
coju	*Coris julis*	Labridae	RWC
ctru	*Ctenolabrus rupestris*	Labridae	Prey
deco	*Deltentosteus collonianus*	Gobiidae	Prey
dede	*Dentex dentex*	Sparidae	TCC
dequ	*Deltentosteus quadrimaculatus*	Gobiidae	Prey
dian	*Diplodus annularis*	Sparidae	Prey
dibi	*Diplecogaster bimaculata*	Gobiesocidae	Prey
dipu	*Diplodus puntazzo*	Sparidae	Prey
disa	*Diplodus sargus*	Sparidae	Prey
divu	*Diplodus vulgaris*	Sparidae	Prey
epca	*Epinephelus caninus*	Serranidae	TWC
epco	*Epinephelus costae*	Serranidae	TCC
epma	*Epinephelus marginatus*	Serranidae	RWC
game	*Gaidropsarus mediterraneus*	Lotidae	RSA
gavu	*Gaidropsarus vulgaris*	Lotidae	RSA
goau	*Gobius auratus*	Gobiidae	Prey
gobius sp	*Gobius* sp.	Gobiidae	Unknown
gobu	*Gobius bucchichi*	Gobiidae	Prey
gocr	*Gobius cruentatus*	Gobiidae	RWC
gofa	*Gobius fallax*	Gobiidae	Prey
goge	*Gobius geniporus*	Gobiidae	RWC
goni	*Gobius niger*	Gobiidae	RWC
gopa	*Gobius paganelus*	Gobiidae	Prey
govi	*Gobius vittatus*	Gobiidae	Prey
hihi	*Hippocampus hippocampus*	Syngnathidae	RA
hira	*Hippocampus (ramulosus) guttulatus*	Syngnathidae	RA
labi	*Labrus bimaculatus*	Labridae	Prey
lame	*Labrus merula*	Labridae	Prey
lavi	*Labrus viridis*	Labridae	Prey
leca	*Lepadogaster candolii*	Gobiesocidae	Prey
lepido	*Lepidorhombus* sp.	Scophthalmidae	RA
liau	*Liza aurata*	Mugilidae	Prey
limo	*Lithognathus mormyrus*	Sparidae	Prey
lini	*Lipophrys nigriceps*	Blenniidae	Prey
mohi	*Monochirus hispidus*	Soleidae	Prey
muba	*Mullus barbatus*	Mullidae	Prey

Table 2 (continued)

