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Posidonia oceanica wrack beds as a fish habitat in the surf zone

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ABSTRACT

Drifting macrophyte detritus cast along the shore, often called wrack, can wash around, accumulate in the surf zone and constitute a habitat where fishes forage and/or hide. We compared fish assemblages associated with *Posidonia oceanica* wrack beds with those associated with bare sand in the surf zone of Sardinia Island (Italy), NW Mediterranean Sea. In July–August 2020, *in situ* non-destructive visual censuses were performed to count fishes and record their behaviour at 3 locations, each including 3 shores characterized by both *P. oceanica* wrack beds and bare sand. The assemblages were mainly composed of small and juvenile/sub-adult individuals and significantly differed between the two habitats. Nine taxa were shared by both habitat types, seven were exclusively associated with *P. oceanica* wrack and only one species was found exclusively on sand. Higher species richness and fish density (without considering the contribution of gregarious fish in the water column) were observed on *P. oceanica* wrack than on sand. Assemblages were numerically dominated by *Diplodus sargus*, *D. vulgaris* and *Mullus surmuletus*. These species and other fishes, mostly represented by invertivorous (e.g., labrids) and omnivorous species, were often observed feeding on *P. oceanica* wrack and using the resuspended dark-brown vegetal fragments to hide. These findings clearly suggest that *P. oceanica* wrack beds attract fishes from surrounding habitats, some of them of commercial importance, providing food and habitat for juvenile and sub-adult stages.

1. Introduction

Seagrass meadows, like other marine coastal vegetated ecosystems, are highly productive, play a pivotal role in sustaining biodiversity and deliver essential ecosystem services (Duarte et al., 2005; Orth et al., 2006; Duarte and Krause-Jensen, 2017; Unsworth et al., 2018). Their primary production often exceeds the herbivore biomass consumption. The surplus contributes to local carbon burial, subsidises the local detrital food web or drifts towards other ecosystems, where it supplies local communities with an allochthonous food resource and provides habitats for a variety of vertebrate and invertebrate species (Mateo and Romero, 1997; Polis et al., 1997; Moore et al., 2004; Duarte et al., 2005; Heck et al., 2008; Haegen et al., 2012; Hyndes et al., 2014; Zimmer, 2019). From a quantitative viewpoint, it has been estimated that up to 80% of the seagrass primary production can be exported annually to other ecosystems, such as submarine canyons, sublittoral rocky reefs, submerged marine caves and sandy shores (Colombini and Chelazzi, 2003; Dimech et al., 2006; Heck et al., 2008; Cresson et al., 2012; Rastorgueff et al., 2015).

Along sandy shores, deposits of drifting seagrass (and seaweed) detritus, often called "wrack" (Rossi and Underwood, 2002; Dugan et al., 2003), are common in many areas around the world. They may accumulate in the supralittoral zone, form berm-like structures (Short, 1999) and play a role in the geomorphological beach dynamics, especially in low energy beaches (Vacchi et al., 2017). Wrack can also enrich with nutrients and organic matter the otherwise organically-poor substrates and allow the subsistence of benthic invertebrates, seabirds and dune vegetation (Dugan et al., 2003; Colombini et al., 2009). On sheltered and embayed shores, wrack can exchange between the supralittoral beach and the surf zone, where this organic material can float and deposit on the seafloor and form patches of an organically-enriched brown bed interspersed within an unvegetated bare sandy matrix (Simeone et al., 2013; Vacchi et al., 2017; McLachlan and Defeo, 2018). Drifting wrack can be used by small gregarious fishes as a shelter (Hasegawa et al.,

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2017) and by many juvenile fishes to hide from predators and/or as a food source, often because preys are associated with this drifting wrack (Lenanton et al., 1982; Robertson and Lenanton, 1984; Crawley et al., 2006; Baring et al., 2018). Similarly, wrack beds could act as shelters in the surf zone i) providing a more complex substrate than bare sand and allowing small fishes to hide, ii) constituting a chromatic background where fishes may camouflage their silhouette, and (iii) increasing water turbidity due to water motion so that small fishes become hardly detectable by visual predators such as fishes or marine birds (Robertson and Lenanton, 1984; Lenanton and Caputi, 1989). Wrack beds can also provide feeding resources i) directly, for fishes eating detrital particles, and ii) indirectly, because the detritus hosts a variety of invertebrate prey (Hyndes and Lavery, 2005; Andrades et al., 2014; Baring et al., 2014, 2018). By feeding among wrack beds and moving across space, fish could contribute to exchanges of seagrass carbon across habitats and ecosystems (Beck et al., 2001; Heck et al., 2008; Hyndes et al., 2014; Bussotti et al., 2018).

On Mediterranean sandy shores, seagrass wrack and its accumulations as berm-like structures are mainly composed of leaves, rhizomes and roots of the endemic *Posidonia oceanica* (L) Delile (Mateo et al., 2003; Costa et al., 2019) and the term *banquettes* is used to indicate their accumulations (Boudouresque and Meinesz, 1982; Boudouresque et al., 2016).

