Site-attachment behaviour of *Oblada melanura* (Linnaeus, 1758) (Osteichthyes: Sparidae) benthic larvae: a quantitative approach

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SUMMARY: The site-attachment behaviour of *O. melanura* settlers was examined in an estuarine area of western Greece. The approach that was followed included underwater assignments of shoal identities and continuous recording of specific behavioural traits. Variations between ontogenetic stages with respect to the pattern of residence at the sites were quantified via an index (the residence-persistence index (RPI)) devised for this purpose. Our findings suggest that this species initiates settlement in small shoals that occupy specific sites at the substratum where they reside for various days. This behavioural trait is stage-specific and gradually diminishes as the fish complete metamorphosis, while at the same time they change their social organisation. Such an ontogeny-dependent site-attachment behaviour has not been described before and is markedly different from that described for other members of the Sparidae family.

Keywords: Oblada melanura, settlement, site-attachment, ontogenetic shift, Sparidae.

RESUMEN: COMPORTAMIENTO DE ASOCIACIÓN AL SUSTRATO DE LAS LARVAS BENTÓNICAS DE *OBLADA MELANURA* (LINNAEUS, 1758) (OSTEICHTHYES: SPARIDAE): UNA APROXIMACIÓN CUANTITATIVA. – En este trabajo se ha examinado el comportamiento de asociación al substrato de los individuos recién asentados de *Oblada melanura* en un área estuárica de Grecia occidental. El estudio se hizo en base a la identificación de los bancos y al seguimiento continuo de las características conductuales específicas a lo largo del tiempo. Las variaciones ontogenéticas respecto a la pauta de residencia en los diferentes lugares han sido cuantificadas mediante un índice (índice de residencia-persistencia (*RPI*) específicamente desarrollado para este fin. Nuestros resultados sugieren que esta especie inicia el asentamiento en pequeños bancos que ocupan lugares específicos del substrato en donde residen varios días. Esta característica conductual es específica del estadio de desarrollo y disminuye gradualmente a medida que los peces acaban su metamorfosis, mientras que, al mismo tiempo, cambian su organización social. Esta conducta de asociación con el lugar de asentamiento, dependiente de la ontogenia, no se había descrito anteriormente y es marcadamente diferente a la que ha sido documentada para otros miembros de la familia Sparidae.

Palabras clave: Oblada melanura, asentamiento, asociación al substrato, cambio ontogénico, Sparidae.

INTRODUCTION

Settlement and post-settlement are processes of great importance in determining population structure and dynamics (Doherty, 2002). Recognising their significance, numerous behavioural studies related to the period prior to settlement (e.g. Breitburg, 1991; Leis and McCormick, 2002; Trnski, 2002; Fuiman and Cowan, 2003; Leis, 2004; Leis *et al.*, 2006) as well as to the period following settlement (e.g. Hoelzer, 1988; Kaufman *et al.*, 1992; Petrie and Ryer, 2006) have been conducted.

One important post-settlement behavioural aspect that has been well recognised for many groups of fishes is site-attachment, describing the restricted activity of individuals to a small section of the available suitable habitat. As stated by Huntingford *et al.* (1998) for salmonids, this behaviour can have significant implications for population processes. Site-attachment behaviour has been well described for adult and juvenile stages following metamorphosis, particularly for species that settle solitarily or exhibit territoriality (e.g. Lembo *et al.*, 2002; Workman *et al.*, 2002; Potthoff and Allen, 2003). To our knowledge, it has never been examined for benthic stages preceding metamorphosis.

