Marine Biology (1995) 124: 35–42

A. García-Rubies · E. Macpherson

Substrate use and temporal pattern of recruitment in juvenile fishes of the Mediterranean littoral

Received: 31 March 1995/Accepted: 12 May 1995

Abstract The microhabitat use and seasonality of the juveniles of 24 littoral species in the north-west Mediterranean Sea were studied between March 1993 and March 1994. Labrids species recruit during summer months, from July to September, whereas sparids recruit at different times of the year. Canonical correspondence analysis revealed that the species recruit in well-defined habitats. Sparid species recruit primarily in the shallowest zone (0 to 2 m), and most of them prefer varied bottoms (sand, gravel or small blocks). Some species of the genus *Diplodus* have similar habitat requirements, but show a clear seasonal segregation, with each species occupying successively the same zones at a different time of the year. Labrid species show a high degree of seasonal and spatial co-occurrence, and are normally found on rocky substrates with high algal cover. Two species (*Mullus surmuletus* and *Symphodus cinereus*) recruit mainly in *Posidonia oceanica* beds, while other species (*Serranus cabrilla*, *Coris julis*, *Symphodus ocellatus*, *S. rostratus*), are abundant in both seagrass beds and on rocky substrates.

Introduction

Most littoral fishes undergo a profound transformation during development, from a pelagic larval phase to a benthic phase at the time of recruitment. Since it determines the number of individuals that recruit to the adult population and thus affects community structure, this transformation plays a significant role in population dynamics (Victor 1986; Sale 1991; Doherty and Fowler 1994).

In recent years, considerable work has focused on the determining factors affecting fish recruitment and on the influence of a variety of factors (e.g. microhabitat, density of the adult population, predation, competition, prey availability) on the density of young individuals recruiting to the adult population (Jones 1984, 1991; Sale et al. 1984; Shulman 1985; Sweatman 1985; Victor 1986; Forrester 1990; Robertson 1990; Doherty 1991; Booth 1992). Substrate type is one of the main factors involved in this process (e.g. Williams and Sale 1981; Sale et al. 1984; Shulman 1984; Carr 1991; Levin 1991), and it affects the abundance, mortality, and growth rate of recruits (Connell and Jones 1991).

Most work has been carried out off Australia and New Zealand and in the Caribbean Sea, with only a very few studies being made in other regions. Despite the importance of recruitment processes in the littoral zone in the Mediterranean Sea, research has centered on adult fish communities (e.g. Bell and Harmelin-Vivien 1982; Bell 1983; Harmelin 1987; García-Rubies and Zavala 1990; Illich and Kotrschal 1990; Macpherson 1994) or on their larval phases (Sabatés 1990). Only recently was a study on the habitat of recruits of certain species of sparids published (Harmelin-Vivien et al. 1995).

The object of the present study was to analyse the characteristics of the habitat used by the juveniles of the main littoral species in the north-west Mediterranean Sea at the time of recruitment, and the temporal distribution of recruitment over the course of the year.

Materials and methods

The study was conducted in the Medes Islands protected area, and along the shore at l'Estartit and Blanes (north-west Mediterranean, Fig. 1). Observations were made between March 1993 and March

---

Communicated by A. Rodríguez, Puerto Real

A. García-Rubies
Instituto de Ciencias del Mar (CSIC), Passeig Juan de Borbó, s/n, E-08039 Barcelona, Spain

E. Macpherson (✉)
Centro de Estudios Avanzados de Blanes (CSIC),
Cami de Santa Bárbara s/n, E-17300 Blanes, Girona, Spain

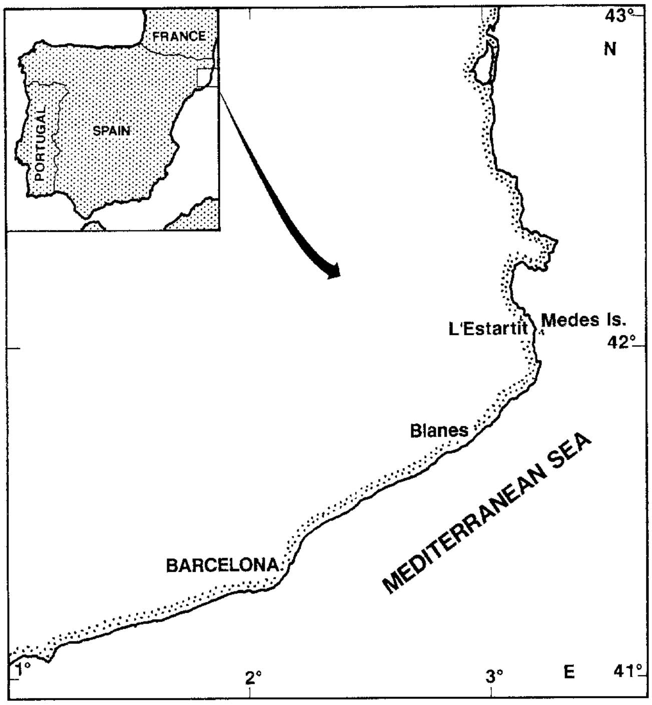


Fig. 1 Study area and location of sampling localities

1994 at depths of 0 to 30 m. Data were collected by SCUBA diving or by snorkelling in shallow water (< 1 m) . The study area was visited regularly by two observers four to eight times each month to detect seasonal effects on recruitment. In all, 102 dives were carried out, covering a total of 150 h observation.