The above-mentioned accumulations may account for 10–55% of the total primary production of *P. oceanica* and are recognized to be important for coastal carbon cycling, for habitat and food provision to many marine and terrestrial invertebrates (Pergent et al., 1994, 1997; Mateo et al., 2003, 2006; Gallmetzer et al., 2005; Boudouresque et al., 2012; Costa et al., 2014, 2019) and for limiting beach erosion (Vacchi et al., 2017). *P. oceanica* meadows are considered as a priority habitat for conservation in the European Union Habitat Directive (Dir 92/43/EEC), on the basis of a large body of scientific evidence showing their fundamental contribution to supporting biodiversity, life cycles of many fish and invertebrate species and a variety of ecosystem services (Duarte, 2000; Campagne et al., 2015). However, specific protection policies for seagrass detritus accumulations are seldom adopted. *Posidonia oceanica* wrack is frequently removed from the beaches to meet the requirements of the touristic demand (Boudouresque et al., 2016; Rotini et al., 2020), with significant ecological consequences for the supralittoral beach (Defeo et al., 2009) and, on sheltered shores, for the surf zone, by limiting the exchange of organic material.

As for other seagrass wrack accumulations in the surf zone worldwide, fish species might use them as a habitat providing food and refuge (Personnic et al., 2014; Boudouresque et al., 2016), but scientific evidence regarding this potential role of *P. oceanica* wrack beds is limited and, to the best of our knowledge, no specific studies have been conducted to quantify its role with regard to fish assemblages in the surf zone.

The purpose of the present study, therefore, is to investigate if and how fish assemblages change between *P. oceanica* wrack beds and bare substrates in the surf zone in the Sardinia Island (Western Mediterranean, Italy) sandy shores. Here *P. oceanica* meadows colonise several coastal substrates (Vacchi et al., 2017) and the removal of wrack is a common practice (Chessa et al., 2000; De Falco et al., 2008). As for other embayed beaches elsewhere, the wrack derives from adjacent seagrass meadows and its deposition on the beach starts as a strandline at the landward edge of the wave action, proceeds seaward up to the shoreline, is eroded away by the waves, float in the inner surf zone and is redeposited forming patches at the end of an erosion cycle, indicating an important exchange between submerged and emerged beaches (Simeone et al., 2013). In all the Sardinia Island, *P. oceanica* wrack occurs in the higher accumulation in lower-energy beaches, that could be explained by the major extension of *P. oceanica* meadows in sheltered coastal sites (De Falco et al., 2008). In the present study, we expect that: (1) fish species composition, assemblage structure would be different and there would be more species, and more individuals on *P. oceanica* wrack patches than on bare sands; (2) fish would feed and hide more often in patches of *P. oceanica* wrack than on bare sands.

2. Material and methods

2.1. Study area and data collection

During July–August 2020 we sampled three locations 100 s km apart from each other, along the coasts of Sardinia Island (Western Mediterranean Sea, Italy; Fig. 1). The locations were i) Stintino (40°90′ N, 08°23′ E), ii) Olbia (40°55′ N, 09°29′ E) and *iii)* Villasimius (39°08′ N, 9°31′ E), situated close to or partially within the borders of the Marine Protected Areas of 'Isola dell'Asinara', 'Tavolara-Punta Coda Cavallo' and 'Capo Carbonara', respectively. At each location, we randomly selected the surf zone of 3 different sandy shores (hereafter called 'sites'), 100s–1000 s m apart. All sites were sheltered, embayed shores,

Fig. 1. Sampling locations hosting the nine study sites (beaches). P = Pazzona, S = Le Saline, Sp = Spalmatore (Stintino); CS = Cala Sabina, CB = Cala Brandinchi, CPip = Cala Pipara (Olbia); CP = Cala Pira, C= Campulongu, PG = Porto Giunco (Villasimius).

where *Posidonia oceanica* wrack forms quite thick *banquettes* along the shore and wide patches in the submerged surf zone (Fig. 2 a, b: see photo of Pazzona beach as an example). At each site, we sampled fish assemblages in two habitat types: i) randomly chosen *P. oceanica* wrack patches (hereinafter referred as PW) extending homogeneously enough (>50 m long) to run multiple fish assessments (i.e., visual census transects; see details later); ii) bare sandy substrates (hereinafter referred as SAND).

Fish were visually sampled by snorkeling, using 10 × 2 m UVC (underwater visual census) transects, following Harmelin-Vivien et al. (1985) during late morning. Three random transects were performed for each PW and SAND habitat at each site. Density and size of fish encountered were recorded along each transect. For fish schools larger than 10 individuals, abundance was estimated by using abundance classes (i.e., 11–30, 31–50, 51–100, 100–200 individuals) and by taking into account the mid-point for estimating the average density per transect. In our sampling, the only taxon observed in large schools and, therefore, whose density was estimated was *Atherina* sp. Observers were trained with fish silhouettes of known total length and had more than 20 years of experience in using UVC methods.

Fish were sampled within the depth range of 0.5–2 m and transects were selected so as to accommodate 3 transects while avoiding habitat type edges.

Multiple aspects of fish behavior were observed during visual census: for each censused fish, we recorded both swimming/feeding and hiding/camouflage behaviors. For each fish censused across each transect we considered a fish as "feeding" when, depending on the species, it was observed "pecking" in the water column or on the bottom, actively grooving into the sediments or searching food items through the seagrass wrack. About hiding/camouflage behaviors and predator/prey interactions, we differentiated between predatory ambushing behavior and prey hiding.

