Temporal and spatial variability of settlement success and recruitment level in three blennoid fishes in the northwestern Mediterranean

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ABSTRACT: We studied the settlement success and recruitment level of 3 common species of blennoids (A. ridibundus, A. sphyra, Paramblypterus incognitus and Tripterygion trigonocephalum) at the NW Mediterranean coast at 3 localities separated ca 50 km apart, over a period of 4 yr (1994 to 1997). Settlement success is defined as the maximum number of new individuals observed during the settlement period and recruitment level as the number of new individuals at the end of the settlement period. We also determined which descriptive variables of the substratum had a significant influence on settlement, and whether the presence of adults had an effect on settlement. The results from the stepwise multiple regression analysis indicated that the type of substrate cover and the presence of adult conspecifics played a significant part in the abundance of settlers and post-settlers on the rocky shores for all 3 species. The variation in the abundance of settlers of A. sphyra was best explained by the category 'bare rock'. Settlement variance of P. incognitus and T. trigonocephalum was mainly explained by the substrate covered with 'small turf of algae'. Field experiments demonstrated a strong relationship between 'bare rock' density and A. sphyra settlement and between 'small turf of algae' density and P. incognitus and T. trigonocephalum settlement. However, the strong correlation between settlers and adult conspecifics in the stepwise multiple regression seems to be causal. For the 3 blennoids, preferences for a specific substrate type in settlement can explain, on small scale, the abundance of settlers in a locality. The maximum density of settlers was only dependent on the amount of preferred substrate available along a transect and independent of the size of a transect. The spatial and temporal patterns of the recruitment level differed from those observed in settlement success. For A. sphyra, no significant temporal and spatial differences were found for settlement success but were for recruitment level. For P. incognitus, no significant differences were found for settlement success, but a significant spatial variation was observed for recruitment level. For T. trigonocephalum, the most-stable differences were found for settlement success between years, which appeared in patterns of recruitment level. This suggests that the interannual differences were very strong and were maintained throughout the post-settlement period. For this species, significant differences of settlement success were also found between localities, however, they were not maintained over the season. Our results demonstrate that post-settlement processes can alter settlement patterns.

KEY WORDS: Settlement • Recruitment • Population dynamics • Habitat selection • Fish • Mediterranean

INTRODUCTION

The input of new individuals to a population is one of the most important processes in the life history of fishes, and to a large extent, affects their population dynamics (Cushing 1996). The addition of new individuals in most fish populations is determined by events occurring at settlement, defined as the period when pelagic larvae reach the bottom, and between this period and recruitment, defined as the time at which the juveniles remaining at the end of the settlement period incorporated into the adult populations (see the review by Caley et al. 1996). The number of larvae that reach the bottom is affected by a variety of abiotic (e.g. currents, wind, waves;
In the present paper, we have studied the settlement success and recruitment level of 3 common benthic littoral species of benthoids (Aidablennius sphynx, Peteniablennius incognitus and Tripterygion tripteronotus) from the NW Mediterranean Sea one of the most studied. Three localities were studied separated ca 50 km from each other over a period of 4 yr. We selected these species because they are taxonomically close, they live in the same littoral zone and habitat, and they tend to the bottom and recruit to the adult population at nearly the same time. These similarities can provide interesting information about the generality of the patterns observed.

The objectives of the present study were the following: (1) to determine which habitat characteristics have a significant influence in settlement, considering the descriptive variables of the substratum and the presence of adult conspecifics, and (2) once the habitat variables that affect settlement had been delimited, to analyse the importance of spatial and temporal variations of settlement success and recruitment level. We considered the settlement success to be the maximum number of new individuals observed during the settlement period and recruitment level to be the number of new individuals at the end of the settlement period that will incorporate into adult populations.

STUDY SPECIES AND AREA

Benthoids and 3-tin benthoids (Families Blenniidae and Tripterygiidae, respectively) form one of the most common groups of the Mediterranean rocky shore fishes (Cernea et al. 1996). On the coast of the NW Mediterranean Sea one finds about 18 species, along the shallow zones of the littoral mainly in the upper 0 to 1 m below the surface (Zander 1986). The 3 most abundant species are Aidablennius sphynx, Peteniablennius incognitus, and Tripterygion tripteronotus with a maximum of 7 individuals of each species m−2 (Illich & Kotschal 1990, Macpherson 1994). It is these 3 species which will be discussed in the present study.