Bottom type is highly diverse in the study area, and includes most of the common types of substrates present in the north-west Mediterranean, comprising sand, gravel, rocky areas and *Posidonia oceanica* beds (Ros et al. 1984; García-Rubies and Zavala 1990).

The smallest specimens of the species observed were taken as recruits. Recruits were generally smaller than 1.5 cm, except in the case of *Mullus surmuletus*, *Labrus merula*, and *L. viridis*, which were slightly larger, suggesting that recruitment in these species took place shortly before the observation time.

On each dive, the observer swam slowly above the bottom until one or more recruits were sighted. A 1 × 1 m PVC frame was then deployed, taking the position of the recruit(s) as the centre. Species, number of individuals, and their estimated size were recorded. The habitat parameters recorded for each frame were depth, substrate type, and slope. Substrate type was expressed as percentage coverage of the total surface area, according to the following categories: sand/gravel (< 1 cm diam), pebbles (< 1 to 10 cm), small blocks (< 10 to 30 cm), medium blocks (< 30 cm to 1 m), large blocks (> 1 m diam). Smoothness of the rock, i.e., the presence or absence of discernible discontinuities, such as caves or holes, was taken as a qualitative variable. Coverage by algae and the sea grass *Posidonia oceanica* was also recorded according to four categories of percentage coverage: 0 to 10%, 11 to 25%, 26 to 50%, and > 50%. Algae were assigned to one of four size classes in height (0 to 5 cm, 6 to 10 cm, 11 to 15 cm, and > 15 cm). The slope was recorded as gentle (0 to 15°), pronounced (16 to 30°), steep (31 to 60°), very steep (61 to 90°), and overhang (> 90°). In all, 465 frames with recruits of one or more species were observed.

Two data matrices (samples – species and samples – habitat parameters) were constructed from the biological data (species and number of individuals) and habitat features. Canonical correspondence analysis (CCA), which has been shown to be one of the most robust and most suitable methods for relating environmental variables to species abundance (Ter Braak 1986; Palmer 1993), was applied to the matrices.

Finally, the existence of possible interspecific aggregation or segregation effects was considered by applying two-by-two contingency tables to the data on the presence and absence of recruits of each species in each frame (Pielou 1969).

Results

Recruits were recorded for 24 species (Table 1). *Serranus cabrilla*, *Diplodus vulgaris* and *Coris julis* were the species present in the largest number of sampling frames. *D. cervinus*, *Labrus viridis* and *Symphodus doderleini* were the least frequent species. *Oblada melanura* and *Sarpa salpa* had the highest densities per frame (> 30 individuals m^{-2}); *Serranus cabrilla*, *D. cervinus*, *L. bimaculatus*, *L. merula*, *L. viridis* and *Symphodus doderleini* had the lowest densities (1 individuals m^{-2}) (Table 1). As mentioned in "Materials and methods" the recruits of certain species (*Mullus surmuletus*, *L. merula* and *L. viridis*) were first observed at sizes slightly larger than 1.5 cm, which suggests that recruitment took place sometime before the observations were made. Other species (*D. annularis* and *Spondyliosoma cantharus*) were observed only in *Posidonia oceanica* beds and have not been included in the study because of low frequency of occurrence.

Several species (*Diplodus sargus*, *Oblada melanura*, *Chromis chromis*, *Coris julis*, *Symphodus tinca* and *Thalassoma pavo*) tended to form single-species shoals, but no species exclusion was apparent, and up to five different species might coexist in a single frame.

Seasonality

Most species studied recruit during the summer months, from July to September (Fig. 2). The recruitment period for sparids was protracted, starting in October and running until July/August of the following year. *Diplodus puntazzo* recruited in October to the beginning of November, while recruitment in *D. vulgaris* and *Sarpa salpa* started at the beginning of November. *D. puntazzo* had a single, well-defined recruitment period, whereas *D. vulgaris* employed a strategy of intermittent recruitment, with two distinct peaks, one at the beginning of November and another in March/April. The recruitment pattern for *S. salpa* was similar to that of the preceding species, with a second recruitment peak in spring (end of May), although this was much less intense than the first peak. Mass recruitment of *D. sargus* occurred between the end of May and the end of June, with a very distinct peak at the beginning of June. *Oblada melanura* also followed a strategy of intermittent recruitment from the beginning of July to mid-August, with a peak at the beginning of August. *Lithognathus mormyrus* recruited from the end of July

Table 1 Average density (*Avg*, individuals m^{-2}) and standard deviation (*SD*) of recruits of each species by plot. Only plots where species was present (*N*) were considered