2.2. Data analyses

We assessed the distribution patterns of fish assemblages between PW and SAND by means of generalized linear models for the multivariate density data with the function 'manyglm' from the mvabund R package (Wang et al., 2012). Data were analysed without the contribution of the schooling species *Atherina* sp., whose density was estimated using abundance categories. Using 'manyglm' we could model the mean–variance relationship in our data by selecting a negative binomial distribution family as link function (Warton et al., 2012; Roberts, 2017; Warton and Hui, 2017). As predictor variables, we considered "Habitat" (2 levels: PW and SAND) and "Location" (3 levels: Stintino, Olbia, Villasimius) as crossed factors and "Site" (3 levels) as nested in "Location" with 3 replicated transects for each combination of factors. Dispersion of points from the centroid was also tested for the triangular matrix generated using Bray-Curtis index on the matrix of density data using 'betadisper' function from vegan R package (Anderson, 2001; Oksanen et al., 2014). Non-metric multidimensional scaling (nMDS, Bray–Curtis distances) was used to visualize the results of the multivariate generalized linear models (r package vegan).

To model the number of species and fish density as a function of "Habitat, Location and Site", we used generalized linear mixed models (GLMM) with the 'glmmTMB' function in the R package glmmTMB (Brooks et al., 2017). We also analysed the abundance of *Atherina* with a multinomial baseline-category logit model, that allows to model not only dichotomous (binary), but also polychotomous responses, using the function mblogit from the R package mclogit 0.8.7.3 (Elff, 2021; see also Agresti, 2002). "Habitat" and "Location" were crossed predictors in the fixed part of the model and "Site" in the random part (fish density or number of species ~ Habitat x Location + (1|Site)). The distribution of the fish species that displayed a difference between habitats, based on the multivariate results from the mvabund data, was further explored considering a GLMM that included their size as a covariate (density ~ Habitat x Location + (1|Site/Location) + fish size). The fish feeding behaviour was also analysed using a binomial GLMM model with logit link, where data indicated the feeding status of the fish (1 = feeding, 0 = not feeding). We included "transect" in the random part and used log (number of fish) as an offset in order to take into account for the different replicates within transect (status fish ~ offset(log(N of individuals) + Habitat x Location + (1|Site|Location)+(1|transect/Site)). The data on counts and species number were fitted with a Gaussian, Poisson or a negative binomial distribution. Normality and homogeneity of residual variances for full GLMM models with the different distributions were evaluated graphically and using the R package DHARMa in order to define the best fitting distribution (Hartig, 2020). The species number was best fitted using a Gaussian distribution, whereas fish density best fitted a negative binomial with log link function.

We then used a model comparison approach to assess the relative strength of different competing models that included different combinations of the explanatory variables. Specifically, we evaluated the fit of the full model (M1) against simplified models that excluded the continuous variable size when present, removed the interaction or one of the main factors. To test for the overall significance, we also compared all models to a null model with no predictors. We compared models using Akaike's Information Criterion for both the cathegorical and the abundance data, corrected for sample size bias (AICc). For the abundance data, we could use the R package bbmle (Bolker et al., 2021) and estimate delta-AICc (a measure of the strength of evidence of each model relative to the best model, which has the lowest AICc value: $\Delta i = AICc,i - AICc,min$), and AIC weights ($w_i$, the probability that model i is the best fitting model). The resulting best fitted model was further explored by estimating significant levels of differences using pairwise *post-hoc* comparisons with least-squared mean estimates and *t*-test analyses corrected for Tukey's multiple comparisons (eemeans function in the package eemeans).

3. Results

3.1. General description of fish assemblages

We recorded a total of 17 fish taxa belonging to 8 families (Table S1).

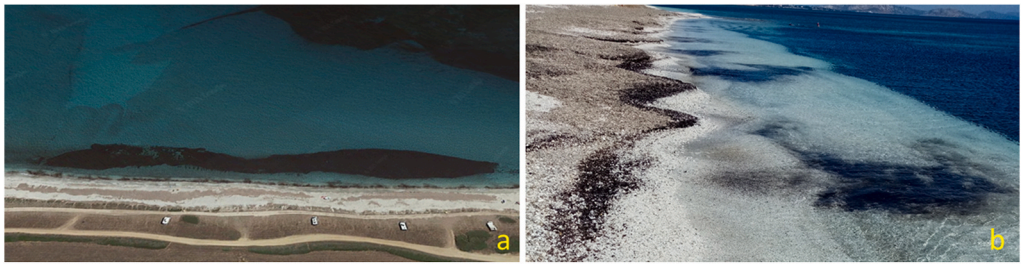

Fig. 2. *Banquettes* along the beach and PW patches in the surf zone (a, b: Pazzona beach, Stintino). a: satellite imagery freely available from Google earth; b: photo credit: Simona Bussotti.

Fish assemblages were numerically dominated by *Atherina* sp., followed by the sparids *Diplodus sargus* and *D. vulgaris*, and then the red mullet *Mullus surmuletus* (Table S1). Nine fish taxa were common to both habitat types (PW and SAND, *Posidonia* wrack and bare sands, respectively), 7 were exclusively associated to PW (i.e., the labrids *Coris julis*, *Symphodus cinereus*, *S. ocellatus* and *S. tinca*; the serranid *Serranus scriba*; the sparid *Diplodus annularis* and *Sarpa salpa*), while the flatfish *Bothus podas* was only found on SAND.

3.2. Differences between habitats

The species composition of the fish assemblages was clearly different between the two habitats (PW vs SAND), regardless of the interactions with location or site (Table 1). Assemblages also differed spatially, among both locations and sites.

The nMDS plot showed a separation between fish assemblages associated with PW and SAND, with SAND assemblages more dispersed than PW ones, especially for the locations of Villasimius and Olbia (Fig. 3; dispersion analyses on the interaction location x habitat: pseudo-$F = 7.46$, $p < 0.001$).