Some life history characteristics of these fishes are known (e.g. Koppel 1988, Abel 1993). The breeding season is from February until July. Mating males usually build nests during this season and attend the deposited eggs (e.g. Wirtz 1978, Almada & Santos 1995, Kraak 1996), which are laid on the rocky shore-line. Once hatched, larvae disperse offshore. Little information is available on this process and on the pelagic phase of the life cycle. For some Mediterranean benthoid species, larval development is known and described (Subates 1984). The larvae of the 3 studied species are differently distributed in the plankton: the larvae of Tripterygion tripteronotus hardly with-
draw from the coast (ca 100 to 300 m), whereas the lar-
vae of A. bifomis and P. cinctus can be found various
miles off shore (S политы and pers. comm.). Blemnids and 3-fim blemnids, in
general, have a short life span from 2 to 5 yr (Görinna
data). Adults and juveniles of these common species
are preyed upon by other fish species (e.g. Serranus
caballus, Citharidae melanops authors pers. obs.)

Very little is known about settlement processes and
the settler's habitat needs. The rocky substrate of
the shallow zone along the Spanish coast of the NW
Mediterranean is covered by the same dominant com-

MATERIAL AND METHODS

The present study was divided into 3 parts based
on the 2 objectives above. First, we investigated the habi-
tat characteristics that best explain the abundance
of new settlers by a correlative approach. Second, to test
the effects of the significant habitat characteristics (alga
cover and presence of conspecific adults, see 'Result's),
we experimentally manipulated both vari-
able to detect possible causal relationships with abun-
dances of settlers. In the last part, settlement and
recruitment were analysed for differences between
localities and years.

Habitat selection. Three localities along the rocky
shores of the Costa Brava, in the NW Mediterranean
Sea, were sampled. The localities were Port de la Selva,
the Medes Islands, and Blanes, (Fig. 1), and are
roughly 50 km apart. Data collection has been carried
out along rocky walls, following transects between
the surface and 1.5 m depth, during the 4 settlement
seasons from 1994 to 1997.

Data on settlement and habitat were collected by
sampling 14 transects in July and August of every year.
Five transects were sampled by snorkeling in Port de
la Selva (totaling to 109 m²), 6 transects in the Medes
Islands (52 m²), and 3 transects in Blanes (69 m²).
The area of each transect varied between 6 and 46 m²
because the number and length of the transects were

limited by topographic characteristics of the locale
and ease of access during the whole settlement season.
Each wall was horizontally separated by discontinu-
ities such as sandy beaches or deep intrusions, and
vertically in depth by sandy bottoms or pebbles. While
algal and barnacle communities were similar at the
3 localities, the bivalve Mytilus galloprovincialis was
not present in Blanes.

Three dives transect 1 yr 1 were carried out at each
locality during the settlement season. Along each tran-
sect, the observer swam very slowly, from one end of
the transect to the other, and a 1 m² square frame was
gently placed on the bottom in order not to disturb
and scatter the fishes, in frame divers recorded (A)
the percentage of each substratum type: (1) bare rock,
(2) small turf algae, 0.5 to 1 cm, (3) long turf algae, 1 to
2 cm, (4) Lottia turf algae > 2 cm, (5) Mytilus gal-
loprovincialis (B) rugosity, 4 defined classes, using
the chain method (Larkhurst & Larkhurst 1976), and
(C) slope, classified as gentle (0 to 15°), pronounced
(16 to 30°), steep (31 to 60°), and very steep (>60°).
The substrate type 'bare rock' included zones with the
encrusting alga R. verrucosa and the occasional
presence of short algae (<0.5 cm in height, e.g. Enter-
orrhaphis clathrata). Individuals of all species (blemnids
and 3-fim blemnids) present in each 1 m² quadrant
were counted and their sizes recorded, but only the 3
most abundant species, A. bifomis, P. cinctus and A.
barbatula, have been analysed. Size was estimated by
plastic trays bearing the silhouettes of individuals of
different size-classes.
(0.5 cm increments) to minimize errors (e.g. Garcia-Johnson & Macpherson 1995, Harmelin-Vivien et al. 1995). New settlers of the 3 species, with total length of about 1.0 to 1.5 cm, were easily distinguished from each other: A. sphynx is practically unpigmented when settling, whereas P. incognitus was slightly pigmented similar to the adult color pattern. T. tripeteronotus was recognizable by its body shape and a color pattern similar to adults.

A stepwise multiple regression analysis was made on each of the 3 localities to determine which habitat variable best explained the abundance of the new settlers. In total, 9 independent variables were taken into consideration: the percentages of the 3 cover categories, rugosity, slope and the 2 fish variables (number of adult conspecifics and non-conspecifics). Normal probability plots were produced to check whether the assumption of normality is violated and no assumptions were plotted against standard deviations to check for outliers.