Short name	Full name	Family	Functional category
mugil sp	*Mugil* sp.	Mullidae	Prey
muhe	*Muraena helena*	Muraenidae	RSA
musu	*Mullus surmuletus*	Mullidae	TSD
nema	*Nerophis maculatus*	Syngnathidae	Prey
obme	*Oblada melanura*	Sparidae	Prey
opba	*Ophidion barbatum*	Ophidiidae	TSD
opgr	*Opeatogenys gracilis*	Gobiesocidae	Prey
opro	*Ophidion rochei*	Ophidiidae	TSD
paac	*Pagellus acarne*	Sparidae	Prey
paer	*Pagellus erythrinus*	Sparidae	Prey
paga	*Parablennius gattorugine*	Blennidae	Prey
papa	*Pagrus pagrus*	Sparidae	TCC
paro	*Parablennius rouxi*	Blennidae	Prey
pate	*Parablennius tentacularis*	Blenniidae	Prey
pava	*Parophidion vassali*	Ophidiidae	Prey
pomi	*Pomatoschistus minutus*	Gobiidae	Prey
poqu	*Pomatoschistus quagga*	Gobiidae	Prey
pomato	*Pomatoschistus* sp.	Gobiidae	Prey
sasa	*Sarpa salpa*	Sparidae	Prey
scca	*Scyliorhinus canicula*	Scyliorhinidae	TCC
scno	*Scorpaena notata*	Scorpaenidae	RA
scpo	*Scorpaena porcus*	Scorpaenidae	RA
scsc	*Scorpaena scrofa*	Scorpaenidae	RA
scum	*Sciaena umbra*	Sciaenidae	RWC
seca	*Serranus cabrilla*	Serranidae	RWC
sedu	*Seriola dumerili*	Carangidae	TCC
sehe	*Serranus hepatus*	Serranidae	RWC
sesc	*Serranus scriba*	Serranidae	RWC
sparus	*Sparus* sp.	Sparidae	TCC
spau	*Sparus aurata*	Sparidae	TCC
spca	*Spondyliosoma cantharus*	Sparidae	Prey
spch	*Spicara chryselis* (*maena*)	Centracanthidae	Prey
spma	*Spicara maena*	Centracanthidae	Prey
spsm	*Spicara smaris*	Centracanthidae	Prey
spsp	*Sphyraena sphyraena*	Sphyraenidae	TCC
syac	*Syngnatus acus*	Syngnathidae	Prey
syci	*Symphodus cinereus*	Labridae	Prey
sydo	*Symphodus doderleini*	Labridae	Prey
symed	*Symphodus mediterraneus*	Labridae	Prey
symel	*Symphodus melanocercus*	Labridae	Prey
symelo	*Symphodus melops*	Labridae	Prey
syoc	*Symphodus ocellatus*	Labridae	Prey
syroi	*Symphodus roissali*	Labridae	Prey
syros	*Symphodus rostratus*	Labridae	Prey
sysa	*Synodus saurus*	Synodontidae	RA
syti	*Symphodus tinca*	Labridae	Prey
syty	*Syngnatus typhle*	Syngnathidae	RA
thpa	*Thalassoma pavo*	Labridae	Prey
trde	*Tripterygion delaisi*	Tripterygiidae	Prey
trdr	*Trachinus draco*	Trachinidae	RA
trla	*Trigloporus lastoviza*	Triglidae	Prey
trme	*Tripterygion melanurus*	Tripterygiidae	Prey
trra	*Trachinus radiatus*	Trachinidae	RA
trtr	*Tripterygion tripteronotus*	Tripterygiidae	Prey
ursc	*Uranoscopus scaber*	Uranoscopidae	RA
vapr	*Vanneaugobius pruvoti*	Gobiidae	Prey
zefa	*Zeus faber*	Zeidae	TWC
zoop	*Zosterisessor ophiocephalus*	Gobiidae	RA
NoID	NoID	Unknown	Unknown

the variability of the fish community abundance matrix across all transects with survey method having the most significant effect and explaining 32% of the variability (PERMANOVA, p = 0.0001). The time of day, season, latitude, and minimum sampling depth also had each individually, a significant influence (p = 0.0136, 0.0021, 0.0037, and 0.0011, respectively).

Effect of predators on the remaining fish community

Controlling for the significant physical variables (method, latitude, and season), total predator abundance and total resident predator abundance both had a significant effect on the remaining fish community (p = 0.0054 and 0.0076, respectively, Tables 3 & 4, Fig. 3). Three predator-specific behavior and hunting techniques (resident wait-chase, resident stalk-attack, and transient wait-chase predators) each had a significant effect on the remaining fish community (p = 0.0027, 0.0002, and 0.0380, respectively).

Effect of predators on prey community and effect of prey on predator community within each sampling method

The predator species exhibiting the strongest association with the prey community were resident ambush predators *Scorpaena notata* and *Zosterisessor ophiocephalus* (skid trawl), transient chase-capture species *Scyliorhinus canicula* (skid trawl) and *Seriola dumerili* (visual census), and resident stalk-attack species *Muraena helena* (beam trawl) (Table 5).

