

Diel and vertical movements of preflexion fish larvae assemblages associated with *Posidonia oceanica* beds

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SUMMARY: Habitat complexity is a strong determinant of fish assemblage structure. Enhanced food resources and protection from predators are generally considered the main benefits of vegetated areas. We investigated the diel and vertical movements of preflexion fish larvae within and above the leaf canopy of *Posidonia oceanica* to determine if it acts as an important habitat for larval stage fish. Samples were taken with moored plankton nets during the night and day at two depths (13 and 15 m) over five consecutive days in July 2000 in the Marine Protected Area off Tabarca Island (Spain, SW Mediterranean Sea). In total, 353 fish larvae were captured. The most abundant taxa were *Sardinella aurita*, Sparidae, *Engraulis encrasicolus* and Gobiidae. Sparidae were more abundant within the leaf canopy during the day but increased in waters 2 m above the canopy at night. In contrast, *Sardinella aurita* were present throughout the entire water column during both the day and night. We conclude that the *P. oceanica* leaf canopy is important as a transitional shelter for the early stage larvae of some demersal fish species.

Keywords: preflexion fish larvae, *Posidonia oceanica*, habitat complexity, shelter, Sparidae, *Sardinella aurita*.

RESUMEN: MOVIMIENTOS VERTICALES DIARIOS DE LARVAS DE PECES EN ESTADÍO PRE-FLEXIÓN ASOCIADOS A LAS PRADERAS DE *POSIDONIA OCEANICA*. – El tipo de hábitat determina la estructura del poblamiento larvario de peces. Los principales beneficios que proporciona un hábitat con vegetación son el incremento de las fuentes de alimento y una mayor protección frente a los predadores. Este estudio se ha centrado en praderas de *Posidonia oceanica* para evaluar su papel como zonas de refugio, función que ha sido poco estudiada. Este trabajo se ha llevado a cabo en la Reserva Marina de Tabarca (España, SW Mar Mediterráneo). Las muestras se recolectaron con redes de plancton fijas en periodos diurnos y nocturnos, y a dos profundidades (13 y 15 m), durante 5 días consecutivos en el mes de Julio de 2000. Se capturaron 353 larvas y 256 fueron identificadas. Los taxones más abundantes fueron *S. aurita*, Sparidae, *Engraulis encrasicolus* y Gobiidae. Sparidae dominó al nivel de las hojas de la pradera durante el día, incrementando su presencia en la columna de agua durante la noche; mientras que la *S. aurita* se encontró a lo largo de toda la columna de agua en los dos periodos estudiados. Nuestro estudio confirma el papel de las praderas de *P. oceanica* como zona de refugio transitoria para los primeros estadios de larvas de peces, aunque limitado a algunas especies demersales.

Palabras clave: larvas preflexion, *Posidonia oceanica*, complejidad del hábitat, refugio, Sparidae, *Sardinella aurita*.

INTRODUCTION

The dynamics of the larval stage of teleost fishes can be a major determinant of the structure and dynamics of adult assemblages (Doherty and Williams, 1988; Sinclair, 1988). Survival during this stage is mediated by factors such as food and shel-

ter availability, predator abundance, larval behaviour and physical conditions (Cushing, 1975; Leis, 1991). The role of seagrass beds in the life history of juvenile fishes has been considered widely (e.g. Bell and Westoby, 1986; Bell *et al.*, 1987; Parrish, 1989; Robertson and Blaber, 1992; Beck *et al.*, 2001; Dorenbosch *et al.*, 2005). The habitat structure pro-

vided by seagrasses is considered to be one of the most important factors at a local scale, as it offers both shelter and food resources (Gotceitas and Colgan, 1989). Generally, vegetated beds favour higher growth rates of juveniles, greater survival and successful recruitment (Shulman, 1984). Seagrass beds have long been considered to be the most productive and architecturally complex systems, providing enhanced food resources and greater protection from predators compared to unvegetated substrates (Carr, 1994). The high primary productivity of the seagrass beds and associated epiphytic and benthic algae ensure that an abundant supply of organic matter is available as the basic energy source for more or less complicated food webs. Moreover, the three dimensional structure of the vegetation, with its network of roots and rhizomes and often dense leaf canopy, offers hiding places that protect against predation. The vegetation structure also confers physical and chemical qualities to the environment that may attract fauna. These characteristics make them a suitable recruitment area for fishes (Hemminga and Duarte, 2000).

