

# Spatial and temporal patterns of settlement among sparid fishes of the genus *Diplodus* in the northwestern Mediterranean

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**ABSTRACT:** Juvenile settlement of 3 sparid fish species, *Diplodus puntazzo*, *Diplodus sargus* and *Diplodus vulgaris*, was studied over 3 yr at 20 stations located at 5 sites in the NW Mediterranean Sea: 1 site in Spain (Girona), 2 in France (Banyuls and Marseille) and 2 in Italy (Portofino and Elba). When all sites and years were combined, 71% of the settlers recorded belonged to *D. vulgaris*, 25% to *D. sargus* and 4% to *D. puntazzo*. Settlement was seasonal, with *D. sargus* settling in May-June, *D. puntazzo* in October-November, and *D. vulgaris* in 2 pulses, the first in November-December and the second in January-February. Settlement intensity varied spatially, temporally, and among species. At a small spatial scale (within site), settlement intensity varied between stations and particularly between years. At a large spatial scale (among sites), settlement intensity varied among sites, with Marseille and Girona generally experiencing higher settlement than other sites. No difference in settlement intensity was observed between protected and unprotected areas. The settlement of *D. sargus* was higher in 1994 than in 1993 and 1995 at all sites, suggesting the influence of meso-scale hydroclimatic conditions on the settlement success of this species. The settlement of *D. vulgaris* was higher in 1993 in the western part of the NW Mediterranean, and in 1994 in the eastern part. No consistent spatial trend over time was seen for *D. puntazzo*. Thus, settlement intensity of *Diplodus* species to nearshore habitats in the NW Mediterranean exhibited high year-to-year variations at both local and regional scales.

**KEY WORDS:** Settlement · Sparid fish · NW Mediterranean · Spatial variability · Temporal fluctuations

## INTRODUCTION

Many fish species inhabiting the nearshore habitats of the NW Mediterranean Sea are of great importance to artisanal fisheries, less so for the biomass of their catches than for their high value relative to Atlantic species (Bas et al. 1984). Despite the growing interest in these species, many aspects of their biology remain

unknown, particularly their spatial and temporal patterns of settlement into benthic habitats. Fluctuations in settlement and juvenile recruitment may influence the population dynamics of fish species and are potential determinants of the sizes of local populations and exploitable fish stocks (Beverton & Holt 1957, Beverton 1984, Connell 1985, Cushing 1988). Recruitment of juvenile fishes may be highly variable at different spatial scales, from metres to hundreds of kilometers. Large interannual variations in the intensity of recruitment may also occur (Shulman 1985, Fowler et al.

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1992, Doherty & Fowler 1994). In temperate zones, many studies of juvenile recruitment of benthic fishes have been done for gadids (Lough et al. 1989, Folkvord et al. 1994), flatfishes (Riley et al. 1981, Berghahn 1986, Bolle et al. 1994, Miller 1994, Pauly 1994), scorpaenids (Carlson & Straty 1981, Carr 1991), labrids (Tupper & Boutilier 1995, Levin 1996) or sea bass (Jennings & Pawson 1992). Data on the recruitment of benthic coastal fishes, particularly sparids, in the Mediterranean Sea are scarce, and generally related to the arrival of 0-group fishes in bays or coastal lagoons (Cambony 1984, Quignard et al. 1984, Jug-Dujakovic 1988). No quantitative information is available for sparid fishes on rocky shores, except for a few studies on the microhabitat requirements at settlement of several species (Garcia-Rubies & Macpherson 1995, Harmelin-Vivien et al. 1995, Biagi et al. 1997). Sparid fishes of the genus *Diplodus* live in coastal habitats,

from shallow waters down to >50 m deep, with reproduction taking place in deep waters (Divanach 1985). After 1 mo of larval life, they settle in very shallow benthic habitats, where they remain for several months. After reaching 4.5 to 5.5 cm in length, the juveniles of the 3 species studied here disperse outside the nursery area to join the adult population (Macpherson 1998).