Effect of predators on prey species richness

We found a significant negative effect of total percent abundance of all predators and the total species richness of the
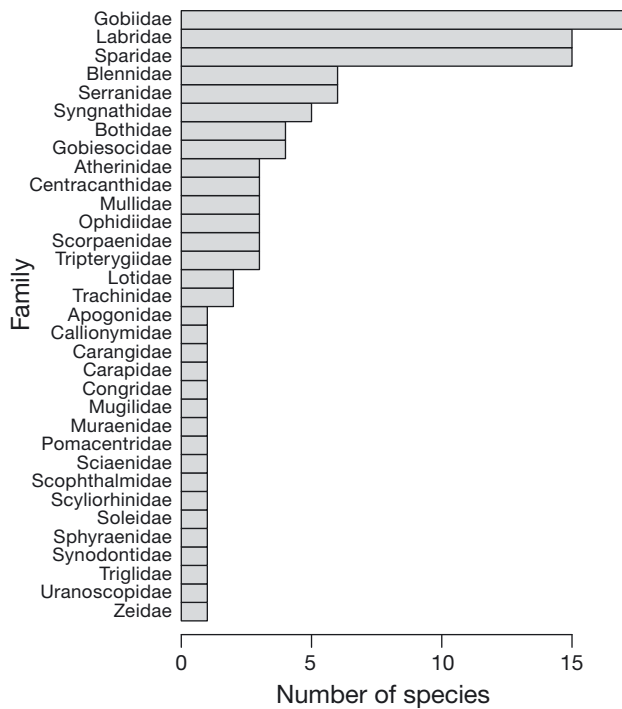
Fig. 2. Total number of fish species sampled in *Posidonia oceanica* meadows in all studies by family

Table 3. Analysis of variance using PERMANOVA of the effect of predators on prey abundance matrix for *Posidonia oceanica* meadows, controlling for the physical variables

Predictor variables	Effect of the predators on the prey abundance matrix			
	df	F	R^2	p
Method	2	7.40	0.307	0.0001
Latitude	1	4.68	0.097	0.0005
Season	2	2.72	0.113	0.0019
All predators	1	3.31	0.069	0.0054
Residuals	20		0.415	

Table 4. Analysis of variance using PERMANOVA of the effect of resident predators on prey abundance matrix for *Posidonia oceanica* meadows, controlling for the physical variables

Predictor variables	Effect of the resident predators on the prey abundance matrix			
	df	F	R^2	p
Method	2	7.35	0.307	0.0001
Latitude	1	4.65	0.097	0.0005
Season	2	2.71	0.113	0.0016
Resident predators	1	3.17	0.066	0.0076
Residuals	20		0.417	

Table 5. p values of correlations between the indicated species and the axes of the NMDS ordinations of the prey community or predator community in *Posidonia oceanica* meadows, within each of the 3 sampling methods. All values <0.1 are reported