The settlement hypothesis is an important argument for the conservation of seagrass beds with respect to other communities. For these reasons, *Posidonia oceanica* has been widely claimed to be an important nursery area for fishes in the Mediterranean Sea (Pérès and Picard, 1964). However, although there are some studies on the role *P. oceanica* seagrass beds play for juvenile fish (Bell and Harmelin-Vivien, 1982; Garcia-Rubies and Macpherson, 1995; Jiménez *et al.*, 1996; Francour, 1997), there is no research that evaluates the importance of *P. oceanica* during the larval phase of fishes. The objective of this study was to assess the role of *Posidonia oceanica* as a habitat for fish larvae communities. We hypothesized that *P. oceanica* affects the diel distribution of fish larvae along the water column and that larvae will be more abundant close to the leaf canopy than in the open water immediately above the canopy. Furthermore, we tested whether the leaf canopy is used mainly as a refuge during the day, with larvae moving in the water column during the night. The objectives of this study were: a) to assess differences in the abundances of fish larvae between the leaf canopy and the water column; b) to determine diel differences in the abundances of larvae; and c) to establish if diel and habitat related patterns of presence and abundance were taxa specific.

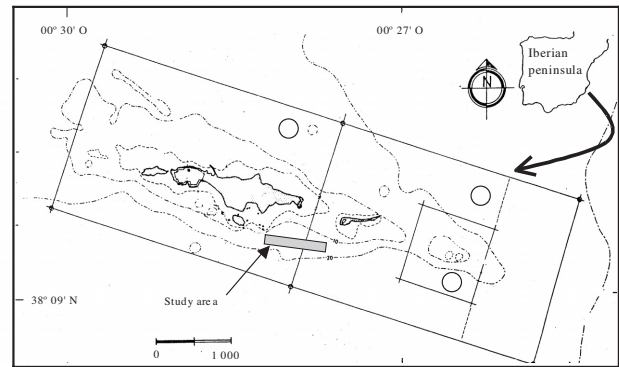


FIG. 1. – Map of the study location at Tabarca Island on the south-east coast of Spain in the Mediterranean Sea.

MATERIALS AND METHODS

Study area and net sampling

This study was carried out in the southern part of the Marine Protected Area of Tabarca Island, (SE Spain, SW Mediterranean Sea) (Fig. 1) at 15 m depth, between 25 and 29 July 2000, which coincided with the season when ichthyoplankton densities are highest in this area (Bordehore *et al.*, 2001). A well developed meadow of *Posidonia oceanica* surrounds the island, with high density and coverage values (Ramos, 1985).

Fish larvae were collected by means of stationary moored long-conical nets (330 μ m mesh, 56 cm diameter and 160 cm long) maintained at two different heights above the seabed: one net on the *P. oceanica* leaf canopy (15 m depth) and a second net situated 2 m above the canopy (13 m depth). Both nets could swing freely with current changes and each carried a 2030 General Oceanics flowmeter in order to estimate the volume of water filtered. This approach was selected to avoid the variability due to the likely changes in habitat characteristics if trawl nets were used, given that habitat characteristics are responsible for a large part of the fish assemblage structure both for adults (Garcia-Charton *et al.*, 2004) and larvae (Bell *et al.*, 1987).

At each height above the leaf canopy, samples were taken during day and night periods. During each period, three replicate samples that filtered seawater over 1 hr were made. This sampling procedure was repeated over 5 consecutive days, obtaining 60 samples for the whole experiment.

Plankton samples were preserved immediately in 4% formalin in seawater buffered with borax. In the laboratory, fish larvae were separated from the rest

of the plankton and then identified to the lowest possible taxonomic level, following Lo Bianco (1931), Aboussouan (1989), Russell (1976), Fahay (1983), Moser (1984), Olivar (1985) and Sabatés (1988). Data of all taxa are expressed as density of larvae per 100 m³.

Data analysis

We employed a mixed analysis of variance (ANOVA; Underwood, 1981) to test differences in total fish larvae density of the most represented taxa among the three factors considered: two fixed orthogonal factors (height above the leaf canopy: 0 or 2 m; and diel period: day or night) and one random factor (time: 5 days) nested in the diel period.

Prior to the ANOVA, heterogeneity of variance was tested with Cochran's C-test. Data were $\sqrt{x+1}$ transformed if variances were significantly different at $p=0.05$, and $\ln(x+1)$ transformed if variance was still heterogeneous. When variance remained heterogeneous, untransformed data were analyzed, as the ANOVA is robust to heterogeneity of variances, particularly for large balanced experiments (Underwood, 1997). Further, we set the F-test alpha at 0.01 for analyses which used untransformed data.