The present study examines the site-attachment behaviour displayed by shoals of *Oblada melanura* benthic metamorphosing larvae (hereafter referred as settlers). Following Pitcher (1986) we use the term 'shoal' for aggregations of settlers, while 'schooling' refers to the coordinated swimming behaviour of a shoal. *O. melanura* is a littoral Mediterranean schooling fish, and from previous studies (García-Rubies and Macpherson, 1995; Harmelin-Vivien *et al.*, 1995) we know that the larvae of this species settle in very shallow waters (2 m or less in depth) over rocky substrata, with the settlers usually occurring at sites with a gentle slope, and in later stages at sites with steeper slopes. Our preliminary observations concerning the settlers of this species indicated that they aggregate on the substratum in shoals whose sizes depend on their ontogenetic stage. Furthermore, the settlers exhibit stationary behaviour during the day, while many shoals seem to be persistently site-attached, retaining their position above certain substratum areas for a variable number of days.

The main objective of the present study was to determine whether site-attachment (hereafter referred to as *residence-persistence*) is stage-specific and whether its duration is related to the fish ontogenetic stage. To this end, we propose a direct approach for quantifying site-attachment behaviour, based on an index devised for this purpose.

MATERIAL AND METHODS

Data collection

Data were collected at the littoral zone of a semi-enclosed bay, 2.5 km east of the Acheloos River estuary (38°20'N, 21°07'E) in the Ionian Sea, western
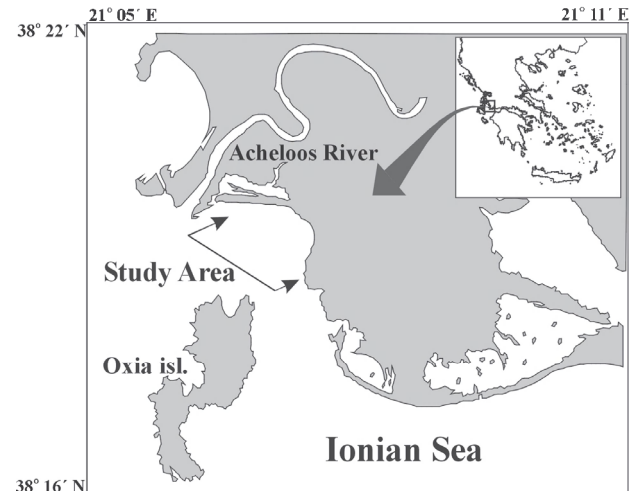

Fig. 1. – Location of the study area in western Greece.

Greece (Fig. 1), using underwater diving apparatus. The bay area consists from east to west of 2 km of sandy littoral, followed by a strip of boulder area approximately 300 m long and 8-10 m wide, both areas having a very gentle slope (7° on average), followed by 3 km of abrupt (76° on average) rocky area. Both boulder and rocky areas were quite uniform throughout the study area. Preliminary observations about the settlement behaviour of this species were conducted in this area during the previous year. These observations set the basis for the proposed methodology in this study. Data collection was initiated after the settlement peak of *Oblada melanura* in early July 2002, as had been determined by previous regular underwater observations in the sampling area (fortnightly surveys all year round, and weekly surveys from the moment when settlement was detected). During the sampling period settlers of all ontogenetic stages were present in the settlement area. *O. melanura* settlers were detected only above or next to rocks or boulders.

Data were collected at sites marked specifically by means of numbered moorings, originally set at places where *O. melanura* settlers were detected. Distances between moorings varied, but the smallest distance between two moorings was set at 6 m. Eighteen such sites were marked along 500 m of coastline and they were surveyed daily during two sampling weeks, at the beginning (3-9) and end (21-28) of July. On the following sampling days other shoals could also appear or reside at these marked sites. The collected data regarding each shoal detected as close as 3 m from each mooring were: a) the number of larvae composing the shoal, identi-

fied as two or more individuals being closer to each other than 10 body lengths (Seghers, 1981; Freeman and Grossman, 1993); b) the ontogenetic stage of the individuals, classified into one of three ontogenetic categories (described below); and c) the distance of the shoals from the moorings, counted as the distance of the centres of the shoals from the moorings. The fish did not exhibit any signs of disturbance as long as the approach was done slowly, a fact also observed by Macpherson (1998) for settlers of other Sparidae species.