**Effect of substratum type and densities on settlement.** All of the following experiments were done on rocky walls in Blanes, Spain, in the upper littoral zone during the 1995 settlement season. Predominant winds and wevers are from the north-east to the east and walls had nearly the same orientation, so that atmospheric and oceanographic conditions were the same along their whole length. Nearby homogeneous walls, of little rugosity and without intrusions or extrusions, were selected. The experiment could only be conducted during the peak settlement period (for Aidaablennius sphynx in July and for Paraablennius incognitus and Tripeteronotus tripeteronotus in August) to get a sufficient number of individuals.

Based on our preliminary results of 1994, ‘bare rock’ was found to explain best the variation in settlement of Aidaablennius sphynx; conversely, we manipulated the density of this substratum type to test its effect on settlement of this species. The same procedure was carried out in Paraablennius incognitus and Tripeteronotus tripeteronotus, using ‘small turf algal (0.5 to 1 cm height)’. To analyse the effect of substratum type, 1 m² quadrats were manipulated by scraping algal from surfaces, leaving selected densities (bare rock for A. sphynx and small turf algal for P. incognitus and T. tripeteronotus) of different percentiles: 20 (low), 50 (medium), and 80% (high); with 4 replicates for each density. A 1 x 1 m PVC frame, subdivided in 16 smaller squares, was used to quantify the percentage of substratum type. The distance between the quadrants was at least 5 m. Each quadrant was isolated from the adjacent areas by additionally scraping a 1.5 m wide section around the perimeter and then applying bleach so no living organism would remain. No artificial effect of bleach application was tested and no settlers were observed in the cleaned strips during the experiment.

This procedure was used instead of artificial small rocks because it is believed to reflect a more natural condition that an individual finds when settling. All the adults and juveniles of benthoid species were removed from the quadrants to eliminate their possible effect on settlement. After 24 h, the number of new settlers per m² was counted for each of the 3 densities and all 4 replicates. This procedure was repeated 3 times during the month of May for settlement for each species. No adults (conspecifics or non-conspecifics) were observed in the quadrants or in the cleaned zone around the quadrants during the experiment.

The effects of algal densities and day of experiment on the abundance of settlers were determined in a 2-factor ANOVA and differences among means were assessed using the Tukey HSD test.

**Effect of presence/absence of conspecifics on settlement.** To analyse the influence of the presence of conspecific adults on the abundance of new settlers, quadrats similar to those used above were used, but with constant substratum conditions in the presence or absence of adults. To test the effect of Aidaablennius sphynx, quadrats of bare rock were used. For Paraablennius incognitus and Tripeteronotus tripeteronotus, a cover density of more than 80% of small turf alga 0.5 to 1 cm in height was used. The density of each of these species is known to be from 1 to 5 ind. m⁻² along this coast (Macpherson 1994). Given this, an adult density of 2 to 3 ind. m⁻² was tested for its influence on settlement. For each of the species, 4 quadrats with and without adults were situated on 2 different walls, separated horizontally on both sides by either deep and wide intrusions or sandy beaches, and vertically by the bottom of sandy substrate or pebbles. The distance between the quadrants was 3 to 5 m. To avoid adult migrations from the nearby areas into the quadrats, all individuals on both walls were collected, leaving only the desired 2 to 3 adults per quadrant. Two days prior to the experiment, the number of adults per quadrant was observed and if the adult densities differed from 2 to 3 ind. m⁻², their numbers were adjusted by replacing or removing individuals. In the majority of the cases the adults were males sitting in their nests which facilitated their remaining in the quadrant. Once verified that adult density remained stable in the quadrats, all juveniles were captured and 24 h later the number of new settlers in each quadrant was counted. This experiment was repeated on 5 different days.

The effects of presence/absence of adult conspecifics and day of settlement were determined in a 2-factor ANOVA and differences among means were compared using the Tukey HSD test.
Study of variations in settlement success and recruitment level between localities and years. To analyze a possible variation in settlement success and recruitment level between localities and years, and in response to both events, the 14 transects were sampled weekly from June to first half of October, when weather conditions permitted. During each dive, settlers of all 3 species were counted and their sizes noted as above. The maximum number of settlers observed per settlement season was assumed to indicate settlement success, for each transect and year. Recruitment level for each species was estimated using the number of individually left after the end of the settlement season, when no new settlers (unpigmented or slightly pigmented fish) were observed.

Because of the different numbers of transects for each locality, daily from transects within localities were pooled. As a result of the differences in lengths of these transects, numbers of settlers were standardized to int. m² substrate. Suitable habitat for Asellusinuis sphenyx was bare rock. For Paraphleianus incomitus and Tritypetonyx tripertorotonus cover of small turf algae (0.3 to 1 cm in height) were used. These algae covers were determined as the preferred substrate for each species (see Results). The variation of settlement and recruitment between localities and years was then determined in a 2-factor ANOVA. The differences among means were assessed using the Tukey HSD test.