Non-parametric multivariate techniques were used to compare assemblages in different heights above the leaf canopy and diel period. All multivariate analyses were performed using the PRIMER statistical package. Prior to calculating the similarity matrices, the data were pooled by summing the 3

replicas for each diel period to reduce the stress of MDS representation, and fourth root transformed to weigh the contributions of common and rare species in the similarity coefficient (Clarke, 1993). Triangular similarity matrices were calculated using the Bray-Curtis similarity coefficient (Clarke and Warwick, 1994). Non-metric multidimensional scaling (nMDS) was used as the ordination method. Species that had more influence on similarities within groups and dissimilarities between groups from different heights above the leaf canopy and diel periods were defined using the SIMPER (similarity percentages) procedure (Warwick *et al.*, 1990). The PERMANOVA permutational multivariate analysis of variance (Anderson, 2005) was used to assess the significance of the interaction between heights from leaf canopy and diel period. The PERMANOVA program tests multivariate hypotheses for experiments with one or more factor in any fully balanced multi-way ANOVA design based on any distance measure using permutation methods. With this procedure we evaluated the multivariate hypothesis that larval fish assemblages at different heights above the leaf canopy would differ depending on the diel period due to fish larvae using the vegetation as a refuge during the day.

RESULTS

A total of 353 fish larvae were collected and 226 were identified to the family level, mainly due to the

TABLE 1. – Mean abundance of fish larvae per 100 m³ captured during the day and at night for each sampling depth in July 2000.

Families	0 m		2 m	
	Day	Night	Day	Night
Bleniidae	-	0.20 ± 0.11	-	0.13 ± 0.09
Bothidae	0.06 ± 0.06	1.33 ± 0.09	-	0.13 ± 0.09
Callyonimidae	-	-	0.07 ± 0.07	-
Carangidae	-	-	-	0.40 ± 0.40
Cepolidae	-	-	0.07 ± 0.07	0.06 ± 0.06
Clupeidae	-	1.60 ± 0.70	0.60 ± 0.23	2.53 ± 0.94
Engraulidae	0.20 ± 0.20	0.40 ± 0.16	0.66 ± 0.35	0.33 ± 0.13
Gobiidae	-	0.40 ± 0.23	0.13 ± 0.09	0.40 ± 0.16
Gobiesocidae	-	1.33 ± 0.09	-	0.06 ± 0.06
Gonostomatidae	-	-	-	0.06 ± 0.06
Labridae	-	1.33 ± 0.09	0.07 ± 0.07	0.26 ± 0.15
Myctophidae	-	0.06 ± 0.06	-	0.26 ± 0.15
Pomacentridae	-	1.33 ± 0.09	-	0.26 ± 0.12
Scorpaenidae	-	-	-	0.13 ± 0.09
Serranidae	0.06 ± 0.06	0.06 ± 0.06	0.13 ± 0.09	0.40 ± 0.16
Sparidae	0.53 ± 0.215	1.40 ± 0.41	0.20 ± 0.11	1.93 ± 0.43
Triglidae	-	0.06 ± 0.06	-	0.06 ± 0.06
Yolk-sac larvae	1.06 ± 0.48	1.40 ± 0.40	2.66 ± 0.55	1.06 ± 0.30
Undetermined	0.53 ± 0.21	0.46 ± 0.16	0.46 ± 0.27	1.13 ± 0.23

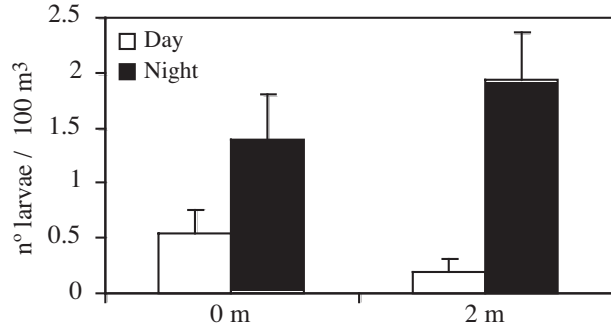


FIG. 2. – Number of Sparidae larvae/100 m³ for the factors Height and Diel period.