Species	Avg	SD	(*N*)
Serranidae			
Serranus cabrilla (Linnaeus, 1758)	1.07	0.25	(59)
Mullidae			
Mullus surmuletus Linnaeus, 1758	6.17	4.66	(6)
Sparidae			
Diplodus cervinus (Lowe, 1838)	1.00	0.00	(2)
Diplodus puntazzo (Gmelin, 1789)	2.88	3.25	(52)
Diplodus sargus (Linnaeus, 1758)	9.79	5.88	(33)
Diplodus vulgaris (Saint-Hilaire, 1817)	14.47	17.73	(62)
Lithognathus mormyrus (Linnaeus, 1758)	3.70	1.57	(10)
Oblada melanura (Linnaeus, 1758)	31.03	18.90	(30)
Sarpa salpa (Linnaeus, 1758)	100.82	97.66	(11)
Pomacentridae			
Chromis chromis (Linnaeus, 1758)	10.54	11.53	(13)
Labridae			
Coris julis (Linnaeus, 1758)	12.71	15.66	(84)
Ctenolabrus rupestris (Linnaeus, 1758)	1.13	0.34	(16)
Labrus bimaculatus Linnaeus, 1758	1.00	0.00	(4)
Labrus merula Linnaeus, 1758	1.00	0.00	(4)
Labrus viridis Linnaeus, 1758	1.00	0.00	(3)
Symphodus cinereus (Bonnaterre, 1788)	1.46	0.69	(37)
Symphodus doderleini Jordan, 1891	1.00	0.00	(3)
Symphodus mediterraneus (Linnaeus, 1758)	1.90	1.26	(40)
Symphodus melanocercus (Risso, 1810)	2.33	1.95	(40)
Symphodus ocellatus (Forsskal, 1775)	7.68	6.57	(22)
Symphodus roissali (Risso, 1810)	1.40	0.87	(25)
Symphodus rostratus (Bloch, 1797)	1.26	0.75	(23)
Symphodus tinca (Linnaeus, 1758)	4.27	3.20	(45)
Thalassoma pavo (Linnaeus, 1758)	2.42	2.14	(26)

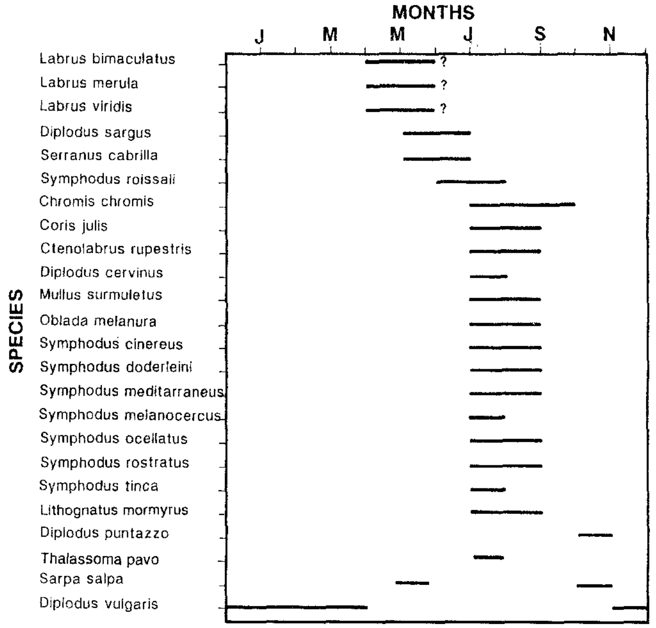


Fig. 2 Seasonality of recruitment. Bars indicate months when new recruits (0.5 to 1.5 cm) were observed (see "Results – Seasonality" for more detailed description of the patterns). First three species (*marked* ?), were slightly larger than 1.5 cm and were probably recruited earlier

to August, and recruitment of the least-abundant species, *D. cervinus*, appeared to take place at the same time. However, because of the small number of recruits observed, it would be premature to assert that recruitment in this species takes place during a single, well-defined period.

Labrids recruited mainly between July and September, with a pronounced peak between the end of July and the beginning of August (Fig. 2). Except for *Labrus bimaculatus*, *L. merula* and *L. viridis* for which recently settled recruits were not observed, mass recruitment in the labrids started in June (*Symphodus roissali*) and July (*S. melanocercus* and *S. tinca*) and continued through August (*Coris julis*, *Ctenolabrus rupestris*, *S. cinereus*, *S. doderleini*, *S. mediterraneus*, *S. ocellatus* and *S. rostratus*). The last labrid to undergo recruitment was *Thalassoma pavo* at the end of August and beginning of September. Of the species belonging to other families, *Serranus cabrilla* (Serranidae) recruited between May and June and *Chromis chromis* (Pomacentridae) recruited in a series of batches from the end of July to the beginning of September.