| Correlation Species	p value
Skid trawl	
Predators on prey ordination	
Scyliorhinus canicula	0.032
Scorpaena notata	0.033
Zosterisessor ophiocephalus	0.044
Coris julis	0.044
Mullus surmuletus	0.054
Prey on resident predator ordination	
Symphodus doderleini	0.004
Symphodus cinereus	0.007
Tripterygion delaisi	0.008
Diplodus vulgaris	0.020
Nerophis maculatus	0.020
Chromis chromis	0.030
Lepadogaster candolii	0.058
Gobius vittatus	0.075
Labrus viridis	0.098
Prey on transient predator ordination	
Lepadogaster candolii	0.005
Chromis chromis	0.007
Symphodus doderleini	0.007
Parablennius tentacularis	0.015
Tripterygion delaisi	0.031
Visual census	
Predators on prey ordination	
Seriola dumerili	0.030
Epinephelus costae	0.048
Sciaena umbra	0.090
Prey on resident predator ordination	
Diplodus puntazzo	0.002
Chromis chromis	0.036
Symphodus doderleini	0.060
Tripterigion delaisi	0.087
Gobius bucchichi	0.095
Prey on transient predator ordination	
Tripterygion delaisi	0.030
Gobius auratus	0.081
G. vittatus	0.081
Beam trawl	
Predators on prey ordination	
Muraena helena	0.080
Mullus surmuletus	0.083
Prey on resident predator ordination	
Spicara smaris	0.040
Diplodus vulgaris	0.080
Prey on transient predator ordination	
Symphodus mediterraneus	0.041
Spicara maena	0.080
Deltentosteus quadrimaculatus	0.083
Diplodus annularis	0.083
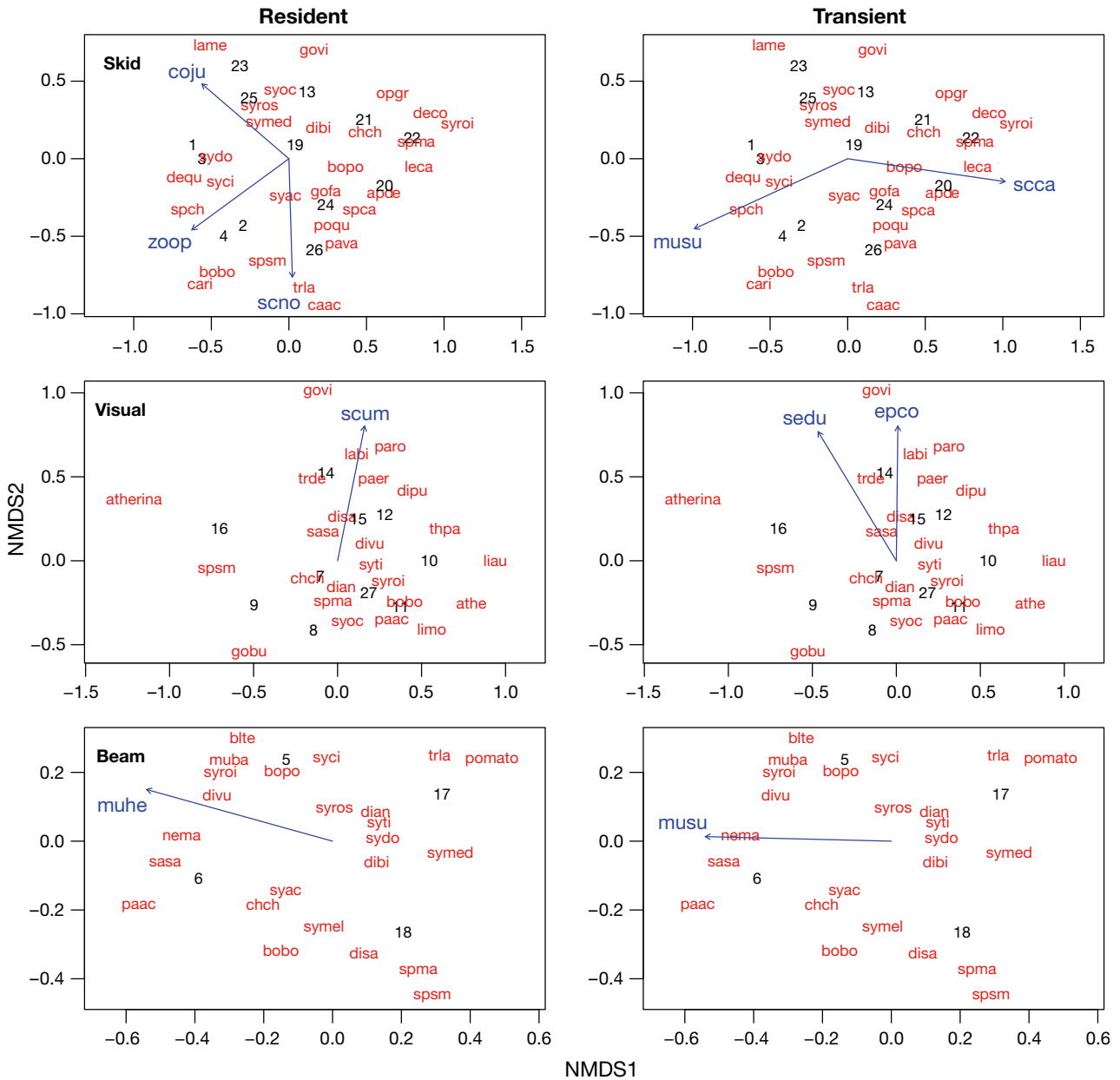
Fig. 3. Non-metric multidimensional scaling plots with vectors indicating direction and magnitude of correlation between ordinations and resident (left) and transient (right) predators within sampling methods skid trawl (top), visual census (middle), and beam trawl (bottom). The numbers within the plots represent individual transects within the datasets indexed in Table 1. For species abbreviations, see Table 2. For probability values of correlations (all <0.1) see Table 5

prey community (Fig. 4, p = 0.0067), with approximately 23 prey species in the absence of predators, and 14 prey species at a predator abundance of 35%.