Ontogenetic stages

The settlers were classified into three ontogenetic stages following the morphological criteria described by Ranzi (1933) for the settlers of this species. These were: 1) early-stage settlers, which had not formed the row of melanophores at the base of their dorsal fins and the white halo on both sides of the already formed black spot at the caudal peduncle; 2) middle-stage settlers, from the completion of the above characteristics to the acquisition of a uniform brownish colour (created by numerous melanophores spread uniformly over their body); and 3) late-stage settlers, from the acquisition of the brownish colour to the completion of metamorphosis, at the complete acquisition of external adult morphological characteristics, which also coincides with the completion of squamation at the head (Nikolioudakis personal communication). In preliminary work, samples of settlers of the three ontogenetic stages described were captured and total length was measured to the nearest tenth of a mm. Sizes ranged from 9.5 mm to 15.9 mm for the early-stage settlers, 12.8 mm to 17.0 mm for the middle-stage settlers and 13.5 mm to 19.0 mm for the late-stage settlers.

Shoal identity

The descriptive criteria used for assigning identities to the shoals detected were: a) the ontogenetic stage of their members (belonging to one of the three stages described above); and b) the shoal size. When a shoal of the same size composed of settlers of the same ontogenetic stage was observed at the same site on different days it was considered as being the same shoal. As sampling was accomplished on a daily basis, any transition of a specific shoal to a different ontogenetic stage could be easily detected; hence shoal identity was not lost. 'Size' refers

to abundance classes, defined approximately by the geometric progression of 2, as proposed by Harmelin *et al.* (1985) for the in situ classification of adult fish schools. Thus, 9 abundance classes were formed having 1, 2-5, 6-10, 11-30, 31-50, 51-100, 101-200, 201-500 and 501-1000 individuals. Each abundance class was assigned a categorical number from 1 to 9 correspondingly.

Data analysis

Shoal size per ontogenetic stage

Mean shoal size differences for the three ontogenetic stages were tested for significance by means of the non-parametric analysis of variance (Kruskal-Wallis) test. Individual differences were further compared by Dunn's test for multiple comparisons (Sokal and Rohlf, 1995).

Residence-persistence

There are various aspects in the display of prolonged stay (residence-persistence) at a site. A shoal may exhibit strong site-fidelity, residing at the chosen site for long periods (here the strongest expression of site-fidelity would occur when the shoal resides at the site throughout the sampling period), or it may exhibit very weak site-fidelity, leaving the site after a variable length of residence and returning again another day, also residing for a variable length of time. The weakest site-fidelity occurs when the shoal appears at the site only twice, at the beginning and in the end of the sampling period. Between strongest and weakest expressions of site-fidelity, all possible variations may occur. Meanwhile, shoal sizes may be modified. The proposed index for the description of the residence-persistence pattern considers the fluctuations in shoal sizes and the uncertainties of shoal identity related to this, along with the pattern of residence (continuity and duration of stay).

The proposed Residence-persistence Index (*RPI*) has the following mathematical expression:

$$RPI = \frac{\sum_{i=1}^{k} e^{-|g_r - g_i|}}{1 + k} \quad \text{for } g_i \neq 0$$

where:

g_r = the categorical number of the most frequently detected abundance class. This is referred to as the

432 · S. KIPARISSIS et al.

resident categorical number. If there is no abundance class with a higher occurrence then the resident categorical number is considered to be the one corresponding to the abundance class first detected.

g_i = the categorical number of the abundance class of the shoal on sampling day i. In cases of shoal absence, g_i is considered to be equal to zero. In such a case a zero (0) score is granted for that day.

k = number of comparisons between sampling days (no. of detections – 1).