In this study, the spatial and temporal patterns of settlement were analysed for 3 species of Sparidae from the genus *Diplodus* at local and regional spatial scales over 3 consecutive years. Results were combined from several contemporaneous studies done from May 1993 to June 1996 at 5 sites located in Spain, France and Italy. These data allowed a multiscale assessment of *Diplodus* settlement in the NW Mediterranean Sea over a linear distance of >600 km. The influence of protection level on fish settlement was also tested by sampling inside and outside marine protected areas

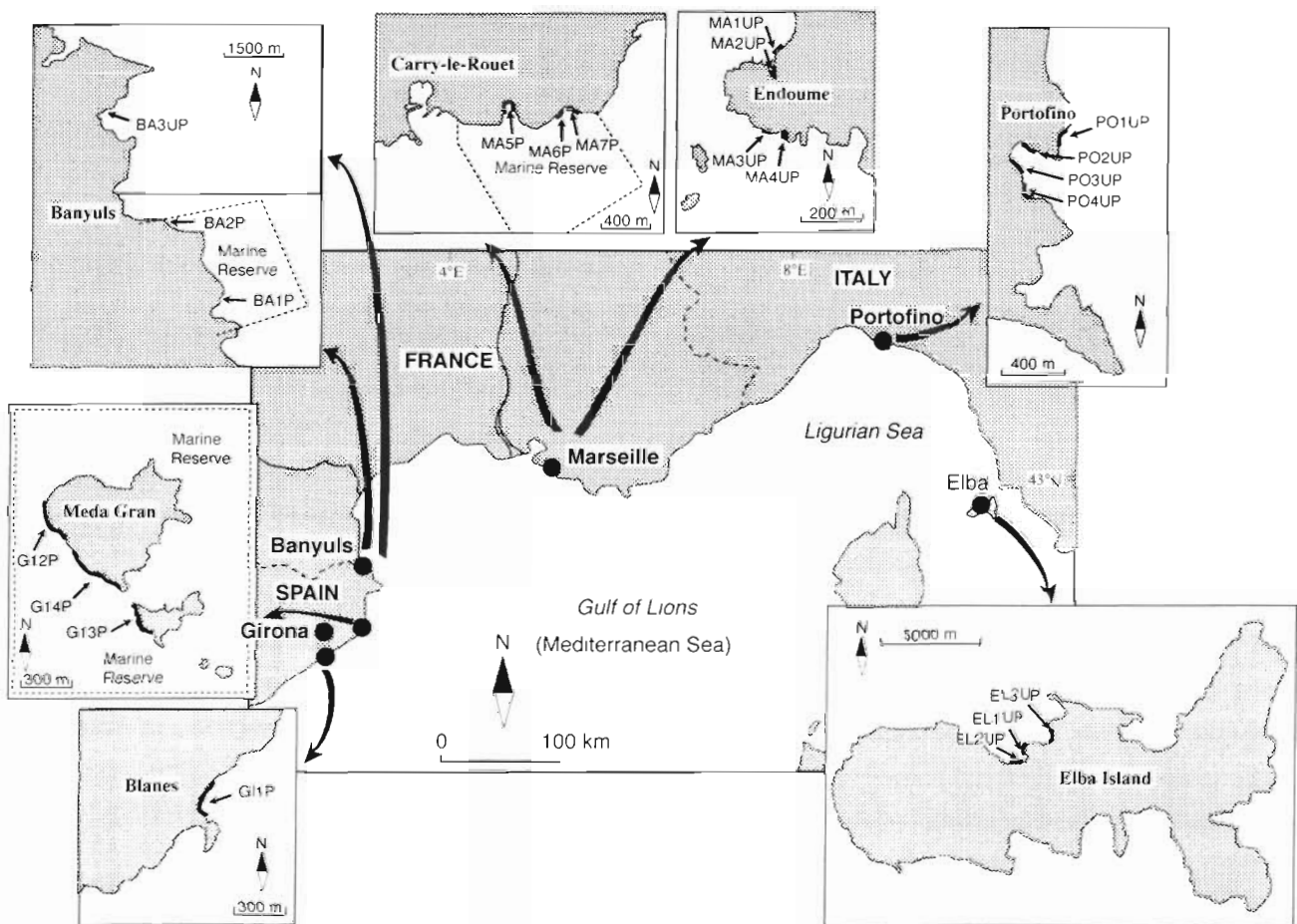


Fig. 1. Locations of the 5 sites studied in the NW Mediterranean Sea, showing stations sampled at each site. Marine protected areas are delineated with dashed lines. Location of stations in protected (P) or unprotected zones (UP) is indicated by station abbreviation. Three stations were studied in Girona (G11UP: 300 m in length, G12P: 150 m, G13P: 150 m), 3 in Banyuls (BA1P: 238 m, BA2P: 189 m, BA3UP: 208 m), 7 in Marseille (MA1UP: 27 m, MA2UP: 24 m, MA3UP: 30 m, MA4UP: 32 m, MA5P: 335 m, MA6P: 129 m, MA7P: 176 m), 4 in Portofino (PO1UP: 63 m, PO2UP: 73 m, PO3UP: 74 m, PO4UP: 104 m), and 3 at Elba Island (EL1UP: 165 m, EL2UP: 148 m, EL3UP: 106 m).

when possible. Following the definitions of Gibson (1994) and Levin (1994), 'settlement' corresponds to the arrival of new individuals from the pelagic habitat into benthic habitats, and 'recruitment' is the number of juveniles surviving an arbitrary period of time (generally a few months) after settlement.