We also tested if settlement and recruitment success were influenced by the sizes of the transects. The same standardized data set was above was used. A general linear regression model was applied to analyze the relationship between the abundance of settlers and recruits and the amount of suitable substrate available for each transect. In addition to the statistics described above, we tested for outliers by plotting means versus standard deviations. Cochran's test was used to test for heterogeneity of variances. However, no transformations were effective, therefore, raw data were used since sample sizes were sufficiently large to minimize Type I error (Underwood 1997).

RESULTS

The weekly censuses showed that settlement season started in second half of June for Asellusinuis sphenyx, in the first half of July for Paraphleianus incomitus and Tritypetonyx tripertorotonus, lasting until October for all 3 species. Settlement patterns were found to be similar for all 3 benthic fish: few settlers per day and no shoal aggregations on the substrate.

Once settled, fish remain benthic and live in the same habitats as adult specifics. Settlers of A. sphenyx and T. tripertorotonus remained on the surface of the rock, their colour pattern matching the substratum. Settlers of P. incomitus also have their colour matching the environment, although they used the rugosity of the rocks as hiding places. Peak settlement was recorded during the second half of August and first half of September, between 8 and 11 wk after the arrival of the first settlers for A. sphenyx, and 5 to 8 wk for P. incomitus and T. tripertorotonus. The last few settlers of P. incomitus and T. tripertorotonus were observed in the last half of September, and of A. sphenyx in the first half of October. No clear differences in the timing of first arrival of settlers was observed between localities and years.

Effect of habitat characteristics on settlement

The means of the 7 different substratum characteristics did not change significantly between each transect of each locality during the settlement season (Kruskal-Wallis test, p > 0.05, in all cases) or between years (Kruskal-Wallis test, p > 0.80, in all cases). This consistency was in a large part a result of the algae Corallina elongata, which maintains a near constant coverage over years and within seasons (Ballisteros 1987). For this reason, and in order to simplify further analyses for each locality, data from transects were pooled for each locality.

The results from the stepwise multiple regression analysis indicate that the type of algal cover and the presence of adult specifics significantly affect the abundance of settlers and post-settlers on the rocky shore of all 3 species (Table 1). However, the preferred substrate type and other wall characteristics differ between the species. The variation in the abundance of Asellusinuis sphenyx is best explained by the category "bare rock". The amount of variance explained by the multiple regression of this type of cover is high in all 3 localities with the highest correlations occurring in Islas and Port de la Selva. Negative correlations were obtained for long turf algae, Mytilus galloprovincialis rugosity and slope in some localities.

Settlement variation of Paraphleianus incomitus and Tritypetonyx tripertorotonus was mainly explained by the substrate covered with small turf of algae. In both species the amount of variance explained is higher in Port de la Selva than in the other localities. The importance of the other substrate characteristics differ between the species e.g. rugosity is positively related with P. incomitus, slope negatively with T. tripertorotonus.
Table 1. Stepwise regression coefficients for sources of variation of settlement of (A) A. didactylus sp., (B) Parabalanus incongruus, and (C) Tripeterygion tripetraeetus, for different localities. The dependent variables are the % characteristics of the habitat type (algal cover, Mytilus galiopolitanus, rugosity, and slope) and 2 fish variables (number of adult conspecifics and non-conspecics). Only significant relationships are shown (**p < 0.001, *p < 0.01, *p < 0.05).