There were more fish taxa and higher fish density associated with PW than SAND if *Atherina* sp. was not considered (Fig. 4 a-c). Fish density and species number best fitted a model with only "habitat" as an explanatory variable (Table 2). Except the models including "habitat", the other models displayed extremely poor fits (all $w_i < 2\%$). The abundance of *Atherina* sp. best fitted the null model (Table 2).

The multivariate analysis of deviance identified 4 species showing significant differences between PW and SAND. Three of them, namely *Diplodus annularis*, *D. vulgaris* and *Mullus surmuletus*, showed significant differences only between habitats (p values < 0.005), whereas *D. sargus* showed differences both between habitats ($p < 0.001$) and among locations ($p < 0.05$). *Diplodus sargus*, *D. vulgaris* and *M. surmuletus* were more abundant on PW than SAND (Fig. 4, d-f), while *D. annularis* only occurred in PW and no further analyses were run on this species.

3.3. Size distribution of fish species identified by multivariate analysis

In both PW and SAND, *D. sargus* was predominantly represented by very small and medium-sized individuals (from 3 to 20 cm total length, TL; Fig. 5, Fig. S1), whereas we did not detect very small individuals of the congeneric *D. vulgaris*. *D. vulgaris* individuals measuring <10 cm TL were only present on PW, whereas those between 10 and 16 cm TL were censused in both habitats. Individuals of *M. surmuletus* ranged between 6 and 12 cm TL.

The size distribution of these 3 species best fitted models that always included the factor "habitat". The AICc comparisons showed that the models with only "habitat" were the best fit for both *D. vulgaris* and *M. surmuletus*, whereas the model including both "habitat" and "fish size" as explanatory variables was the best fit for *D. sargus*. The other models had extremely poor fits (all $w_i < 0.2$ in Table 3). The estimated differences between PW and SAND were always highly significant ($p < 0.001$, Pairwise Tukey's test comparisons). The model for *D. sargus* also showed a significant effect of "fish size" on the density distribution ($p < 0.001$).

Table 1
Multivariate Analysis of Deviance (mvabund R package) for fish assemblages, considering the full model: ~ Location + Site (Location) + Habitat + Location x Habitat + Site (Location) x Habitat with negative binomial. P-value is calculated using 999 iterations via PIT-trap resampling.

	Res.Df	Df.diff	Dev	Pr(>Dev)
Location (L)	51	2	63.14	0.009
Habitat (H)	50	1	130.86	0.001
Site (L)	41	9	137.35	0.002
L x H	39	2	21.33	0.290
Site (L) x H	36	8	56.30	0.158

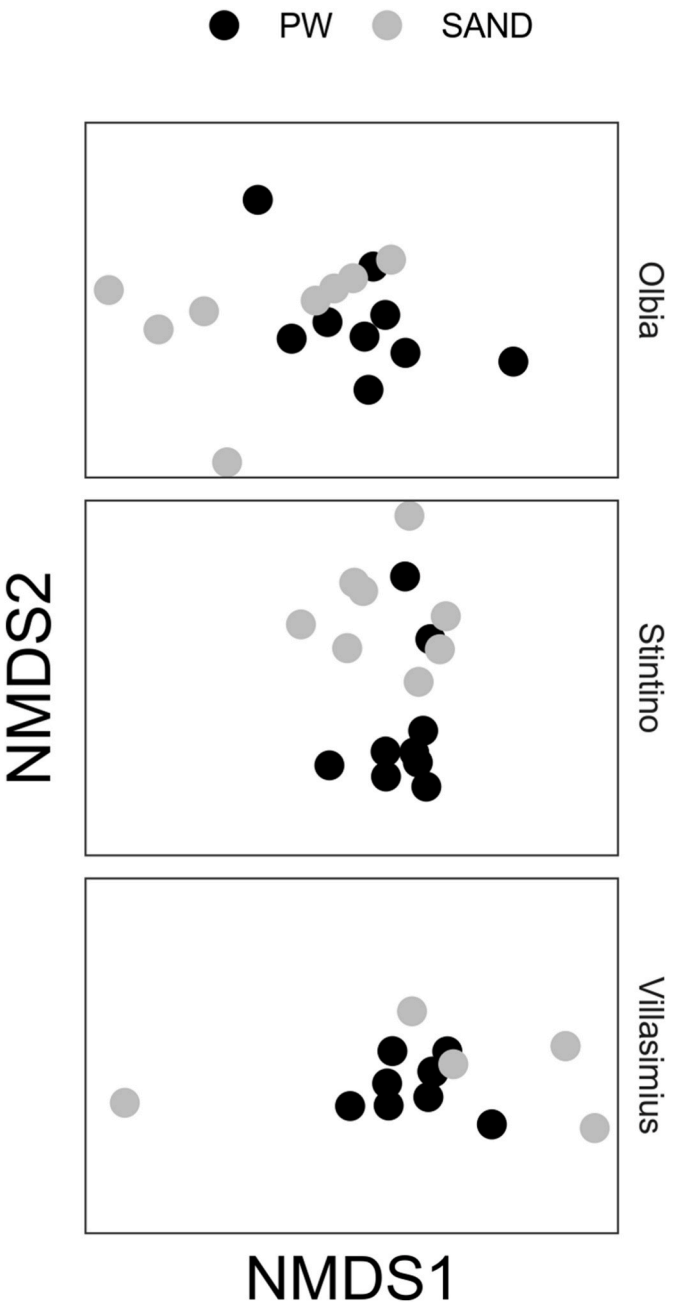

Fig. 3. Non-metric multidimensional scalings (nMDS) of fish assemblage structure for each location separately, assessed on density data (Bray–Curtis distances) and showing differences between the two habitats investigated. Each point represents a transect ($n = 3$) from each of the 3 sites. Missing points indicate that no fishes were observed in the transect. Locations are plotted separately to ease the legibility of the ordination plot.