The specific objectives in this study were 3-fold: (1) to quantify the spatial and temporal variability in the timing of settlement, (2) to quantify the spatial and temporal variability in the magnitude of settlement, and (3) to test whether settlement differs between protected and unprotected areas.

## MATERIAL AND METHODS

**Study sites.** Settlement of 3 sparid fish species, *Diplodus puntazzo*, *Diplodus sargus* and *Diplodus vulgaris* was studied at 5 sites located along the NW coast of the Mediterranean Sea: 1 site in Spain (Girona), 2 in France (Banyuls and Marseille), and 2 in Italy (Portofino and Elba) (Fig. 1). At each site, 3 to 7 stations, located in protected and non protected areas when possible, were sampled. All 20 stations were located in known nursery areas: shallow water coves protected from prevailing winds and presenting a gentle slope with coarse sand, gravel, pebbles or boulders (Garcia-Rubies & Macpherson 1995, Harmelin-Vivien et al. 1995). The sizes of the stations differed depending on the morphological characteristics of the coast and ranged between 24 and 335 m in length (Fig. 1).

**Methods.** Visual censuses were performed weekly at each station from May 1993 to June 1996. Intercalibration of teams was done prior to the start of sampling to minimize biases due to different observers. Censuses were conducted along shore, from the surface to 7 m using snorkels and SCUBA; this depth range encompassed the entire vertical distribution of settlers of the 3 species. Juvenile sparids were counted and their length estimated (in 5 mm size classes) during each census using a plastic board bearing silhouettes of individuals of different sizes. Four replicate censuses were made at all stations except for the protected stations at Marseille, where 1 census per week was conducted. Data were not collected in 1993 for *Diplodus sargus* in Banyuls, Portofino and Elba. Data were not collected for *D. vulgaris* in Banyuls in 1995. The duration of each dive ranged from 30 min (stations <50 m in length) to 2 h (stations >300 m in length). As visual counts were performed with a weekly periodicity, we assumed that the date of first count was not very different from the date of first settling. To study the spatial and temporal patterns of benthic settlement, we decided to take into account the maximum number of individuals ( $N$ ) recorded at each station each year

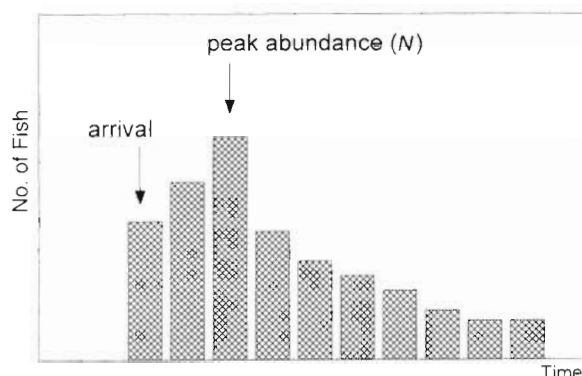


Fig. 2. *Diplodus* spp. Schematic representation of the settlement pattern of 3 *Diplodus* species.  $N$  is the number of individuals recorded at peak abundance

(Fig. 2). The peak number of settlers gave the best estimate of settlement for that year, as the number of fishes recorded at each station greatly varied in time. It increased rapidly during the settlement period, reached a peak and then decreased progressively when mortality predominated over arrival. As stations differed in size within and between sites, we standardized data ( $D$ ) by dividing the maximum number of individuals ( $N$ ) recorded at each station by the coastal length of the station expressed in metres ( $L$ ):  $D = N/L$ . Thus,  $D$  was the maximum number of settlers recorded per linear coastal metre at the station level. At the site scale a mean standardized settlement intensity ( $D_m$ ) was calculated each year by combining data from all stations. If  $D$  accounted best for settlement intensity at the station level, it did not necessarily reflect the final abundance of juveniles recruited into the population, as the initial number of settlers might be highly and diversely modified by differential mortality rates, as discussed by Macpherson et al. (1997). The minimum size at settlement was around 10 mm total length (range 8 to 15 mm TL) in the 3 species.