The first aspect considered by the RPI is the similarity between the most frequently detected shoal size (considered as the representative shoal size) and the daily shoal size detections. In cases of absolute resemblance g_r will be equal to g_i and thus $e^{-|g_r-g_i|}$ will be equal to 1, contributing to the total index value the maximum daily score. The $e^{-|g_r-g_i|}$ function that generates the daily scores for each shoal gives significant credit to differences only up to 2 abundance class categorical numbers. Larger differences are assigned very low scorings and thus their contribution to the total index value is very small. This scoring method "rewards" similarities and undervalues large discrepancies in shoal sizes (size being the only discrepancy in the descriptive criteria accepted), reflecting the low possibility of a shoal being the same as the resident shoal when the difference in the size by which it reappears is large.

The second aspect considered by the RPI is the pattern of residence (continuity and duration), both being expressions of site-fidelity. The numerator is the sum of all daily scores derived from the successive comparisons (k value) during the whole period of residence (a longer residence will result in larger sum of daily scores and consequently in a larger numerator). To gain proportion, the index is standardised by dividing the numerator by the number of comparisons (k value). The k value also represents the maximum score that may be granted to a shoal in cases of continuous presence, and in that respect the standardised index becomes a proportion of the observed residence to the ideal one. Moreover, when standardised, the index gives a proportion of residence continuity, since absences caused by the temporary abandonment of the site or by the displacement in distances longer than 3 metres, add 0 values to the numerator, significantly decreasing the index value. The increase by 1 of the k value in the denominator adds the element of duration, giving a larger weight in long periods of presence by significantly decreasing the total index value in cases of very short residences (small k value), while its effect is minimum in cases of very long residences (large k value).

GLM analysis

In a subsequent step, generalised linear modelling techniques (GLMs) (McCullagh and Nelder, 1983) were used in order to analyse variations in RPI and examine the relative importance of ontogenetic stage and shoal size in explaining these variations. The choice of the most appropriate link function and error distribution was made on the basis of residual plots.

Preliminary analysis demonstrated that a Gaussian error structure model (i.e. a general linear model) was suitable for analysing variations in the RPI. Models were fitted by means of the S-PLUS statistical package as detailed by Venables and Ripley (1997). Interactions among explanatory variables were not included in the models due to lack of sufficient data. Statistical inference was based on the 95% significance level.

RESULTS

According to the aforementioned shoal identification criteria, in both sampling periods at the marked sites there were 173 shoal detections in total, attributed to 63 individually identified shoals. Twelve of these shoals belonged to the early-stage, 9 to the middle-stage and 42 to the late-stage ontogenetic categories. The microhabitat types in which these shoals were detected were either boulders on a substratum with a very gentle slope and no vegetation on them, or crevices and embayments in a rocky littoral with an abrupt slope, also without vegetation. The position of each shoal in relation to the substratum was different at the different ontogenetic stages. The new recruits formed small benthic shoals that remained a few centimetres above the substratum and sought refuge among the rocks when they were disturbed. In later stages, these shoals were gradually positioned higher in the water column. The shoals of different ontogenetic stages did not mix even when they were present at the same site. Besides having a different position in the water column, they reacted differently when disturbed.

Unique detections

The percentage of unique detections (shoals detected only once at the marked sites), can give

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TABLE 1. – Descriptive residence characteristics for the shoals of the three ontogenetic stages and mean shoal residence at the sites

Ontogenetic stage	Unique detections	Sequential reappearance	Non-sequential reappearance	Mean residence duration at the marked sites
Early-stage	17%	75%	8%	3.1 d·shoal⁻¹
Middle-stage	22%	66%	11%	2.1 d·shoal⁻¹
Late-stage	31%	36%	42%	1.8 d·shoal⁻¹

us a clue to the degree of site-fidelity or activity level around the sites for the shoals of the three ontogenetic stages. The more site-attached a shoal is, the more often it will be resighted at the same site, while roving behaviour will result in a larger number of unique presences. The same effect will be produced by a high activity level that results in displacements of more than 3 m around the occupied site.