<table>
<thead>
<tr>
<th>Independent variable</th>
<th>Blanes Coefficient</th>
<th>Blanes Partial r²</th>
<th>Blanes p</th>
<th>Major Islands Coefficient</th>
<th>Major Islands Partial r²</th>
<th>Major Islands p</th>
<th>Port de la Selva Coefficient</th>
<th>Port de la Selva Partial r²</th>
<th>Port de la Selva p</th>
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</thead>
<tbody>
<tr>
<td>(A) A. didactylus sp.</td>
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<tr>
<td>No algae (to scarce)</td>
<td>0.249</td>
<td>0.491</td>
<td>***</td>
<td>0.855</td>
<td>0.359</td>
<td>***</td>
<td>0.444</td>
<td>0.472</td>
<td>***</td>
</tr>
<tr>
<td>Long turf algae</td>
<td>-0.347</td>
<td>0.011</td>
<td>*</td>
<td>-0.715</td>
<td>0.126</td>
<td>***</td>
<td>-1.150</td>
<td>0.051</td>
<td>***</td>
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<td>Mytilus</td>
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<td>Rugosity</td>
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<td>Slope</td>
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<tr>
<td>Adult conspecifics</td>
<td>0.483</td>
<td>0.051</td>
<td>***</td>
<td>-0.659</td>
<td>0.047</td>
<td>***</td>
<td>0.276</td>
<td>0.022</td>
<td>***</td>
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<tr>
<td>(B) Parabalanus incongruus</td>
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<tr>
<td>Small turf algae</td>
<td>0.206</td>
<td>0.136</td>
<td>**</td>
<td>0.243</td>
<td>0.022</td>
<td>*</td>
<td>1.076</td>
<td>0.448</td>
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<td>Rugosity</td>
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<tr>
<td>Adult conspecifics</td>
<td>0.095</td>
<td>0.087</td>
<td>***</td>
<td>0.591</td>
<td>0.323</td>
<td>***</td>
<td>0.348</td>
<td>0.037</td>
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<tr>
<td>(C) Tripeterygion tripetraeetus</td>
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<tr>
<td>Small turf algae</td>
<td>0.376</td>
<td>0.332</td>
<td>***</td>
<td>0.676</td>
<td>0.343</td>
<td>***</td>
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<tr>
<td>Rugosity</td>
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<tr>
<td>Adult conspecifics</td>
<td>0.168</td>
<td>0.171</td>
<td>*</td>
<td>-0.149</td>
<td>0.119</td>
<td>***</td>
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</table>

Test of the effect of algal density on settlement

The results from the 2-factor ANOVA show that only the percentage of algal cover explains the variance of abundance of settlers. No significant differences exist over time. Furthermore, algal cover and sampling date interaction show no significant relationship (Table 2); consequently, data collected on different days were pooled for further analyses. A. didactylus sp. was settled in quadrats with high abundance of "bare rock" (80%). Settlement did not occur if this subphase type was less frequent than 50%. Mean abundances were significantly higher (Tukey HSD test) in quadrats with low algal densities, but high abundance of "bare rock" (high > medium > low, p = 0.0001), and no differences between medium and low densities of "bare rock" were found (p = 0.98). Parabalanus incongruus preferred to settle on high algal densities (>80%) of "small turf of algae". Mean settlement abundances were significantly higher in quadrats with high algal densities than with medium (50%) and low (<20%) densities (p = 0.04, Fig. 2). Tripeterygion tripetraeetus showed an intermediate pattern, with no preference between medium and high densities of algal cover. When the densities of 50% turf algae and 50% bare rock could be selected, quadrants with low density (<20%) were avoided (p < 0.0002). Based on results from experiments on algal densities and habitat characteristics, the hypothesis that algae cover on this coastal affects settlement of larval fish is accepted. A strong effect of substrate type on settlement of A. didactylus sp., Parabalanus incongruus and Tripeterygion tripetraeetus seems to exist.

![Fig. 2. Effect of 3 densities of preferred substrate on the density of benthic settlers (mean ± SE). "Bare rock" cover type was tested for A. didactylus spamy (AS), "small turf algae" cover type for Parabalanus incongruus (PS), and Tripeterygion tripetraeetus (TT). Three different levels of preferred substrate densities (low, 20%; medium, 50%; and high, > 80% cover) were used.](image-url)
Table 2. Results of a 2-factor analysis of variance used to determine if the number of newly settled individuals of the species (A) Ascidia mentula (B) Paracentrotus lividus, and (C) Triploid triploidy triploidizm is influenced by the salinity density in the experimental quadrants (1 m²). Three different densities of algal cover per quadrant were tested: low (<20%), medium (50%) and high (>80%), with 4 replications at each density. Selected algal cover varied between species: no algae (0% cover), small algae, ±1.5 cm for A. mentula, and small turf algae, ±1.0 cm for P. lividus and T. triploidizm (see Results for further explanation). Day refers to sampling days.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>p</th>
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<td>2</td>
<td>2.082</td>
<td>2.996</td>
<td>0.190</td>
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<tr>
<td>(B) Paracentrotus lividus</td>
<td>2</td>
<td>7.601</td>
<td>58.044</td>
<td>0.000</td>
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<td>(C) Triploid triploidizm</td>
<td>2</td>
<td>0.249</td>
<td>3.855</td>
<td>0.091</td>
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Table 3. Results of a 2-factor analysis of variance used to determine if the number of newly settled individuals of the species (A) Ascidia mentula, (B) Paracentrotus lividus, and (C) Triploid triploidizm is influenced by the presence or absence of adult conspecifics in the experimental quadrants (1 m²). Between 1 and 3 adults were present per quadrant. Day represents sampling days.