A 2-factor analysis of variance (ANOVA) was used to examine variability in settlement intensity on both small and large spatial scales. Within each site (small scale), differences in settlement intensity were tested among stations and among years. Data were included only from years where all stations at a site were sampled. Data were log-transformed [ $\log_e(D+1)$ ] prior to analysis to homogenize variance (Bartlett's test,  $p > 0.05$ ). Mean settlement ( $D_m$ ) was tested among sites and years. Comparisons between specific sites were made using a Student-Newman-Keuls test. A 3-way ANOVA with stations nested within sites and with years as another factor was not possible owing to missing data. The effect of protection level on settlement intensity was tested by combining data from Girona, Banyuls and Marseille, where stations were located

both in protected and unprotected areas. Differences were tested by Mann-Whitney *U*-test of comparison of means.

## RESULTS

### Seasonality of settlement

Seasonality of settlement of juvenile fish on Mediterranean rocky shores was high for each of the 3 species. *Diplodus sargus* settled mainly from May to June, *D. puntazzo* from October to late November, and *D. vulgaris* from November to February, generally in 2 pulses (Fig. 3). The maximum number of settlers was recorded from 2 to 4 wk after the arrival of the first settlers. The time elapsed between the first count and the peak in abundance gave an indication of the minimum duration of the settlement period. A shift between years in the timing of settlement was observed in all sites. Settlement of *D. sargus* occurred earlier in 1995 (May) than in 1993 and 1994 (June) and for a longer period, as the peak was observed more than 6 wk after the arrival of the first settlers instead of 2 to 3 wk the preceding years (Fig. 3A).

The arrival and the abundance peak of *Diplodus puntazzo* occurred 1 mo later in 1993 (November) than in 1994 and 1995, and the duration of the settlement period was twice as long in 1993 as in the 2 following years (Fig. 3B). *D. vulgaris* settled in 2 well-separated pulses, the first centred around the end of November (from late October to late December) and the second from January to February, in 1993 and 1994 (Fig. 3C). However, in 1995, the first pulse only was observed in all sites, and the second pulse did not occur. The settlement period generally lasted for 2 to 3 wk for this species, whatever the pulse. As the first and second pulses of settlement of *D. vulgaris* occurred in different calendar years, we used the year of the first arrival to put data into years (e.g. data on settlement from October 1993 to February 1994 appear as '1993').

### Small-scale spatio-temporal variability

The spatial variability of settlement at a small scale was high for each species (Tables 1 to 3). Differences greater than 1 order of magnitude were observed between adjacent stations separated by only tens to hundreds of metres. The rank of stations generally varied from year to year, as emphasized by the significant interaction between station and year. The factor 'Station' was highly significant at all sites for each species, indicating that mean number of settlers differed highly between stations within sites. However, this factor