Among the early-stage shoals, 83% were resighted during the sampling periods at least twice, 75% of them sequentially, while only 17% of them were detected only once. At the other end, 78% of the late-stage shoals were resighted, but only 36% of them sequentially, while 31% of them were detected only once. The middle-stage shoals exhibited intermediate percentage values: 77% of them were resighted, 66% sequentially and 22% of them were sighted only once (Table 1). Moreover, the early-stage shoals were present for a longer period on average at their residence sites, this period decreasing correspondingly for the middle and late-stage settlers (Table 1).

Shoal sizes

Settlers of the early-stage formed on average the smallest shoal sizes among the three ontogenetic stages (Table 2). The ranges of shoal sizes for the three ontogenetic stages are given in Table 2. Analysis of variance on ranks (Kruskal-Wallis) showed

TABLE 2. – Average shoal sizes (expressed by their medians) for the three ontogenetic stages and their ranges. Shoal size refers to number of individuals and numbers in parenthesis refer to abundance class category.

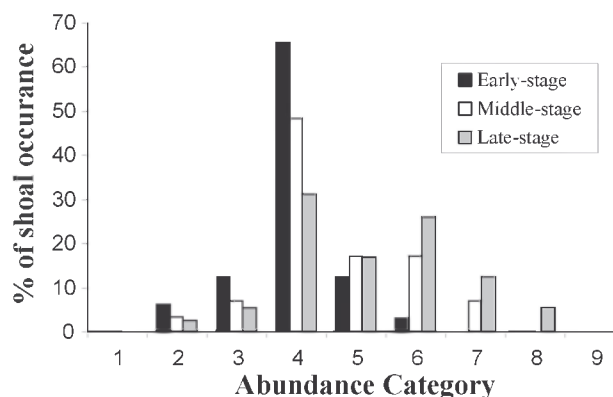| Ontogenetic stage	No. of detections	Shoal size median	Minimum shoal size	Maximum shoal size
Early-stage	32	20	2 (2)	56 (6)
Middle-stage	29	30	5 (2)	200 (7)
Late-stage	112	48	4 (2)	350 (8)

FIG. 2. – Distribution of the percent occurrences per abundance category for the three specified ontogenetic stages

significant differences among the mean shoal sizes (sizes represented by abundance class categorical numbers) for the three ontogenetic stages (H = 22.662, p <0.001). A posteriori multiple comparisons (Dunn's test), showed significant differences between early and late-stage shoal sizes, while middle-stage shoal sizes did not differ statistically from either one.

The distribution of the shoal sizes for the early-stage shoals showed a trend towards small abundance categories, with 84.4% of the shoals occurring in the first 4 categories, while 58.6% of the middle-stage and 39.4% of the late-stage shoals occured in these first 4 categories. The abundance class 4 (11-30 individuals) was the most frequently encountered at all ontogenetic stages (65.6% for the early, 48.3% for the middle and 31.25% for the late stage). The largest percentage of the late-stage shoals (60.6%) were distributed between categories 5 and 8 (Fig. 2).

Distribution of *RPI* values

The frequency distribution of the PRI values shows a distinct trend of the early-stage shoals towards high index values (continuous residence), all of which were greater than the intermediate values (0.46-0.50). On the other hand, late-stage index values stretched towards low index values (low residence durations or infrequent occupation of the sites), with 31% above 0.46. The middle-stage shoals obtained intermediate index values, with 43% above 0.46 (Fig. 3). The range of index values were: for the early-stage shoals between 8.0 and 0.456, for the middle-stage shoals between 0.584 and 0.123 and for the late-stage shoals between 0.592 and 0.0031.
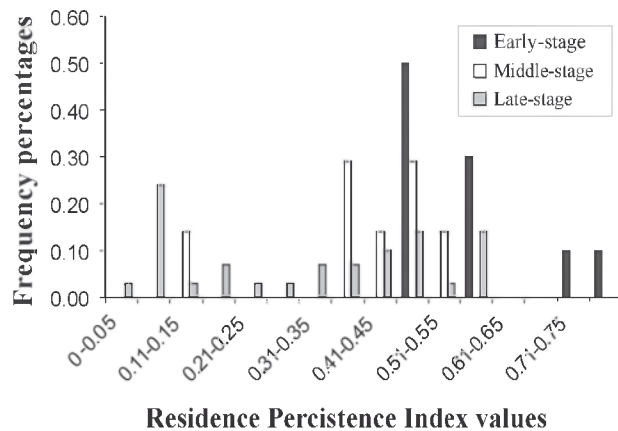
FIG. 3. – Shoal frequency percentages of *RPI* values for the three specified ontogenetic stages