<table>
<thead>
<tr>
<th>Source</th>
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<td>0.038</td>
<td>0.441</td>
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<td>Adults (B)</td>
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<td>2.588</td>
<td>0.118</td>
</tr>
<tr>
<td>A × B</td>
<td>2</td>
<td>0.029</td>
<td>0.333</td>
<td>0.653</td>
</tr>
<tr>
<td>Error</td>
<td>30</td>
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<tr>
<td>(B) Paracentrotus lividus</td>
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<td>0.124</td>
<td>0.742</td>
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<td>A × B</td>
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<tr>
<td>Error</td>
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<tr>
<td>(C) Triploid triploidizm</td>
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<td>0.102</td>
<td>0.485</td>
<td>0.747</td>
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<td>0.980</td>
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<tr>
<td>Error</td>
<td>30</td>
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</table>

Variations in settlement success and recruitment level between localities and years

Settlement success of the 3 species studied for different localities and years is shown in Fig. 4. For all analyses, variances from Tukey HSD tests were carried out (see Material and Methods), but for simplicity only significant pairwise comparisons are noted. ANOVAs showed no spatial (between localities) or temporal (between years) differences in settlement success for Ascidia mentula or Paracentrotus lividus (Table 4). For Triploid triploidizm, however, settlement success varied significantly between 1998/99, with higher settlement success in 1999 than in other years (Tukey HSD test, p < 0.001), and between localities with higher settlement success in Medes (Tukey HSD test, p < 0.05). The number of recruits (A. splphyl x 0.64, P. lividus x 0.64 and T. triploidizm x 0.86, p < 0.0001 in all cases) was positively and significantly correlated with the maximum number of settlers for each species. However, the 2-way ANOVA performed on recruitment level data showed a different result than the results from settlement success (Table 4, Fig. 5). Recruitment for A. splphyl was significantly higher in Port de la Selva than in Blanes (Tukey HSD test, p = 0.05), recruitment level of 1997 was significantly higher than in previous years (Tukey HSD test, p = 0.02). For P. lividus, spatial and temporal patterns of recruitment level were quite similar as for settlement success, the exception was Port de la Selva.

Fig. 3. Effect of the presence and absence of adult conspecifics on the settler densities (mean ± SE) of Ascidia mentula (AS), Paracentrotus lividus (PL), and Triploid triploidizm (TT).

<table>
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<th>Absence</th>
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<tr>
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<table>
<thead>
<tr>
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<td>1.5</td>
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<td>2.0</td>
<td>2.5</td>
<td>3.0</td>
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</tbody>
</table>
with significantly higher levels than Blanes (Tukey HSD test, p = 0.001). For T. triperonotus, recruitment level did not vary significantly between localities, but was clearly different between years, with higher levels in 1997 than in previous years (Tukey HSD test, p = 0.0003).

To test the relationship of the amount of suitable substrate on settlement success, a general linear regression between the maximum abundance of settlers per transect and the amount of suitable substrate available per transect was carried out. Data from all localities and years were pooled. A significant relationship was found for A. bifida (r^2 = 0.42, p = 0.001) and P. incognitus (r^2 = 0.77, p = 0.001) and for P. incognitus, r^2 = 0.78, p = 0.001) (Fig. 6A,B). No relationship was found for T. triperonotus (r^2 = 0.19, p = 0.001) for T. triperonotus. As noted from the statistical results above, for T. triperonotus, highest densities were found in Medes and in 1997. When a linear regression was repeated using only the data sets for Medes (r^2 = 0.32, p = 0.01) and for all localities in 1997 (r^2 = 0.72, p = 0.001), a better relationship was found (Fig. 6C). The combination of the 2 gives the highest correlation between maximum numbers of settlers and amount of available suitable habitat (r^2 = 0.95, p = 0.005). To test if settlement was lower on isolated patches of suitable habitat versus continuous, larger areas of suitable habitat, different models were applied on settlers, standardized by the area of suitable habitat (no. per m^2 suitable habitat), and the amount of suitable habitat available per transect. No relationship was found for all 3 species. Thus, the abundance of settlers per surface area of suitable habitat is independent of the amount of the preferred substrate available along a transect (Fig. 7).

**DISCUSSION**

Substratum characteristics clearly influence the small-scale settlement of the 3 benthic fishes. New individuals of *A. bifida* occupied quadrants with a higher percent of rocky areas with no algal to scarce algal cover or covered by encrusting or occasional small algae. The other 2 species, *P. incognitus* and *T. triperonotus*, settled on clearly different substrata dominated by small turf algae. On the otherhand, the presence or absence of adult conspecifics seems to have a significant effect on settlement of the 3 species. Similar relationships have been described for other tropical and temperate fishes in which habitat characteristics influence settlement (Sale et al. 1984, Doherty 1993, Levin 1991, Williams 1991). Some authors have analyzed the relationship between the density of new settlers and some substratum variables, finding different patterns. Marli- ave (1977) found that newly settling littoral fishes (e.g. Artedius lateralis, Lepisostus armatus) show substratum preferences based on tactile cues and light transmission. Carr (1991, 1994) demonstrated that spatial and temporal variation in the density of the giant kelp Macrocystis pyrifera explained much of the variation in the recruitment of Paralabrax clathratus as well as in other rockfish species. Macpherson (1998) found