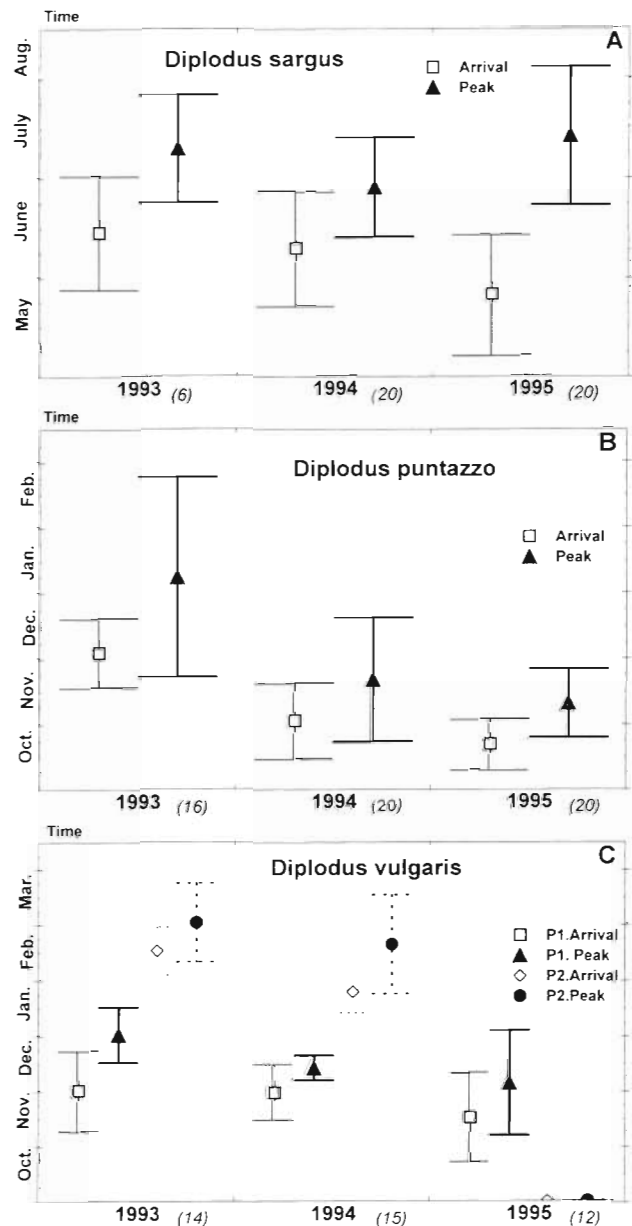


Fig. 3. *Diplodus* spp. Mean dates ( $\pm$  SD) of arrival and peak abundance at settlement of (A) *D. sargus*, (B) *D. puntazzo*, and (C) *D. vulgaris* (P1: pulse 1, P2: pulse 2) in the north-western Mediterranean from 1993 to 1995. Number of data per year is indicated in italics

generally explained a lower percentage of variance than did the factor 'Year', which predominated at all sites, except at Elba for *Diplodus puntazzo* and *D. vulgaris*. The small-scale spatial variability in settlement of *D. sargus* was high (Table 1). The rank of stations varied from year to year in all sites, except at Marseille, where settlement was always higher at station MA3UP. Similar trends in year-to-year variation in set-

Table 1 *Diplodus sargus*. Within-site variability of *D. sargus* settlement intensity in space and time. Results of the 2-way analyses of variance performed on transformed data using  $\log_e(D+1)$ , where  $D$  is the maximum number of settlers per linear coastal metre. % variance: percentage of the total variance explained by each factor. \*\*\* $p < 0.001$

Site	Factor	df	F	p	% variance
Girona (Spain)	Station	2	1015.7	***	22.7
	Year	1	4999.5	***	55.9
	Station $\times$ Year	2	950.8	***	21.3
Banyuls (France)	Station	2	112.3	***	10.9
	Year	1	1179.8	***	57.2
	Station $\times$ Year	2	316.6	***	30.8
Marseille (France)	Station	3	131.9	***	22.7
	Year	1	582.1	***	66.9
	Station $\times$ Year	3	24.1	***	8.7
Portofino (Italy)	Station	3	664.8	***	28.1
	Year	1	4184.4	***	58.9
	Station $\times$ Year	3	301.0	***	12.7
Elba (Italy)	Station	2	436.1	***	33.1
	Year	1	1298.2	***	49.2
	Station $\times$ Year	2	225.2	***	17.0

tlement intensity for this species occurred at all sites. From Spain to Italy, 1994 was a year of higher settlement for *D. sargus* than were 1995 and 1993 (Fig. 4). The decrease in settlement intensity from 1994 to 1995 was 44% in Marseille, whereas it reached 80% in Girona, 75% in Banyuls, 78% in Portofino, and 74% at Elba Island. In 1993, settlement was lower than in 1995 in both Girona and Marseille.

The spatial variability in *Diplodus puntazzo* settlement at a small scale was also high (Table 2). The rank order of stations changed with year in all sites, except at Elba, where station EL3UP was always ranked first. Settlement of *D. puntazzo* varied differently from year to year at each site (Fig. 5). In Girona, no difference occurred from 1993 to 1994, but a drastic decrease (92%) was observed in 1995. In Banyuls, Portofino and Elba an increase was observed from 1993 to 1994, followed by a clear decrease in 1995, but the lowest settlement was recorded in 1995 for Banyuls and Portofino and in 1993 for Elba. In Marseille, settlement of *D. puntazzo* was high both in 1993 and 1995 and significantly lower in 1994 (mean decrease 85%).