Because *D. sargus* size was important for explaining density distribution, we further explored the data with a model that included the interaction between "fish size" and "habitat". The AICc comparisons did not show any improvement of model fit by including this interaction term ($w = 0.99$ and 0.005 for no interaction and interaction, Table S5).

3.4. Fish behavior

Multiple aspects of fish behavior were observed during visual assessments. All the most frequent and abundant species (namely *Diplodus sargus*, *D. vulgaris*, *M. surmuletus*, *Sarpa salpa*, *Lithognatus mormyrus*, *Oblada melanura* and *Synphodus tinca*) were observed feeding more often

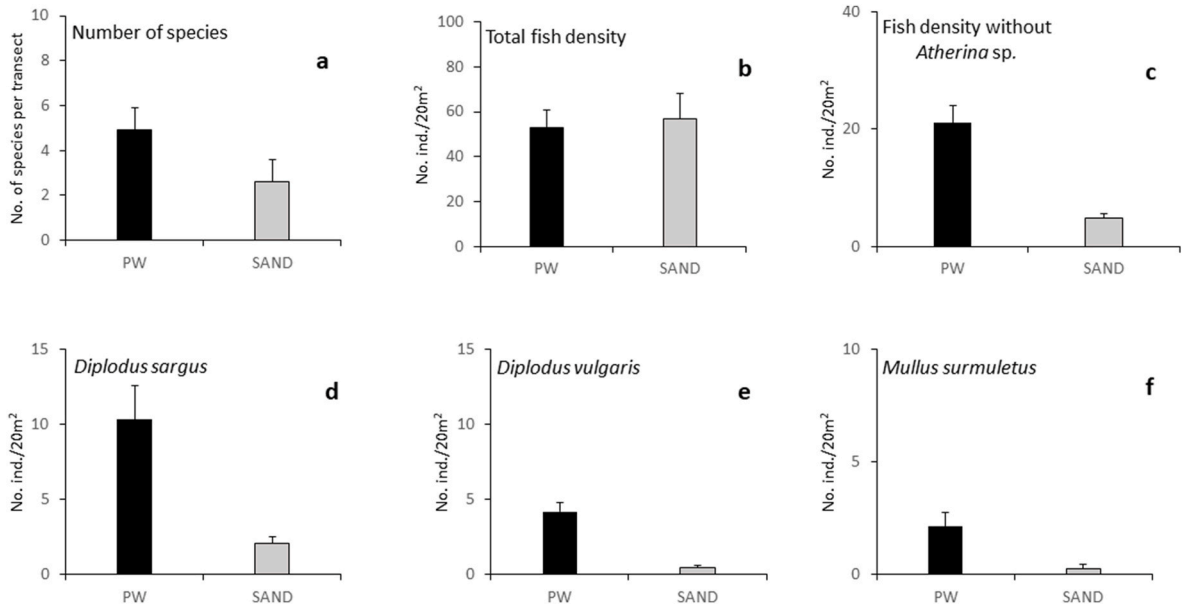

Fig. 4. Mean values of (a) species richness (average species number per transect; mean + SE), density (mean number of individuals 20/m^2 + SE) of total fish with and without the numerical contribution of *Atherina* sp. (b and c) and of important species (d–f) in each habitat type investigated. PW = Posidonia Wrack; SAND: bare sand.

Table 2
Model selection for total density of individuals, and for the number of species and for abundance of *Atherina* sp). Models are arranged according to their decreasing fit to data. Density was fit to a negative binomial distribution. Number of species was fit to the normal distribution. See detailed results in Supplementary Materials (Tab. S3, S4).

	Explanatory variables included in the model	logLik	AICc	dLogLik	dAICc	df	Weight
Density	Habitat	−179.2	367.0	16.1	0.0	3	0.929
	Habitat + Location+1|Site	−173.8	373.5	21.5	6.5	6	0.035
	Location	−191.0	395.0	4.3	28.0	4	<0.001
	Null model	−195.3	395.7	0.0	28.7	2	<0.001
	Full Model	−172.2	396.5	23.0	29.5	8	<0.001
	1|Site	−172.2	396.5	23.0	29.5	8	<0.001
Species number	Habitat	−99.9	208.4	13.3	0.0	3	0.984
	Habitat + Location	−96.0	218.0	17.1	9.6	6	0.008
	Null	−113.3	231.8	0.0	23.0	2	<0.001
	Location	−112.1	237.2	1.0	28.9	4	<0.001
	Full Model	−92.9	237.8	20.2	29.4	8	<0.001
	Habitat x Location	−92.9	237.8	20.2	29.4	8	<0.001
***Atherina* sp.**	Null		193.2			9	
	Location		198.4			27	