Substrate use

Fig. 3 is a canonical plot for all species. The first two axes explained 34 and 30% of the variance, respectively, and the correlation between the species and environmental parameter matrices for each axis was 0.93 and 0.89, respectively. The first axis of the classification was

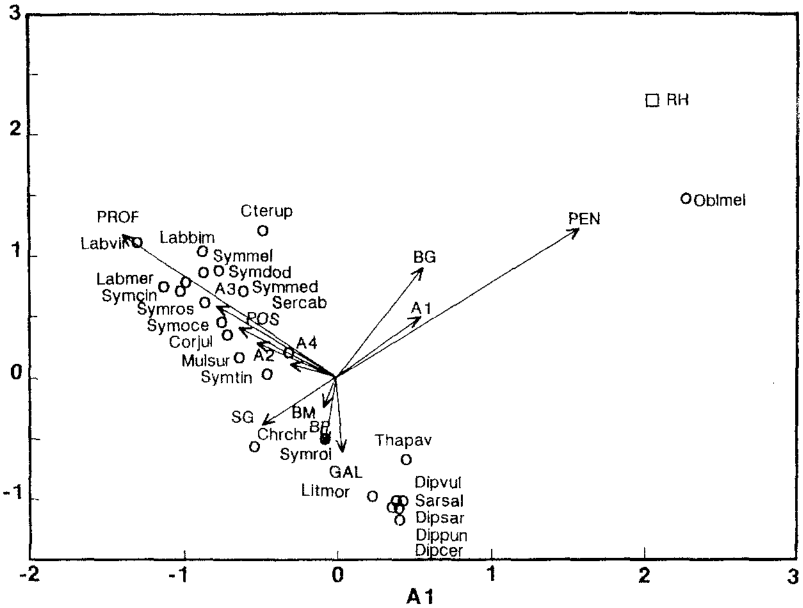


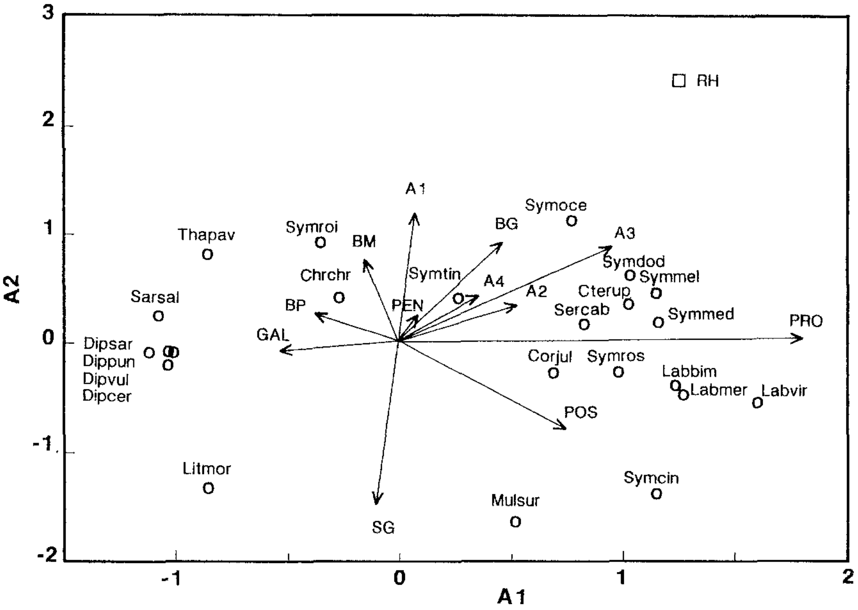
Fig. 3 Canonical correspondence analysis (CCA) ordination diagram for all species (*Chrchr*, *Chromis chromis*; *Corjul*, *Coris julis*; *Cterup*, *Ctenolabrus rupestris*; *Dipcer*, *Diplodus cervinus*; *Dippun*, *Diplodus puntazzo*; *Dipsar*, *Diplodus sargus*; *Dipvul*, *Diplodus vulgaris*; *Labbim*, *Labrus bimaculatus*; *Labmer*, *Labrus merula*; *Labvir*, *Labrus viridis*; *Litmor*, *Lithognathus mormyrus*; *Mulsur*, *Mullus surmuletus*; *Oblmel*, *Oblada melanura*; *Sarsal*, *Sarpa salpa*; *Sercab*, *Serranus cabrilla*; *Symcin*, *Symphodus cinereus*; *Symdod*, *Symphodus doderleini*; *Symmed*, *Symphodus mediterraneus*; *Symmel*, *Symphodus melanocercus*; *Symoce*, *Symphodus ocellatus*; *Symros*, *Symphodus rostratus*; *Symroi*, *Symphodus roissali*; *Symtin*, *Symphodus tinca*; *Thapav*, *Thalassoma pavo*). Environmental variables were: *A*(algae)*1* algae of 0 to 5 cm; *A2* 6 to 10 cm; *A3* 11 to 15 cm; *A4* > 15 cm; *SG* sand/gravel (< 1 cm diam); *GAL* pebbles (< 1 to 10 cm); *BP* small blocks (< 10 to 30 cm); *BM* medium blocks (< 30 cm to 1 m) ; *BG* large blocks (> 1 m diam); *PEN* slope; *POS*, *Posidonia oceanica* beds; *PRO* depth; *RH* rock without discontinuities (considered as qualitative variable)