Settlement of *Diplodus vulgaris* was consistently higher at station BA3UP and at station EL3UP during the 3 years. In the other sites, the rank order of stations varied from year to year (Table 3). Interannual variation in settlement of *D. vulgaris* differed among sites. In the western sites, Girona and Banyuls, the highest abundance of settlers was observed in 1993, whereas the highest settlement intensity in the eastern sites,

Table 2 *Diplodus puntazzo*. Within-site variability of *D. puntazzo* settlement intensity in space and time. Results of the 2-way analyses of variance performed on transformed data using  $\log_e(D+1)$ , where  $D$  is the maximum number of settlers per linear coastal metre. % variance: percentage of the total variance explained by each factor. \*\*\* $p < 0.001$

Site	Factor	df	F	p	% variance
Girona (Spain)	Station	2	1266.8	***	23.4
	Year	2	2518.1	***	46.6
	Station $\times$ Year	4	800.9	***	29.7
Banyuls (France)	Station	2	95.7	***	5.1
	Year	2	1440.3	***	78.9
	Station $\times$ Year	4	126.2	***	15.3
Marseille (France)	Station	3	441.2	***	20.6
	Year	2	1574.6	***	49.0
	Station $\times$ Year	6	319.0	***	29.8
Portofino (Italy)	Station	3	960.0	***	20.6
	Year	1	7254.1	***	49.9
	Station $\times$ Year	3	1424.8	***	29.3
Elba (Italy)	Station	2	1560.4	***	47.1
	Year	2	778.7	***	23.6
	Station $\times$ Year	4	479.3	***	28.9

Table 3 *Diplodus vulgaris*. Within-site variability of *D. vulgaris* settlement intensity in space and time. Results of the 2-way analyses of variance performed on transformed data using  $\log_e(D+1)$ .  $D$  is the maximum number of settlers per linear coastal metre. % variance: percentage of the total variance explained by each factor. \*\*\* $p < 0.001$ , ns:  $p > 0.05$ . Girona data were not analyzed, as only one station at Girona was studied for *D. vulgaris*

Site	Factor	df	F	p	% variance
Banyuls (France)	Station	2	33.2	***	9.7
	Year	1	596.0	***	86.7
	Station $\times$ Year	2	3.4	ns	1.0
Marseille (France)	Station	3	333.3	***	30.0
	Year	1	2051.7	***	61.5
	Station $\times$ Year	3	862	***	7.7
Portofino (Italy)	Station	3	249.5	***	20.6
	Year	1	487.7	***	49.9
	Station $\times$ Year	3	74.5	***	15.1
Elba (Italy)	Station	2	1560.4	***	60.4
	Year	2	778.7	***	29.2
	Station $\times$ Year	4	260.2	***	10.2

Marseille, Portofino and Elba, was observed in 1994 (Fig. 6). *Diplodus vulgaris* generally settled in 2 pulses, the first in November-December and the second, which was generally the highest, in January-February. This pattern was obvious in Marseille, where the 2 pulses were separated (Table 4). In 1995, this species recruited in one pulse only (November) at all sites.