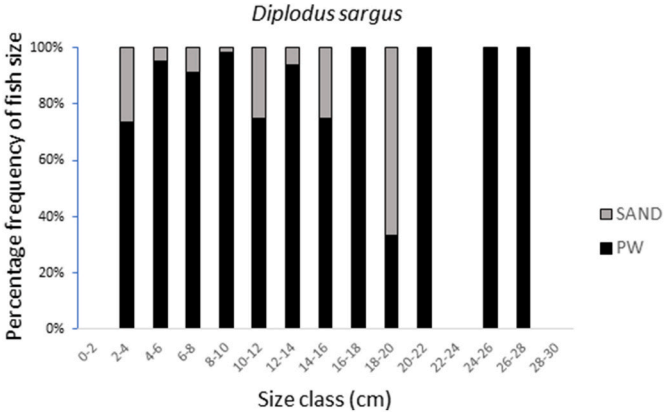

Fig. 5. Size–structure of *Diplodus sargus* in the two habitats investigated expressed as percentage and obtained by pooling all transects from each and location. PW = Posidonia Wrack; SAND: bare sand.

above the wrack than on bare sand (Fig. 6). Specifically, *D. sargus* was mostly observed to peck on the substrate surface and seldom in the water column (just the very small individuals around 4 cm TL). Sometimes, small *D. sargus* and medium-sized *Oblada melanura* were observed feeding upon the particles/small prey resuspended by the feeding activity of other fishes, such as *M. surmuletus* and *S. tinca*. *M. surmuletus* was seen to spasmodically search for prey with barbels and mouth digging into the substrate, while *S. tinca* was observed to "chew and spit" to select prey from sediments and algal debris.

A formal statistical analysis on feeding behavior was performed only for *D. sargus*, because of the limited number of observations available for the other species. The frequency of feeding acts of *D. sargus* was best fitted using a reduced model with "habitat" in the fixed part and "transect" for the random part. The first 3 best-selected models included the variables "habitat" and "transect" (Table 4). The analyses on the contrasts between PW and SAND showed significant differences, with more frequent feeding acts in PW than SAND (t-test = 3.14 p = 0.0013) and no differences within "transects" (Variance: 0.4238; p = 0.651). There was also no correlation between the *D. sargus* density per transect and the frequency of feeding acts.

Table 3
AICc model comparisons for the generalized linear mixed models on the density and size of *D. sargus, D. vulgaris* and *M. surmuletus*. We modeled data using a zero inflated negative binomial distribution for *D. sargus,* a zero-inflated Poisson distribution for *D. vulgaris* and *M. surmuletus*. See detailed results in Supplementary Materials (Tab. S2, S5, S6, S7).

	Explanatory variables in the model	logLik	AICc	dLogLik	dAICc	df	weight
D. sargus	Habitat + Fish size	−320.0	661.9	25.0	0.0	5	0.829
	Habitat+1|Site + Fish size	−316.5	666.0	28.5	4.1	6	0.108
	Fish size	−326.7	668.1	18.3	6.2	4	0.038
	1|Site + Fish size	−323.5	669.0	21.5	7.0	5	0.024
	Location+1|Site + Fish size	−321.8	676.5	23.2	14.6	6	<0.001
D. vulgaris	Habitat	−202.2	413.8	8.9	0.0	3	0.724
	Habitat+1|Site	−200.9	416.5	10.2	2.7	4	0.190
	Habitat + Fish size	−201.8	418.2	9.3	4.4	4	0.080
	Habitat+1|Site + Fish size	−200.8	423.7	10.3	9.8	5	0.005
	Null	−211.1	427.7	0.0	13.9	2	<0.001
M. surmuletus	Habitat	−114.5	238.4	7.1	0.0	3	0.811
	Habitat+ 1|Site	−113.8	242.4	7.8	3.9	4	0.114
	Habitat + Fish size	−114.5	243.6	7.2	5.1	4	0.063
	Null	−121.6	248.8	0.0	10.3	2	0.005
	Habitat+1|Site + Fish size	−113.7	249.3	8.0	10.9	5	0.004
	1|Site	−120.4	250.3	1.2	11.8	3	0.002
	Fish size	−121.5	252.5	0.1	14.0	3	<0.001

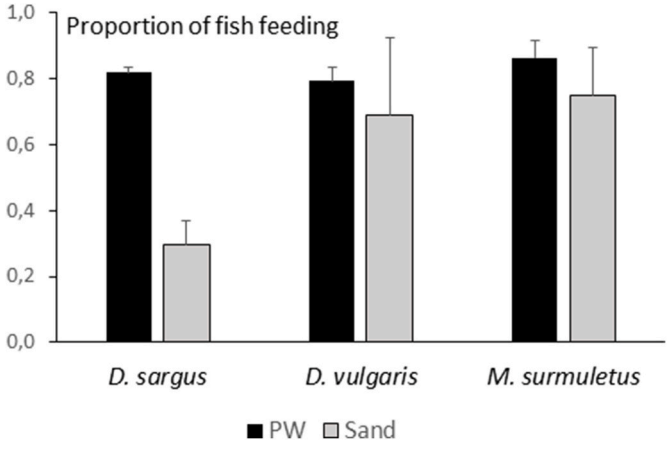

Fig. 6. Frequency of feeding acts of important species in the two habitats investigated. PW = Posidonia Wrack; SAND: bare sand.

Table 4
AICc model comparisons for the generalized linear mixed models on the feeding behavior of *D. sargus*. Data were fitter to the binomial distribution. See detailed results in Supplementary Materials (Tab. S8).