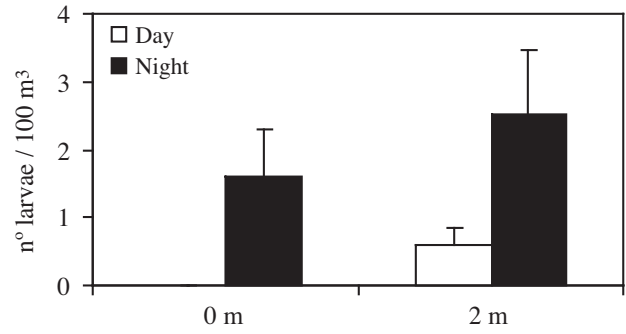


FIG. 3. – Number of *Sardinella aurita* larvae/100 m³ for the factors Height and Diel period.

small size of larvae. 85 specimens were classified as yolk sac larvae and 42 were too damaged to be identified. Total lengths ranged between 1.5 and 7 mm, but few larvae surpassed 3.5 mm. Mean lengths of larvae collected were quite similar during the day (1.86 ± 0.06 mm) and night (2.56 ± 0.13 mm). To test our hypotheses, we grouped the 226 identified larvae into 17 families (Table 1). The most abundant taxa were: Clupeidae (represented by *Sardinella aurita*), which constituted 31% of the analyzed larvae, Sparidae (27%), *Engraulis encrasicolus* (11%) and Gobiidae (6%). Each of the other 13 families represented less than 5% of the total number of larvae. The SIMPER analysis indicated that the taxa that contributed most to the similarity among samples at 2 m above the canopy was *Sardinella aurita* (44%), while at 0 m above the canopy Sparidae (63%) was the family that contributed most. Dissimilarity between heights was determined mainly by Sparidae (24.5%), which dominated at the level of the leaf canopy mainly during the day. Abundance of Sparidae was greater at the leaf canopy level during the day (Fig. 2), increasing along the entire water column during the night; however, diel period was the only statistically significant factor (Table 2). *Sardinella aurita* (24%) was

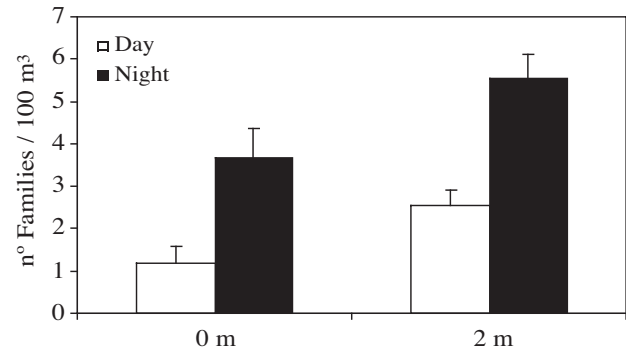


FIG. 4. – Mean number of families recorded during the day and night and at two heights above the *Posidonia oceanica* canopy.

recorded above the leaf canopy on all days but only appeared at 0 m during the nights (Fig. 3); however, there were no significant statistical results for the relation between diel period and height (Table 2). Bothidae and Gobiidae exhibited the same pattern as Sparidae and *Sardinella aurita* respectively (Table 1), although they contributed only slightly to the dissimilarity between heights (3.4% and 6.4% respectively). Serranidae abundances were greater at 2 m above the canopy during both the day and night (Table 1), with a dissimilarity value of 6.7% between different heights. None of these taxa showed significant differences for the factors considered.

TABLE 2. – Results of ANOVA comparing mean abundance of Sparidae and Clupeidae for the three factors considered (Height; He, Diel period; Pe and Time; Ti). *Significant at $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. ^{ns} no significant difference.

Source	DF	Clupeidae MS	F	MS	Sparidae F	F versus
Diel period	1	46.8167	2.00 ^{ns}	2.6364	7.24*	Ti(Pe)
Time (Pe)	8	23.4583	9.64***	0.3643	3.44**	Res
Height	1	8.8167	5.06**	0.0110	0.07 ^{ns}	HexTi(Pe)
Pe x He	1	0.4167	0.24 ^{ns}	0.3194	2.08 ^{ns}	HexTi(Pe)
He x Ti(Pe)	8	2.3583	0.72 ^{ns}	0.1534	1.45 ^{ns}	Res
Res	40	1.7417		0.1060		
total	59	2.4333				

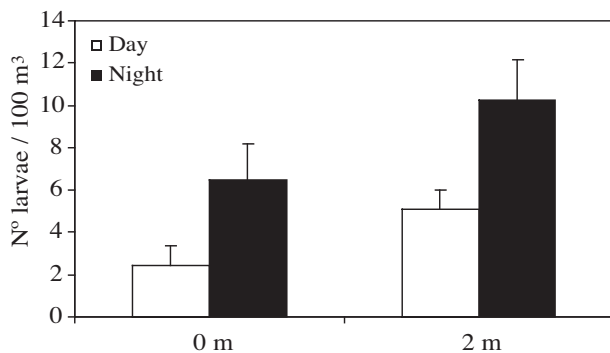


FIG. 5. – Mean number of fish larvae recorded during the day and night and at two heights above the *Posidonia oceanica* canopy.