Effect of ontogenetic stage and shoal size on RPI variation

The GLM analysis of RPI variation in relation to ontogenetic stage and shoal size indicated that only the effect of ontogenetic stage was significant (Table 3). The effect of ontogenetic stage on RPI is shown on the y-axis for the different ontogenetic levels (x-axis) (Fig. 4). Negative values on the y-axis indicate that, at the corresponding levels, the model predicts RPI that is lower than the mean estimated by the model. The opposite holds for positive values. Thus, RPI decreased with ontogenesis and the RPI of the early-stage larval settler shoals was about 20% higher than that of the middle-stage ones. Differences between the middle and late stage were smaller (about 10%) (Fig. 4).

DISCUSSION

Our results suggest that *O. melanura* settlers commence settlement in small shoals, residing at specific sites for a variable number of days. All of the above change gradually as the fish metamorphose, with the late-stage settlers having changed their behaviour considerably. They have almost abandoned the
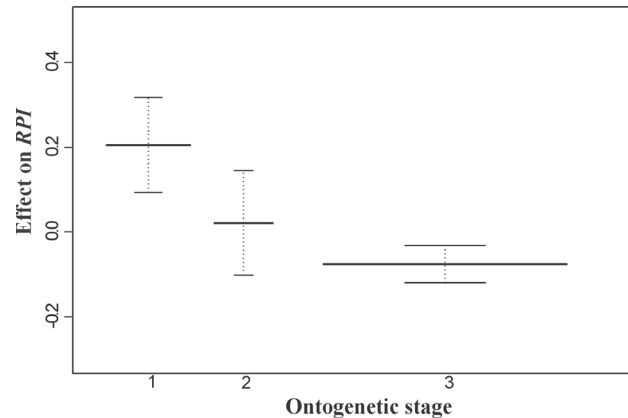

FIG. 4. – General linear-model-derived ontogenetic stage effect on resident persistence index (RPI). The fitted values are adjusted to average zero and the broken lines indicate two standard errors. Bar widths correspond to the observation frequency at each ontogenetic stage level.

residence behaviour, aggregate in shoals of a wide range of sizes, but mainly large (the latter also supported by the observations of Harmelin-Vivien *et al.* (1995)), and they are more kinetic, exhibiting roving behaviour in all of the above resembling the behaviour of the adults of their species. Such an ontogeny-dependent post-settlement residence-persistence strategy has not been described before and is markedly different from that described for other members of the Sparidae family, which commence settlement in large shoals that gradually decrease in size as the fish grow (Harmelin-Vivien *et al.*, 1995; Macpherson, 1998).

For several fish species site-attachment behaviour has been examined, in most cases by means of individual tagging experiments (e.g. Saunders and Gee, 1964; Fable, 1980; Gowan and Fausch, 1996; Marnane, 2000; Lembo *et al.*, 2002; Workman *et al.*, 2002; Potthoff and Allen, 2003). Although tagging procedures may be appropriate for studying behavioural traits in individuals or specific shoals, they cannot be of great help when large numbers of shoals, often of large size, have to be surveyed simultaneously, as in the present case. Moreover, removal of shoals from their original site in order to tag them may produce

TABLE 3. – Analysis of deviance table for the general linear model fitted to residence persistence data.