Fitted Model	logLik	AICc	dLogLik	dAICc	df	Weight
Habitat+1|transect	−189.2	388.5	10.2	0.0	3	0.799
Habitat	−193.5	392.8	5.8	4.3	2	0.091
Habitat+1|Site+1|transect	−188.9	393.8	10.5	5.3	4	0.057
Location+1|transect	−189.1	394.1	10.3	5.7	4	0.047
1|Site+1|transect	−194.6	399.2	4.8	10.7	3	0.004
Null	−199.4	401.3	0.0	12.8	1	0.001
Location+1|Site+1|transect	−189.1	403.1	10.3	14.7	5	<0.001
Location + Habitat+1|transect	−184.1	408.1	15.3	19.7	6	<0.001
Full	−183.8	527.6	15.6	139.2	8	<0.001

In terms of predatory behaviour, we observed that adults of the piscivorous serranid *Serranus scriba* adopted a camouflage colour, i.e., a dark-brown livery, just above (the dark-brown) PW while ambushing juvenile specimens of *Atherina* sp. (swimming in the water column) and *D. sargus* (both swimming in the water column and close to the substrate).

Juveniles of *D. sargus*, depending on size, have a semi-transparent body with visible organs and head. Based on our observations, they seemed to hide their silhouette by taking advantage of the dark-brown fragments of *P. oceanica* leaves resuspended above PW by water movements (sometimes caused by tourists walking in shallow waters, within 1.5 m depth).

4. Discussion

4.1. Distribution of fish assemblages across the Posidonia wrack in the surf zone

In this study we provide the first evidence that Mediterranean fish assemblages in the surf zone of sandy shores (in terms of species richness, density and behaviour) associated with the habitat formed by *P. oceanica* wrack differ from those in adjacent bare sand, in agreement to studies done elsewhere (e.g. Robertson and Lenanton, 1984; Lenanton and Caputi, 1989; Crawley et al., 2006; Barings et al., 2014). It is well known that different nearshore habitat types, such as seagrasses, rocky reefs and sand, tend to host different fish assemblages (e.g., Francour, 1994; Guidetti, 2000; Anderson and Millar, 2004; Chittaro, 2004; Tunesi et al., 2006; Bussotti and Guidetti, 2009; La Mesa et al., 2011; Giakoumi and Kokkoris, 2013). However, fish associated with macrophyte wrack beds have been examined to a less extent (Lenanton et al., 1982; Robertson and Lenanton, 1984; Lenanton and Caputi, 1989; Ayvazian and Hyndes, 1995; Crawley et al., 2006; Baring et al., 2018) and no specific study has focused on the Mediterranean Sea. This is surprising because *P. oceanica* wrack beds are recognized as an important habitat, changing in time, shape and size in relation to local hydrodynamic conditions (Boudouresque et al., 2016; Vacchi et al., 2017).

Some authors reported that several coastal fishes may spend part of their life in the surf zone, likely due to the availability of substrates/habitats to forage or hide in (Laymann, 2000; Esposito et al., 2015) and that the surf zone is dominated by a few taxa (e. g. Modde and Ross, 1981, Vanderklift and Jacoby, 2003; Esposito et al., 2015; Olds et al., 2017), which is in agreement with our findings. We only found 1 species exclusively on sand, i.e., the flatfish *Bothus podas* which is expected since this species is typically associated with sandy substrata where it usually camouflages or burrows (Darnaude et al., 2001; Tunesi et al., 2006). More interestingly, 7 species were exclusively censused on *Posidonia* wrack: the labrids *Coris julis*, *Sympphodus cinereus*, *S. ocellatus* and *S. tinca*, the sparids *Diplodus annularis* and *Sarpa salpa,* and the serranid *Serranus scriba.* Most of the remaining species, which included the numerically dominant *D. sargus* and *D. vulgaris,* and *M. surmuletus*, are well known to mostly inhabit rocky reefs and *P. oceanica* meadows (Francour, 1997; Guidetti, 2000; Ruitton et al., 2000; Garcia-Charton

and Perez-Ruzafa, 2001). The affinity of most species to rocky reefs and *P. oceanica* meadows also explains why there were differences among sites and locations in species composition, despite that the pattern of difference between habitats was consistent through the 9 beach sites and the 3 locations 100 kms apart. Some sampling locations and sites, in fact, were relatively close to rocks and seagrass beds than others. The fishes found on the PW habitat were therefore likely to move from adjacent rocky reefs and *P. oceanica* meadows. Without the presence of PW, these fishes would hardly cross bare sandy habitats that offer no shelter, as observed for other species in other ecoregions (see Robertson and Lenanton, 1984; Ayvazian and Hyndes, 1995; Crawley et al., 2006). suggesting that PW is an important habitat component (see Boudouresque et al., 2016) together with living seagrass beds.

Despite clear differences in density, fish size distribution did not change between habitat types. In both PW and SAND, we found that small- and medium-sized individuals widely dominated the assemblages. High densities of very small individuals were found for the sparid *D. sargus,* which is consistent with its settlement-recruitment period (Vigliola et al., 1998; Bussotti and Guidetti, 2011). Likewise, Crawley et al. (2006), found that, in Southern Australia, winter accumulations of detached macrophytes in the surf zone provide a habitat for juvenile *C. macrocephalus*. In the surf zone, small- and medium-sized fish could minimize predator encounters, because this zone offers restricted access, and little maneuverability and foraging efficiency to large piscivorous fishes (Laymann, 2000; Inoue et al., 2008; Olds et al., 2017). Large predatory fishes could just perform rapid incursions or run their attacks successfully only when the sea is rough (Tobin et al., 2014; Esposito et al., 2015). As observed by Baring et al. (2014) along the southern Australian coast, predatory fishes tend also to move quickly within and between wrack accumulations in the surf zone.