TABLE 3. – Results of the ANOVA comparing mean number of families and mean fish larvae density for the three factors considered (Height; He, Diel period; Pe and Time; Ti). *Significant at $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. ns no significant difference.

Source	DF	MS	F	F versus
Families				
Diel period	1	11.0370	2.90 ^{ns}	Ti(Pe)
Time (Pe)	8	3.8065	9.64 ^{***}	Res
Height	1	7.1328	16.48 ^{**}	HexTi(Pe)
Pe x He	1	0.0013	0.00 ^{ns}	HexTi(Pe)
He x Ti(Pe)	8	0.4327	1.10 ^{ns}	Res
Res	40	0.3949		
total	59			
Fish larvae				
Diel period	1	96.2667	7.33 [*]	Ti(Pe)
Time (Pe)	8	13.1417	10.80 ^{***}	Res
Height	1	21.6000	50.82 ^{***}	HexTi(Pe)
Pe x He	1	1.6667	3.92 ^{ns}	HexTi(Pe)
He x Ti(Pe)	8	0.4250	0.35 ^{ns}	Res
Res	40	1.2167		
total	59			

The mean number of families recorded (Fig. 4) was significantly higher 2 m above the seagrass than at the canopy level, and significantly higher during the night compared to the day, although there were no significant differences between periods (Table 3). The same pattern was found for mean densities of fish larvae (Fig. 5; Table 3), showing significant differences for both the period and height factors. They exhibited considerable temporal variability at the day scale. The MDS plot (Fig. 6) did not clearly reflect the significant differences found in the interaction term by the PERMANOVA (Table 4). In this analysis, the pair-wise *a posteriori* comparison between the two sampling heights above the canopy showed significant differences in the fish larvae assemblage between heights during the day ($t = 1.99$; $p < 0.05$) but not during the night ($t = 0.70$; $p > 0.05$), which indicates changes in the pattern of vertical distribu-

tion of some specific taxa in the water column over a 24 hour period.

DISCUSSION

Our results suggest that some fish families are more abundant close to the leaf canopy during the day and move into the water column at night (e.g. Sparidae, Bothidae), while other taxa exhibit the opposite behaviour (e.g. *Sardinella aurita*, Gobiidae). Similarly, different patterns were reported in other studies for the diel and vertical distribution of fish larvae, with densities of larvae either decreasing in shallower layers during the day period (e.g. *Diplodus sargus*; Olivar and Sabatés, 1997) or appearing deeper during the night (e.g. *Clupea harengus*; Munk *et al.*, 1989). Leis (1986) found different behavioural patterns and concluded that most taxa remain at greater depths during the day and move upwards at night. Other studies (e.g. Kingsford, 2001) report this kind of behavioural pattern even for preflexion larvae that are more abundant during the dark periods.

In this study, the largest amount of fish larvae captured was in the preflexion stage. The main reason for this may be due to the type of fixed nets used

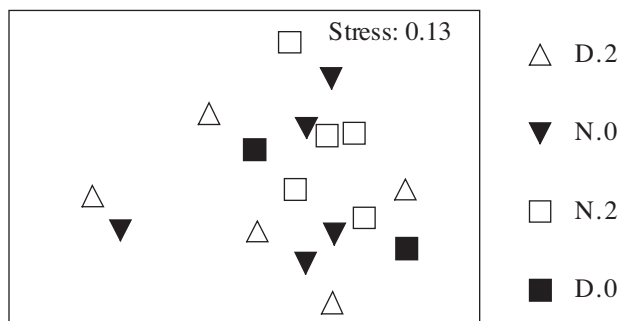


FIG. 6. – Non-parametric multi-dimensional scaling plot of fish larvae for the factors: Height (2=in the water column; 0= on the *Posidonia oceanica* leaf canopy) and Diel period (D=day; N=night).