clearly correlated with substrate slope. This parameter was closely associated with the large rocky blocks without apparent discontinuities (smooth rock) covered by encrusting or small algae. The second axis was correlated mainly with depth, and species were classified according to their depth distributions. Three species groupings were apparent: a strictly shallow-water group comprising all the sparids and *Thalassoma pavo*; an intermediate group consisting of *Chromis chromis* and *Symphodus roissali*; and a deeper-dwelling group consisting of the rest of the species observed. The first axis fully characterized the habitat of *Oblada melanura*, which was thus isolated from the rest of the species in the shallow-water group. *C. chromis* and *S. roissali* exhibited an intermediate depth distribution distinct from both the strictly shallow-water group and the less well-defined group of species with relatively deeper depth distributions.

In view of the clearly predominant effect of substrate slope on the first axis in the classification, a second classification was carried out excluding *Oblada melanura*. The second and third axes in the first classification then became the first and second axes in the second classification (Fig. 4). The first axis, related to depth, explained 44% of the variance, with a correlation between the species and the environmental parameter of 0.91. The second axis explained 16% of the variance, and the correlation between the species and the environmental parameter, in this case sandy or gravel substrate type, was 0.61. Plotting the species on the vectors for the environmental parameters revealed the association between the species and substrate type.

For the strictly shallow-water species. *Lithognathus mormyrus* was associated with sandy bottoms and *Thalassoma pavo* was associated mainly with rocky bottoms with a predominance of small and medium blocks. *Diplodus cervinus*, *D. puntazzo*, *D. sargus*, *D. vulgaris*, and *Sarpa salpa* all shared a similar preference for a substrate consisting primarily of pebbles, but also recruited to substrates of sand or gravel and small or medium blocks. *Symphodus roissali* and *Chromis chromis* exhibited an intermediate depth distribution (mainly 0.5 to 15 m) between the strictly shallow-water species and the deeper-dwelling species, and were clearly associated with small or medium rocky blocks; these species avoided sandy bottoms. Of the deeper-dwelling species, *Mullus surmuletus* and *S. cinereus* occupied bottoms consisting of a large proportion of sand, and the latter species was also clearly correlated with *Posidonia oceanica* beds. The remainder of the species exhibited an affinity mainly for rocky bottoms. *S. tinca* was closely correlated with large, arborescent algae, partly because this species was closely associated with areas where uprooted algae were washed by wave action, such as clearings at the upper edge of *P. oceanica* beds. In contrast, *S. ocellatus* was associated with algal cover on large rocky blocks at a certain depth (mainly

Fig. 4 CCA ordination diagram for all species excluding *Oblada melanura* (*Abbreviations* as in Fig. 3)



5 to 15 m). *Ctenolabrus rupestris*, *S. doderleini* and *S. melanocercus* were also associated with large blocks substantially covered by arborescent algae. Although *Labrus merula*, *L. viridis* and *S. rostratus*, were characteristic species on rocky bottoms, they also exhibited a certain affinity for isolated clumps of *P. oceanica* and sand.

Fig. 5 shows the mean depth distributions for the species considered in this study as a function of their vertical abundance. Sparids were mainly found between 0 and 5 m, whereas labrids preferred deeper waters, mainly between 10 and 20 m.

Co-occurrence of species

A total of 13 statistically significant associations ($p < 0.05$) were observed between the species considered (Table 2). Most co-occurrences were between species within the family Labridae. The main associations between species of other families were *Diplodus puntazzo* with *D. vulgaris* (Sparidae), and *Serranus cabrilla* (Serranidae) with *Symphodus melanocercus* and *Ctenolabrus rupestris* (Labridae).

The low rates of co-occurrence in the recruitment of species with requirements for similar habitats (e.g. *Diplodus sargus* with *D. puntazzo* and *D. vulgaris*) were the result of seasonal differences in the time of recruitment.

The low level of co-occurrence between most species was mainly attributable to differences in habitat use. Aggregations between the species with relatively deep depth distributions (> 5 m) generally involved associations between infrequently recorded labrid species. The most obvious case was the recruits of *Labrus merula*, a species that was positively associated with *Serranus cabrilla*, *Symphodus mediterraneus*, and *S. rostratus*, all of which species were grouped relatively closely together on the first two axes of the canonical classification. These results suggest that these species were not associated with just a single or a few substrate types, but rather with areas with a diverse range of substrate types. Positive associations between *Serranus cabrilla* and *Symphodus melanocercus*, and between *Symphodus mediterraneus* and *S. melanocercus* had a similar explanation (Table 2).