4.2. Fish behaviour across habitats

We found that the most abundant species, the omnivore sparid *D. sargus,* showed more frequent feeding acts on PW than on SAND and that this behaviour was in common with other invertivorous fishes like *M. surmuletus* and several labrids (which have a diet mainly composed of small crustaceans, polychaetes, bivalves or gastropods), other omnivorous sparids (*Diplodus* spp., *Lithognatus mormyrus* and *Oblada melanura*) and the piscivorous *Serranus scriba* (Quignard and Pras, 1986; Sala and Zabala, 1996; Bautista-Vega et al., 2008; Kallianiotis et al., 2005; Thibaut et al., 2017). Our observations substantially agree with the results showed by Baring et al. (2018) in a study conducted in South Australia.

D. sargus along with *O. melanura* were observed swallowing the particles resuspended by the feeding activity of *M. surmuletus and S. tinca. M. surmuletus* is well known to form foraging associations with different species due to the very active foraging behavior involving a vigorous stirring up of sediments by their barbells and mouth (Randall, 1967; Golani and Galil, 1991). *S. tinca* is known to "chew and spit" sand and vegetal debris to then select prey or feeding particles, of which other labrids and the two-banded seabream *D. vulgaris* often take advantage (Zander and Nieder, 1997; Molino, 2008).

These observations suggest that PW beds represent foraging areas. The presence of PW could provide invertebrate preys and, in turn, increase availability of small fishes for piscivorous predators. Studies conducted in southwestern Australia reported particularly high densities of crustacean amphipods in wrack accumulations (Robertson and Lucas, 1983) and in the stomachs of fish feeding on them (Robertson and Lenanton, 1984; Crawley et al., 2006; Baring et al., 2018). Vanderklift and Jacoby (2003), moreover, reported a significant relationship between species number, abundance or biomass of invertivorous fishes and the amount of drifting plant material in sandy substrates adjacent to seagrass beds. Even if similar studies are lacking for the Mediterranean Sea, some papers report significant abundances of prey for invertivorous fishes (e.g., crustaceans, mollusks, meiofauna species) within the detritus accumulating within *P. oceanica* meadows or within bottom depressions, between stones or boulders (Dimech et al., 2006; Gallmetzer et al., 2005; Como et al., 2008; Remy et al., 2018; Mascart et al., 2015; Costa et al., 2019).

Some fishes could use PW beds to minimize predator encounters before reaching adult size, whereas medium-sized fishes could hide to ambush invertebrate or fish prey. We found the piscivorous *Serranus scriba* specimens camouflaged by getting a dark-brown livery while preying just in PW beds upon very small specimens of *Atherina* sp. and *D. sargus*. The semi-transparent body of *D. sargus*, moreover, was hardly detectable within the resuspended wrack fragments, which could be a specific strategy to hide from visual predators. (Re)suspended wrack particles could also reduce the light penetration (Lasiak, 1986; Moore et al., 2004). This mimetic livery is also displayed by juveniles of the congeneric species *D. puntazzo* (showing typical brown bands) in shallow waters, and by small individuals of the labrid *Coris julis* in deeper *P. oceanica* leaf detritus accumulations (Author's, personal observations). Dark liveries and reduced light penetration make these small fishes hardly detectable by fish and avian visual predators, such as cormorants in the study area, similarly to what observed elsewhere (Lenanton et al., 1982; Robertson and Lenanton, 1984).

4.3. Implications for management

This study, besides the specific results discussed here, has direct and indirect implications for management. *P. oceanica* wrack beds could have, in fact, crucial ecological roles, providing food and shelter to juvenile and subadult fish, some of commercial value, such as *Diplodus sargus, D. vulgaris* and *M. surmuletus*, targeted by commercial and recreational fishers. Further studies are required to measure the "manger effect" of wrack beds (attraction/concentration of fish for foraging) and quantify how much *P. oceanica* detritus may contribute to prey availability for these fishes. This study also highlights that the current decline of several vegetated habitats could have negative consequences extending far beyond the areas where seagrasses grow (Heck et al., 2008). Conservation efforts to sustainably manage seagrass meadows should thus also take into proper account the seagrass wrack with protection measures that should be extended to the habitats receiving phytodetritus (Heck et al., 2008; Boudouresque et al., 2016; Unsworth et al., 2018).

We should also consider that the wrack in the surf zone does not come only directly from the *Posidonia* meadows. but also from the wrack accumulated on the supralittoral beach (Vacchi et al., 2017). In touristic regions like the Mediterranean, beach wrack raises certain non-negligible socio-economic issues: tourists, residents and policy makers often perceive the PW as unpleasant and an ecosystem 'disservice', driving beach grooming and sand nourishment procedures for their removal (Ruiz Frau et al., 2019). We hope our study could contribute to making stakeholders more aware that this practice is a threat for the shore and for biodiversity. In order to improve conservation and restoration measures, we strongly believe that scientific evidence together with education programs and support for proper management protocols (Zakhama-Sraieb et al., 2011; Rotini et al., 2020) could help persuade policy makers, local stakeholders and tourists that PW along the beaches and in the surf zone is just "natural" and so beneficial for beach protection against erosion and the associated biodiversity.

CRediT authorship contribution statement

Simona Bussotti: Conceptualization, Data curation, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Paolo Guidetti:** Writing – review & editing, Methodology, Investigation, Data curation, Conceptualization. **Francesca Rossi:** Conceptualization, Data curation, Formal analysis, Investigation, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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