TABLE 4. – Results of PERMANOVA for fish larvae considering the factors Height and Diel period. *Significant at $p < 0.05$. ns no significant difference.

Source	DF	MS	F	F versus
Diel period	1	6573.4582	2.7802 [*]	Res
Height	12	5544.6015	2.3451 ^{ns}	Res
Pe x He	1	6756.5309	2.8577 [*]	Res
Res	16	2364.3623		
total	19			

that favour capturing small larvae but can be avoided by larger larvae (Leis and Carson-Ewart, 1994). Other studies that used the same sampling method obtained similarly low proportions of late stage fish larvae (Bordehore, 2000), in contrast to samples obtained from towed nets that capture larger fish larvae but often destroy small larvae. However, the increased overall catches during the night were probably not due to net avoidance because mean size did not change greatly between the day and night (e.g. mean size of Sparidae was 1.84 ± 0.07 during the day and 2.04 ± 0.04 at night; and Bothidae measured 2.0 ± 0.0 during the day and 2.45 ± 0.2 at night). Although the sampling method used was not suitable for studying all larval phases, our approach allowed us to detect very early stages of fish larvae not yet reported in the Mediterranean Sea in *Posidonia oceanica* meadows. In this sense, the samples collected were useful for testing the hypothesis proposed for early stage larvae.

We found that larvae of some typical bottom-dwelling sedentary species (e.g. Callionymidae, Scorpaenidae, Bleniidae, Labridae and Serranidae) remained in the entire water column during both the day and night. This suggests that they have not reached the development stage necessary to use the demersal habitat, given that vertical migrations of these taxa could be carried out by larger larvae (Fortier and Leggett, 1983; Fortier and Harris, 1989). This interpretation agrees in this respect with several other studies that have determined specific vertical distributions for larger larvae of certain species in offshore open waters (Leis *et al.*, 1996; Olivar and Sabatés, 1997). However, Sparidae and Bothidae were more abundant at the leaf canopy level during the day but increased in the water column above the canopy at night, even though these larvae exhibited similar sizes as the taxa mentioned above. These larvae would appear early in the *P. oceanica* meadows, use them as a refuge during the day and migrate to shallower layers at night. Such excursions are reported widely in the literature (Kendall and Naplin, 1981) and could be a means of determining if the bottom is suitable for settlement, a means of obtaining orientation cues (Leis *et al.*, 1996) or even using the *P. oceanica* meadows as a transitional habitat from offshore spawning zones to the definitive settlement grounds through horizontal and vertical migration and movement by residual or tidal currents (Champalbert and Koutsikopoulos, 1995). This could explain why some families did not

vary at different heights and diel periods while others varied considerably. Furthermore, although some studies reported vertical nocturnal movements of some species motivated by trophic behaviour (Mikhman and Tomanovich, 1977; Bulgakova, 1993; Tudela and Palomera, 1995), planktivory needs visual cues (Strickler *et al.*, 2005). The vertical diel movements recorded for Sparidae and Bothidae in this study are unlikely to have foraging as the main cause because these species feed during daylight periods.

Our results show that *P. oceanica* seagrass beds are used for shelter by some early stage fish larvae. The physical complexity of seagrasses is a major determinant of the structure of the associated community (Orth *et al.*, 1984), and is considered to be especially important for the survival of fish larvae and juveniles (Bell *et al.*, 1987). Fish larvae find shelter from predators in seagrass canopies, which significantly reduces their susceptibility to predation (Nakamura and Sano, 2004). Fish larvae using seagrass increases their ability to avoid predatory attacks (Folkestad, 2005), and selecting a suitable habitat seems to be an active choice (Leis and Carson-Ewart, 1997). Therefore, a larger presence of Sparidae and Bothidae near the canopy during the daylight period can be interpreted as active selection of a habitat as a transitional refuge. Although there is some information about the active behaviour of mature larval fishes selecting suitable habitats for settlement (Bell and Westoby, 1986; Bell *et al.*, 1987; Ault and Johnson, 1998), no information is available with respect to early stage larvae in *P. oceanica* meadows. Our results highlight the important role that *P. oceanica* seagrass beds play during the early larval stage of some fish and their function as a shelter, which favours the enhancement of adult densities and the conservation of fish stocks. Since the presence of *P. oceanica* seagrass beds can be an essential factor in the survival of fish larvae, losses of this Mediterranean community could therefore affect the dynamics of adult populations of some valuable commercial species. Our results provide further support for the need to properly protect the *P. oceanica* habitat by managing littoral resources.

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