<table>
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<th>MS</th>
<th>F</th>
<th>p</th>
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that settlers belonging to 3 species of the genus Diplo-
dus showed a clear preference for specific habitats.
A range of effects of adult conspecifics have been
demonstrated, either a facilitation (Forrester 1990),
inhibition (Shulman 1985, Tupper & Hunte 1994) or no
effect on settlement (Doherty 1983, Sweetman 1985,
that resident conspecifics of Tautogolabrus adspersus
did not affect small-scale variability in recruitment,
where recruitment was higher in areas with dense
understorey of foliace and filamentous algae than in
substrates covered by crustose algae. For this species,
algae cover was an important predictor of variability in
recruit abundance in one region, but not in others
(Levin et al. 1997). Booth (1992) found that juveniles of
Dascyllus abeiola do not interact with adults, being
conspecific juvenile density a major factor influencing
settlement. The presence of conspecifics reduced set-

![Fig. 4. Maximum density (mean per transplant and m² ± SE) of settlers for (A) Abulablennius spixii, (B) Parablennius incogni-
tis, and (C) Triportheus tetrapteronus observed per locality and per year. The maximum density is taken as an estimate of
settlement success. Note that y-axes vary for the 3 species.](image)

![Fig. 5. Density (mean per transplant and m² ± SE) of recruits for (A) Abulablennius spixii, (B) Parablennius incognitus, and
(C) Triportheus tetrapteronus observed at the end of the set-
tlement season per locality and per year. Note that y-axes vary for the 3 species.](image)

tlement in Stopesastes planifrons, but the percent cover of
corals can affect significantly settlement dynamics
(Tolimieri 1995).

Microhabitat choice at settlement of the 3 species
matched quite well the pattern of adult conspecific dis-
tribution. Therefore, the substrate selection could confer
a greater fitness in preferred microhabitat, as has been
observed in Stopesastes planifrons, S. leucostictus and
S. variabilis from the Caribbean Sea (Wellington 1992,
Tolimieri 1995). Settlers of the 3 benthic species showed
similar behaviour as adults (Lender 1996, Abel 1993),
remaining in the same type of habitats. Similar behav-
ior patterns were observed by other authors in littoral
species (Marlase 1977). The overlap between adult and
settler distributions for the 3 species suggests that the
selected habitat at settlement can provide some ad-
vantages for the species, for example, protection and food.
Several authors (Levin 1993, Tullis et al. 1995) suggested that for species where adults and juveniles shared the same habitats, their co-occurrence indicated suitable zones for an adequate development. Consequently, differences in the adult abundances can be attributed to different settlement (Fowler et al. 1992, Risk 1997). In the present study, the relationship between settlers, recruits, and adult distributions has not been evaluated as it has in other studies (e.g. Wellington 1992) and further studies with more detail need to be done. Gibson (1993) emphasised that future studies should be conducted on settlement distribution patterns, analyzing if the patterns are the result of an initial choice by larvae or if preferred substrate is chosen after random settlement, or if it simply results from an elimination of individuals from unfavourable habitats (also see Connell & Jones 1991).

For the 3 blemoids studied here, preferences for a specific substratum type at settlement can explain, on the small scale, the abundance of new settlers in a locality. This abundance will be related to the availability of habitat suitable for the species and, additionally, will be independent of the rocky reef size. Similar results have been provided by other authors in coral reef fishes (Williams 1991, Fowler et al. 1992, Tullis et al. 1995, Risk 1997). Although the variations in habitat can explain much of the variation in settlement success and recruitment (Carr 1994), some important considerations should be taken into account in order to understand the variability on different spatial and temporal scales. The amount of suitable habitat accounts for some of the variation in settlement success, thus, the large varia-

**Fig. 6. Relationship between settlement success and suitable habitat available per transect for (A) Addinellus sphyrae, (B) Parabalanus inconspitus, and (C) Trachypagyri tripus.** For *A. sphyrae* and *P. inconspitus* all years and transects are shown, while for *T. tripus* only 1997 is shown for all transects (see Results for further explanations). Note that *x* and *y*-axes vary for the 3 species.