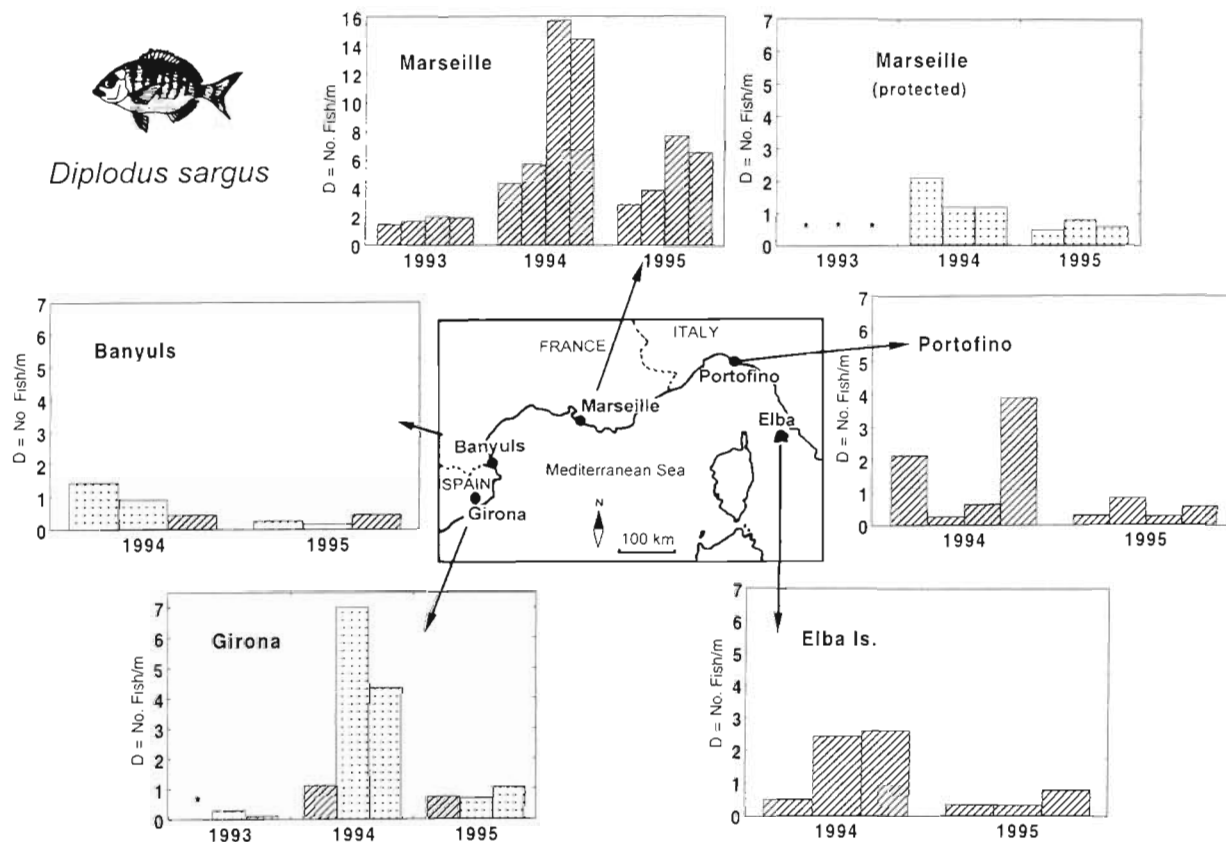


Fig. 4. *Diplodus sargus*. Settlement across the NW Mediterranean between 1993 and 1995 (ranking of stations is similar in each site each year with Stn 1 to the left). Hatched bars: stations located in unprotected zones, dotted bars: stations located in protected zones. \*Stations not surveyed. Note difference in scale for the unprotected Marseille stations

Table 4. *Diplodus vulgaris*. Difference in settlement intensity between pulse 1 and pulse 2 for *D. vulgaris* in Marseille in 1993 and 1994 (means  $\pm$  SD,  $n = 4$ ).  $p$ : significance of SNK test of comparison of means between pulses [ $p(p)$ ] and years [ $p(y)$ ], ns: not significant

	1993	1994	$p(y)$
Pulse 1	3.696 $\pm$ 2.227	1.249 $\pm$ 2.023	ns
Pulse 2	5.529 $\pm$ 0.466	77.421 $\pm$ 42.780	$p = 0.02$
$p(p)$	ns	$p < 0.02$	

### Large-scale spatio-temporal variability

A large difference in the intensity of settlement of *Diplodus sargus*, *D. puntazzo* and *D. vulgaris* was observed among sites during the 3 yr study (Table 5). A significant difference in settlement between sites was found for each species, but significant interaction between site and year existed for 2 species (Table 6). At a large spatial scale, the factor 'Site' explained a higher percentage of variance than the factor 'Year', which was not significant for 2 species. For *D. sargus*,

the rank of sites did not change with time, as indicated by the non-significant interaction between Site and Year, with highest settlement in Marseille, then Girona, Portofino, Elba and finally Banyuls. Significant interannual variation in settlement of *D. sargus* was observed at the large spatial scale, with 1994 values being higher than those of 1995. The intensity of settlement of *D. puntazzo* was significantly higher in Marseille, Elba and Girona than in Portofino and Banyuls, but the rank order of sites varied from year to year. Settlement of *D. puntazzo* was highest in Marseille in 1993 and 1995 and at Elba in 1994. Settlement of *D. vulgaris* was consistently highest in Marseille during the 3 yr study, but the rank of the other sites varied from year to year. Lowest settlement was observed in Portofino in 1993 and 1995 and in Banyuls in 1994.

### Effect of protection level

Mean numbers of settlers were higher in unprotected areas, but these differences were not significant (Table 7). At a small spatial scale, contrasting results