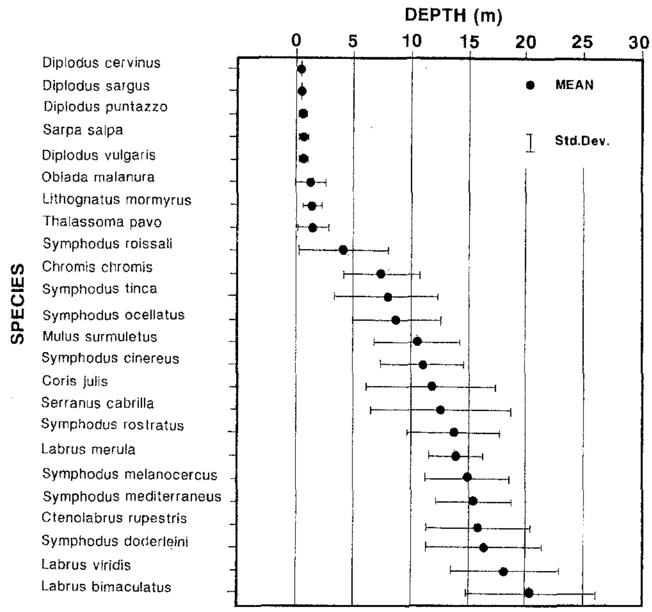


Fig. 5 Mean depth distribution ($\bar{x} \pm$ SD) of recruits of the various species

Table 2 Species pairs for which co-occurrence was significatively positive using two-way contingency tables for presence and absence of species in each m^{-2} plot. Only species present in more than ten $1\ m^{-2}$ plots were considered

Species pair	*p*
Coris julis – Chromis chromis	0.021
Coris julis – Symphodus melanocercus	0.0005
Coris julis – Ctenolabrus rupestris	0.013
Chromis chromis – Serranus cabrilla	0.007
Chromis chromis – Ctenolabrus rupestris	0.032
Diplodus puntazzo – Diplodus vulgaris	< 0.001
Serranus cabrilla – Symphodus melanocercus	0.0001
Serranus cabrilla – Ctenolabrus rupestris	0.0058
Symphodus cinereus – Symphodus tinca	< 0.0001
Symphodus roissali – Symphodus tinca	< 0.0001
Symphodus mediterraneus – Symphodus melanocercus	< 0.0001
Symphodus mediterraneus – Symphodus roissali	< 0.0001
Symphodus melanocercus – Symphodus tinca	0.008

Discussion

The juveniles of each of the 24 littoral species studied in the north-west Mediterranean Sea recruit to well-defined habitats with characteristically distinctive substrate types. As for the adult populations (Bell 1983; García-Rubies 1995), depth was one of the main factors regulating the distribution of recruits. The members of the family Sparidae recruited primarily in the shallowest zone (0 to 2 m), normally in areas sheltered from the prevailing winds. Although the habitat requirements for *Oblada melanura* are quite narrow (smooth rock and a strong slope) and *Lithognathus mormyrus* requires bottoms consisting exclusively of sand or gravel, the remaining species (*Diplodus cervinus, D. puntazzo, D. sargus, D. vulgaris,* and *Sarpa salpa*) all prefer varied bottoms consisting of sand, gravel, or small blocks. These results are in agreement with the findings of Harmelin-Vivien et al. (1995) in the Marseille region. Segregation of these species, all of which shared quite similar habitat requirements, was basically seasonal. Except *D. cervinus* and *D. sargus*, which both recruit at the end of spring, each of the remaining species recruits to the bottom at different times of year, with each species occupying zones previously occupied by another species some time before. This temporal staggering of recruitment may be a mechanism for reducing possible interspecific competition, as has been observed in other fish communities (Doherty 1991). Recruits are to some extent separated from adults on the basis of depth, with the adults occupying a much broader depth range than juveniles of the same species (García-Rubies 1995; Harmelin-Vivien et al. 1995). The other species present in the shallowest zone (*Symphodus roissali, S. tinca, Chromis chromis,* and *Thalassoma pavo*) were segregated from the sparids on the basis of depth by occupying a slightly deeper range (1 to 5 m). In these species, segregation of juveniles from adults was minimal, with the latter occupying a somewhat broader depth range (Harmelin 1987; García-Rubies 1995). *C. chromis* is the only species that exhibited a variable distribution pattern within the water column; the adults are planktivores (Bell and Harmelin-Vivien 1983) that shoal throughout the water column (Harmelin 1987), whereas the juveniles form dense aggregations on rocky bottoms.

There may be several different explanations for the shallow distribution of recruits. Different workers have reported that prey abundance (Jones 1986; Forrester 1990), predation (Doherty and Sale 1985), and the presence of adult conspecifics (Doherty 1982; Sweatman 1985; Victor 1986; Jones 1987) may exert a positive or negative influence on the distribution and abundance of recruits. The shallow distribution of several species of sparids may be interpreted as a sheltering beaviour from possible predators, because predator manoeuvrability may be hampered in shallow water. Nevertheless, the capture of juveniles by various predators [e.g. *Serranus cabrilla, Dicentrarchus labrax,* and *Gobius cobitis* (authors' personal observations)] was noted with some frequency over the observation period. In addition, higher prey-capturability rates may also influence the distribution of juveniles. The littoral zone is affected by wave action, and the high level of turbulence thereby generated in that zone increases encounters between predators and prey (Rothschild and Osborn 1988), as has been reported for copepods (Saiz et al. 1992) and fish larvae (MacKenzie and Leggett 1991). This would afford juveniles certain advantages, in that they could find food more readily than at deeper depths.