Source of variation	*df*	Deviance	Explained deviance (%)	Residual *df*	Residual deviance	P
Null				45	1.88	
Ontogenetic stage	2	0.51	27.13	43	1.37	0.001
Group size	7	0.28	14.89	36	1.09	0.267
Total		0.79	42.02			

unpredictable stress responses. This may explain the dearth of studies referring to site-attachment behaviour of fish settler shoals. The method we propose, using descriptive, directly applicable criteria, aims to overcome the aforementioned restrictions. The disadvantage of the method—which is the inherent uncertainty concerning the assigned identities—is alleviated by rendering daily scores based on the degree of the similarities observed. According to the conditions set by the index, in order for a shoal to get a high index value it must remain at the occupied site with no interruption for at least three days and with no alteration to its descriptive characteristics. Any change of the above will correspondingly reduce the total index value.

Mortality has not been considered in the estimation of the index. Having a reducing effect on overall shoal size, may result—when strong enough to reduce the shoal size beyond the shoal size intervals set by the identification criteria—in lower index values than the true ones. Its effect is therefore always on the conservative side, resulting in ascribing smaller residence-persistence than actually exists. The latter gives us confidence for the existence of this behaviour when it is detected by the proposed method. On the other hand, we could safely infer that shoals that gain high index values, besides being strongly site-attached, must also suffer from low mortality rates during the examined period.

According to Lenfant and Olive (1998), the shoals of *Oblada melanura* disperse during the night with the settlers staying isolated and inactive, while they gather again at first light. Therefore, in our case the shoals that retained their original position on the substratum for several days must have stayed in loose formations at close distances to their residence sites, to which they returned at first light. If the opposite were true, dispersion of the settlers during the night would have resulted in large inconsistencies in shoal identities and consequently in low index values. This implies that the residence at the chosen sites is an active process, that is, a process involving decision-making and effort. Moreover, the prolonged residence at specific sites also indicates a degree of suitability for these sites, in meeting the fundamental requirements for the survival of the settlers (i.e. protection from predators and feeding).

Prolonged residence is related to small shoal size and an early ontogenetic stage of the settlers. A number of reasons could be suspected for this: microhabitat characteristics that may not offer shelter in large shoals, resource availability since foraging is conducted at the sites during the whole residence period, and the low conspicuousness of small shoals to their predators, to mention only a few. Proof regarding the factors and the degree to which each one influences this settlement pattern cannot be provided by the present study because it is beyond its scope.

At the later ontogenetic stages, as the settlers grew in size they lost their dependence from the substratum. This may be related to the larger body size of the settlers of these ontogenetic stages, which enables faster swimming speeds (Vogel, 1994). This in turn offers more chances to escape predators, an ability which is reinforced by the formation of larger shoals (Krebs and Davies, 1981). Thus, a roving behaviour can be adopted by the late-stage settlers, giving them access to a wider range of food resources, a hypothesis supported by the results of Lenfant and Olive (1998), who found increasing diversity of prey taxa in the stomachs of the settlers of this species as they grow in size.

There is no evidence for the specific mechanisms by which the early-stage *Oblada melanura* settlers retain small sizes in their shoals. The adaptive significance of a residing settlement strategy of shoals, compared to the roving strategy followed by the schooling settlers of other sparids in the same settlement area, is also unclear. However, shoals of other species have also been observed occasionally to adopt residence-persistence behaviour, often residing next to *O. melanura* shoals (unpublished data). Therefore, we should consider a more thorough examination of the benefits of such a strategy and of the cues that direct the shoals of the settlers to choose specific residence sites. Macroscopic inspection of the substratum did not reveal any specific characteristics that could justify the selection of a specific site against any others. Therefore, the question arises whether there are specific microhabitat quality features that direct site selection. Important ecological issues may come into question if there are subtle, yet essential, microhabitat features that influence the implementation of such a settlement pattern for this and possibly for other species. The existence of such features may eventually determine the efficiency of an area as a nursery for a given species. Since alterations to the number and efficiency of the nurseries may be a major cause of the adult fish stock decrease (Riley *et al.*, 1981), knowledge of these attributes may prove to be a useful tool for fisheries management.

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