**Fig. 7. Relationship between settlers standardized by the area of suitable habitat and the amount of suitable habitat available per transect for (A) Addinellus sphyrae, (B) Parabalanus inconspitus, and (C) Trachypagyri tripus.** For *A. sphyrae* and *P. inconspitus* all years and transects are shown, while for *T. tripus* only 1997 is shown for all transects (see text for further explanations). Note that *x* and *y*-axes vary for the 3 species.
ility observed in maximum settler density for the 3 benthos suggests that, additionally, other processes are influencing settlement and later recruitment.

Numerous authors have emphasized the importance of analyzing the relationships between settlement, recruitment, and habitat availability at different scales, in order to know how well patterns exhibited at small scales explain patterns observed at larger scales (Doberty 1991, Calle et al. 1996). This analysis is a central topic in ecological studies to determine the mechanisms influencing population dynamics of any species (Dayton & Tegner 1984, Levin 1988). Unfortunately, comparisons of different spatial and temporal scales are rarely done in studies of fishes and invertebrates. Fowler et al. (1962), working on recruits of Chaetodentex naidartii at different spatial scales (from regions separated by hundreds of km at different sites on a coral reef), found that the distribution patterns of recruitment was consistent each year, and several regions always had higher recruitment rates than others. Tolturni (1993) showed that mobile blacktip choice had consequences on the small-scale recruitment patterns of Stegastes planifrons, but not on the large-scale variation. Levin et al. (1997) found that the variation in the densities of newly recruited individuals of Tacto gouldi adnulator was pronounced among areas (separated by 100 to 1000 m) and among localities (separated by ca 10 km), but this pattern was not geographically homogeneous but distinct to geographic regions. Vignola et al. (1998) observed that for 3 species of Diplodus at a large scale (ca 1000 km of coast line) the spatial variability of settlement was higher than the temporal variability, whereas on small scale, within localities, the temporal variability was higher. Settlement success patterns of Acanthistius spiny and Parabopsis insitus did not differ between the 3 localities situated along 150 km coast line and separated ca 50 km from each other. Furthermore, the settlement success did not show any significant differences among years. These results would suggest that processes affecting settlement success at small scale did not differ from patterns observed at larger scales. Tripethygon tripterorontus, however, showed temporal and spatial differences.

These different patterns could be driven by processes occurring at different stages in the life of fishes, during pre-settlement or at any time during and after settlement. The importance of pre-settlement versus post-settlement processes in determining year-class strength has been widely discussed. Larval supply to a locality is thought to be a major cause of variability in settlement success of fishes (Victor 1991) and it has been considered a primary factor in the population dynamics of many fish communities (Sale 1982, Doberty 1991, Ciubetan 1996). Larvae of Acanthistius spiny and Parabopsis insitus have a distribution pattern clearly different than the one observed in Tripethygon tripterorontus. Larvae of the former species are distributed offshore, on the continental shelf and slope (Saboas 1994), whereas larvae of T. tripterorontus are as in most Tripethygon (Bogun 1994, Leis 1994), located inshore, between the coastline and 100 to 200 m offshore (Saboas pers. comm.). These differences in larval distributions, could explain, at least partially, differences observed in the pattern of settlement success. Species situated on the continental shelf are influenced by mesoscale processes, as observed in other Mediterranean species, i.e. Diplodus sargus (Vignola et al. 1998), which would result in a more homogenous spatial pattern of settlement. On the other hand, settlement of T. tripterorontus, could be more dependent on microscale processes, quite common in the tortuous coast of the NW Mediterranean (Ros et al. 1985), and on local oceanographic events, e.g. currents, storms, waves (Kingsford & Chast 1989, Breitburg et al. 1995, Jenkins et al. 1997). The relationship between larval and settlement distributions has been analysed by several authors (see the abovementioned references) for different areas, however, the above stated hypotheses need to be investigated further and the relevant physical oceanographic processes influencing settlement on this coast determined.

The differences observed between spatial and temporal variability in settlement success and recruitment levels for each benthosic species calls the attention to the interpretation of the results. Differences between settlement and recruitment patterns can mask a more complete view of the importance of post-settlement processes and the necessity for further research. The highest significant differences (yearly variability in Tripethygon tripterorontus) were reflected in both settlement and recruitment patterns, which suggests that the interannual differences are very strong and are maintained through the post-settlement period. The minor differences of settlement success between localities for this species, however, were not maintained over the seasons. On the other hand, for Acanthistius spiny, temporal and spatial differences were not found significant for settlement success but were significant for recruitment level. For Parabopsis insitus no significant differences were found for settlement success, but a significant spatial variation in recruitment level was observed. Although correlations between settlement success and recruitment are highly significant (by the order of magnitude), the results from the ANOVA (based on variance between means) demonstrate that post-settlement processes can alter patterns of settlement and therefore, are able to change spatial and/or temporal recruitment patterns. The period following settlement...


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