The distribution pattern for recruits between 5 and 30 m was on the whole more uniform, and in no case was it as marked by preference for a given substrate type as the distribution pattern of species in the shallow zone. Furthermore, the species present in this zone exhibited a high degree of overlap during the recruitment period (summer) and a high level of spatial co-occurrence, particularly in the case of the labrids. Except for *Coris julis*, which preferred sandy bottoms and tended to form single-species aggregations of recruits, the remaining labrid species were normally found on substrates with high algal cover. The distribution of the recruits of *C. julis* was a result of this species' burrowing behaviour on sandy bottoms at night (Lejeune 1987). The distribution of labrid recruits overlapped with the adult distribution range (García-Rubies 1995), as reported earlier by Sayer et al. (1993) for *Ctenolabrus rupestris* off Scotland. The high overlap between the distributions of adults and juveniles, and the association of both adults and juveniles with substrates bearing algal cover, used by adults to build their nests (Lejeune 1984) and for foraging (Bell and Harmelin-Vivien 1983), suggests that algal cover may be a determining factor affecting the abundance of most of these labrid species, as has been observed in other communities of fishes associated with algae (Jones 1984; Carr 1994).

Other workers have made reference to the important role of sea-grass beds in littoral fish recruitment (Bell et al. 1987). *Posidonia oceanica* beds were the exclusive habitat of only two species, *Mullus surmuletus* and *Symphodus cinereus*. Harmelin et al. (1995) reported that *Diplodus annularis* also recruited specifically to beds of that same sea grass. Other species, e.g. *Serranus cabrilla*, *Coris julis*, *Symphodus ocellatus* and *S. rostratus*, likewise recruited to that habitat, but these species were also abundant on rocky substrates. The small number of species recruiting exclusively to *P. oceanica* beds in the present study indicates that the substrate is not a determining habitat for recruitment of juveniles of the species considered. Rocky substrates accounted for recruitment of the largest number of species.

The results of the present study provide a basis for establishing the seasonal and spatial patterns of recruitment in various Mediterranean littoral fish species. Nevertheless, further work is needed to elucidate what additional aspects may influence the distribution and abundance of juveniles. Such information would be a major step forward in our understanding of the structure and dynamics of littoral fish communities.

Acknowledgements We thank to E. Salas and M. Zavala for their assistance in collecting data. The manuscript benefit from input from R. Sacks. This research was funded by European Commission (DG XIV, MED/92/007).

References

Bell JD (1983) Effects of depth and marine reserve fishing restrictions on the structure of a rocky reef fish assemblage in the North-Western Mediterranean Sea. J appl Ecol 20: 357–369

Bell JD, Harmelin-Vivien ML (1982) Fish fauna of French Mediterranean *Posidonia oceanica* seagrass meadows. 1. Community structure. Téthys 10: 337–347

Bell JD, Harmelin-Vivien ML (1983) Fish fauna of French Mediterranean *Posidonia oceanica* seagrass meadows. 2. Feeding habits. Téthys 11: 1–14

Bell JD, Westoby M, Steffe AS (1987) Fish larvae settling in seagrass: do they discriminate between beds of different leaf density?. J exp mar Biol Ecol 111: 133–144

Booth DJ (1992) Larval settlement patterns and preferences by domino damselfish *Dascyllus albisella*. J exp mar Biol Ecol 155: 85–104

Carr MH (1991) Habitat selection and recruitment of an assemblage of temperate zone reef fishes. J exp mar Biol Ecol 146: 113–137

Carr MH (1994) Effects of macroalgal dynamics on recruitment of a temperate reef fish. Ecology 75: 1320–1333

Connell SD, Jones GP (1991) The influence of habitat complexity on postrecruitment processes in a temperate reef fish population. J exp mar Biol Ecol 151: 271–294

Doherty PJ (1982) Some effects of density on the juveniles of two species of tropical, territorial damselfishes. J exp mar Biol Ecol 65: 249–261

Doherty PJ (1991) Spatial and temperature patterns in recruitment. In: Sale PF (ed) The ecology of fishes on coral reefs. Academic Press, London, pp 261–292

Doherty PJ, Fowler T (1994) An empirical test of recruitment limitation in a coral reef fish. Science, NY 263: 935–939

Doherty PJ, Sale PF (1985) Predation on juvenile coral reef fishes: an exclusion experiment. Coral Reefs 4: 225–234

Forrester GE (1990) Factors influencing the juvenile demography of a coral reef fish population. Ecology 71: 1666–1681