DISCUSSION

The present study revealed that, over the last 30 years of published fieldwork quantifying fish communities observed within *Posidonia oceanica* mead-

ows, (1) the lack of uniformity in sampling methodology and low sample size prevents strong generalization about the magnitude of the value of *P. oceanica* as a fish habitat throughout the Mediterranean Sea, and (2) the existing data are not consistent with the proposition that seagrass represents a uniform refuge from predation, but indicate that the value of *P. oceanica* as a refuge varies greatly in response to the abundance of resident predators in seagrass. We discuss each of these points in turn.
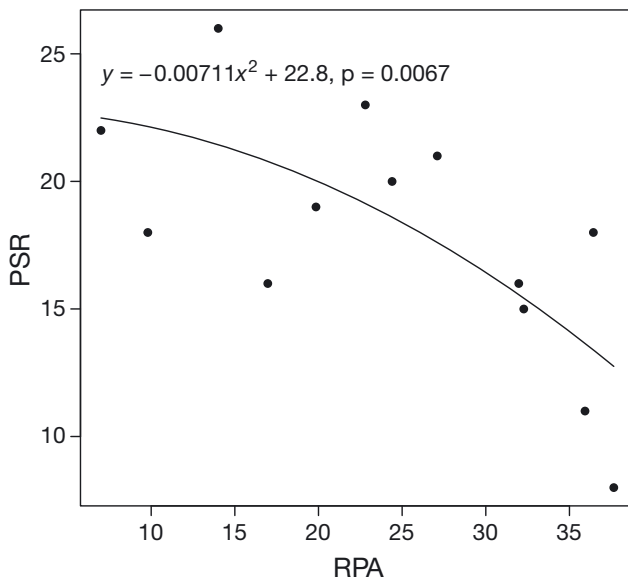
Fig. 4. Relationship between the total percent abundance of resident predators (RPA) and the total number of prey species (PSR) in skid trawl transects. Regression parameters are 0.00711 (SE 0.0021) and 22.8 (SE 1.8)

Effect of sampling method

Despite 30 years of study, we assert that knowledge of the potential value of *P. oceanica* meadows for fish communities (especially compared with alternative natural structured habitat such as reefs, other seagrass species, and macroalgal beds) is still fragmented, preliminary, and anecdotal. This is due primarily to the small number of peer-reviewed studies and because methodological differences (e.g. collection method, time of day, season, geographical location, sampling depth) accounted for approximately 70% of the variation among communities across studies. Different sampling methods lead to different absolute and relative population densities (Willis et al. 2000, Pasquaud et al. 2012), which are not comparable due to a lack of cross-calibration of different methods used in the Mediterranean Sea. For example, the 3 sampling methods in the present study produced 3 somewhat different ordinations of the prey community, each of which showed a somewhat different correlation with key predators. A single overall ordination based on all 3 methods cannot be constructed currently due to the absence of any function for cross-calibration.

As shown in Pasquaud et al. (2012), fishing (sampling) gears differ in capture efficiencies not only due to differences in gear size, tow speed, and mesh opening, but also due to differences in behavioral responses of fish species to the gear and sampling

area. For that reason, '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' (Willis et al. 2000, p. 249). Likewise, for total community studies, using a set of complementary methods may be the only strategy for equalizing catch probabilities among species with significant method-specific catchability (Starr et al. 2010, Oliveira et al. 2014), and accordingly, efforts to diversify mandated sampling methods for stock assessment have been made both within and among nations. State conservation agencies under the EU Water Framework Directive (EC 2000) have frequently adopted multi-method approaches to monitoring fish stocks (e.g. Inland Fisheries Ireland, which uses a multi-gear approach with 4 complementary sampling methods). Outside the EU, Lowry et al. (2012) recommended that plans for monitoring Australian reefs use a coupled approach based on 2 non-destructive core methods for fish census, baited remote underwater video (BRUV) and underwater visual census (UVC). BRUV uses stereo-photogrammetry to obtain high-precision estimates of the size of attracted nekton and notably larger predatory species that are repelled by divers before they can be seen. UVC, especially lure-assisted (Kruschel & Schultz 2012), facilitates census of sedentary species less likely to be attracted to a fixed bait station. This coupled strategy allows for both more equal total encounter rates of species across the community, and continuous cross-calibration of the methods and quantification of the biases of each method.

A complete understanding of the drivers of fish community organization and the value of *P. oceanica* as fish habitat in the Mediterranean Sea will require (1) general recognition of the values of complementary sampling and data comparability, and (2) international adoption of standard methods, towards the goal of (3) assembling a dataset on local fish communities associated with *P. oceanica* at least an order of magnitude larger than that currently existing. Only when these are accomplished will the current high level of confidence in the value of *P. oceanica* as a faunal refuge habitat, as expressed in legal instruments such as the European Union Habitats Directive, be justified by the available data.

Predator–prey community organization

In addition to significant variation in fish communities among sampling methods, we also found signifi-

cant variation within each sampling method attributable to the abundance and behavior of piscivorous predators and their prey. This relationship 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 actively seek prey within 3-dimensional habitat (Kruschel & Schultz 2011, Thiriet et al. 2013). In the present analysis of the meta-data, we found a significant effect of both resident and transient predators on the remaining fish community, including resident ambushers and transient cruise-chasers. Resident predators take advantage of the 3-dimensional structure offered by seagrass, which can improve foraging efficiency by obstructing prey's vision (Laurel & Brown 2006), providing more locations from which predators may attack (Janes 1985) and by enabling the predator to physically approach the prey unnoticed (Horinouchi et al. 2009). However, the relationships between predator and prey differed between methods, perhaps caused by different species-specific catchability.

(1) Skid trawl is efficient at catching seagrass residents, and the resident ambush predators *Scorpaena notata* and *Zosterisessor ophiocephalus* collected with skid trawls significantly affected the *P. oceanica* prey community. These 2 species could be considered the ultimate resident predators: adapted to hunting from within a 3-dimensional structure, they ambush prey with one explosive movement (Schultz & Kruschel 2010). Kruschel & Schultz (2011) showed that an observed absence of small fish from dense patches of the seagrasses *Zostera marina*, *Z. noltei*, and *Cymodocea nodosa* is correlated with a higher predation risk to prey from *Z. ophiocephalus*, a species with a gape size accommodating prey of a wide size range. The same is true for the gape size of *Scorpaena* species, and our results show a negative correlation between both predators and potential prey species such as small individuals of *Symphodus* spp. (*S. ocellatus*, *S. roisali*), *Chromis chromis*, or small gobies (*Deltentosteus collonianus*, *Gobius vittatus*). In addition, *Coris julis* was negatively correlated with most of the prey species, a result that 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 *Chromis chromis* were most important in structuring the predator communities.

(2) Visual census (Harmelin-Vivien & Francour 1992) may only be successful 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 visual census 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 the most important candidates for structuring the prey community, and are negatively correlated with most prey species. This result was not expected, because according to the seagrass superiority hypothesis (Heck & Orth 1980), prey fish are predicted to prefer seagrass in the presence of transient, cruising, visual predators because only in response to predators not physically inside the seagrass canopy do the leaves of *P. oceanica* constitute an effective visual and mechanical barrier to the detection and pursuit of prey. This result might be explained by the possibility that (1) these specific predators are not easily deterred by the physical structure of *P. oceanica*, (2) those studies using visual census happened to occur over sparse *P. oceanica* beds, or (3) visual census was not able to detect epibenthic species that were concealed within seagrass. Among the prey, *Chromis chromis* again was an important indicator of the resident predator community.

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

Gaps and research needs

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 our 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). Our review of the literature 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: (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 and after control-impact studies of the impact of the loss of *P. oceanica* habitat on the local fish community. Our results 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 (see also 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 (Staglicic et al. 2011). These trends suggest that the value of seagrass as a prey refuge has decreased over the last several decades. Our 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 *Posidonia* meadows and other structured habitats in the Mediterranean Sea.

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