García-Rubies A (1995) Poblacions de peixos litorals sobre substrat rocos. Factors que influexen la seva distribució. Ph. D. thesis. University of Barcelona

García-Rubiés A, Zavala M (1990) Effects of total fishing prohibition on the rocky fish assemblages of Medes island marine reserve (NW Mediterranean). Scientia mar 54: 317–328

Harmelin JG (1987) Structure et variabilité de l'ichtyofaune d'une zone rocheuse protégée en Méditerranée (Parc national de Port-Cros, France). Pubbl Staz zool Napoli (I: Mar Ecol) 8: 263–284

Harmelin-Vivien ML, Harmelin JG, Leboulleux V (1995) Microhabitat requirements for settlement of juvenile sparid fishes on Mediterranean rocky shores. Hydrobiologia 301: 309–320

Illich IP, Kotrschal K (1990) Depth distribution and abundance of northern Adriatic littoral rocky reef blennioid fishes (Blenniidae and *Tripterygion*). Pubbl Staz zool Napoli (I: Mar Ecol) 11: 277–289

Jones GP (1984) Population ecology of the temperate reef fish *Pseudolabrus celidotus* Bloch & Schneider (Pisces: Labridae). I. Factors influencing recruitment. J exp mar Biol Ecol 75: 257–276

Jones GP (1986) Food availability affects growth in a coral reef fish. Oecologia 70: 136–139

Jones GP (1987) Some interactions between residents and recruits in two coral reef fishes. J exp mar Biol Ecol 114: 169–182

Jones GP (1991) Postrecruitment processes in the ecology of coral reef fish populations: a multifactorial perspective. In: Sale, PF (ed) The ecology of fishes on coral reefs. Academic Press, London, pp 294–327

Lejeune P (1984) Etude écoethologique des comportements reproducteurs et sociaux des Labridae Mediterranéens des genres *Symphodus* Rafinesque, 1810 et *Coris* Lacepéde, 1802. Ph. D. thesis. University of Liege

Lejeune P (1987) The effect of local stock density on social behavior and sex change in the Mediterranean labrid *Coris julis*. Envir Biol Fish 18: 135–141

Levin PS (1991) Effects of microhabitat on recruitment variation in a Gulf of Maine reef fish. Mar Ecol Prog Ser 75: 183–189

Mackenzie BR, Leggett WC (1991) Quantifying the contribution of small-scale turbulence to the encounter rates between larval fish and their zooplankton prey: effects of wind and tide. Mar Ecol Prog Ser 73: 149–160

Macpherson E (1994) Substrate utilisation in a Mediterranean littoral fish community. Mar Ecol Prog Ser 114: 211–218

Palmer MW (1993) Putting things in even better order: the advantages of canonical correspondence analysis. Ecology 74: 2215–2230

Pielou EC (1969) An introduction to mathematical ecology. John Wiley & Sons, New York

Robertson DR (1990) Differences in the seasonalities of spawning and recruitment of some small neotropical reef fishes. J exp mar Biol Ecol 144: 49–62

Ros J, Olivella I, Gili JM (eds) (1984) Els sistemes naturals de les illes Medes. Institut d'Estudis Catalans, Barcelona

Rothschild BJ, Osborn TR (1988) Small-scale turbulence and plankton contact rates. J Plankton Res 10: 465–474

Sabates A (1990) Distribution pattern of larval fish populations in the northwestern Mediterranean. Mar Ecol Prog Ser 59: 75–82

Saiz E, Alcaraz M, Paffenhöfer, GA (1992) Effects of small-scale turbulence on feeding rate and gross-growth efficiency of three *Acartia* species (Copepoda: Calanoida). J Plankton Res 14: 1085–1097

Sale PF (1991) Reef fish communities: open nonequilibrial systems. In: Sale PF (ed) The ecology of fishes on coral reefs. Academic Press, London, pp 564–596

Sale PF, Doherty PJ, Eckert GJ, Douglas WA, Ferrell DJ (1984) Large scale spatial and temporal variation in recruitment to fish populations on coral reefs. Oecologia 64: 191–198

Sayer MDJ, Gibson RN, Atkinson JA (1993) Distribution and density of populations of goldsinny wrasse (*Ctenolabrus rupestris*) on the west coast of Scotland. J Fish Biol 43 (Suppl A): 157–167

Shulman MJ (1984) Resource limitation and recruitment patterns in a coral reef fish assemblage. J exp mar Biol Ecol 74: 85–109

Shulman MJ (1985) Recruitment of coral reef fishes: effects of distribution of predators and shelter. Ecology 66: 1056–1066

Sweatman HPA (1985) The influence of adults of some coral reef fishes on larval recruitment. Ecol Monogr 55: 469–485

Ter Braak CJF (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67: 1167–1179

Victor BC (1986) Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. Ecol Monogr 56: 145–160

Williams DMcB, Sale PF (1981) Spatial and temporal patterns of recruitment of juvenile coral reef fishes to coral habitats within "One Tree Lagoon", Great Barrier Reef. Mar Biol 65: 245–253