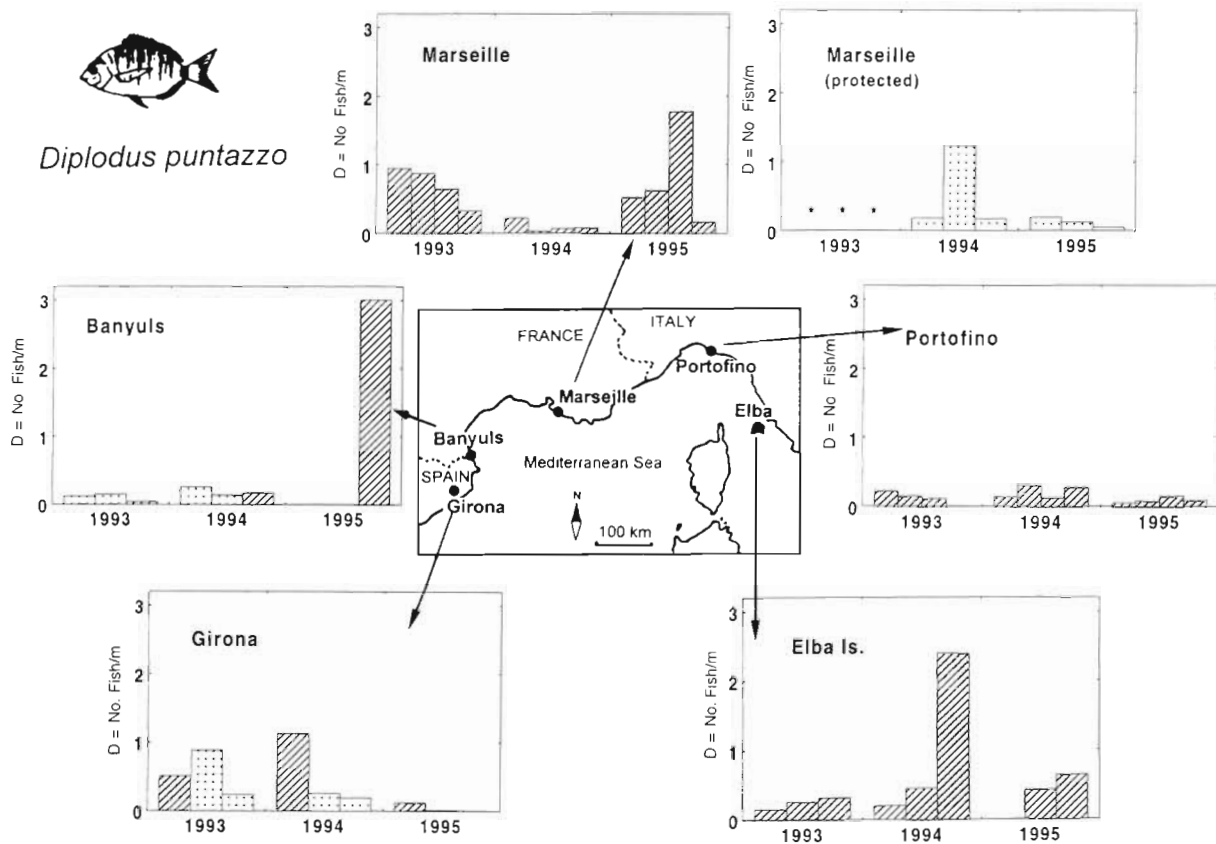


Fig. 5. *Diplodus puntazzo*. Settlement across the NW Mediterranean between 1993 and 1995 (ranking of stations is similar in each site each year with Stn 1 to the left). Hatched bars: stations located in unprotected zones, dotted bars: stations located in protected zones. \* Stations not surveyed

Table 5. *Diplodus* spp. Mean density ( $D_m$ ) of settling *D. sargus*, *D. puntazzo* and *D. vulgaris* at abundance peak (mean number of settlers per coastal metre  $\pm$  SD) in the NW Mediterranean according to sites and years. nd: no data collected

Species	Year	Girona	Banyuls	Marseille	Portofino	Elba
<i>D. sargus</i>	1993	0.134 $\pm$ 0.150	nd	1.778 $\pm$ 0.231	nd	nd
	1994	4.159 $\pm$ 2.948	0.946 $\pm$ 0.500	6.374 $\pm$ 6.214	1.740 $\pm$ 1.654	1.861 $\pm$ 1.163
	1995	0.840 $\pm$ 0.201	0.300 $\pm$ 0.143	3.261 $\pm$ 2.942	0.499 $\pm$ 0.272	0.495 $\pm$ 0.258
<i>D. puntazzo</i>	1993	0.543 $\pm$ 0.323	0.103 $\pm$ 0.062	0.624 $\pm$ 0.412	0.163 $\pm$ 0.064	0.246 $\pm$ 0.084
	1994	0.530 $\pm$ 0.524	0.187 $\pm$ 0.062	0.111 $\pm$ 0.071	0.216 $\pm$ 0.094	1.012 $\pm$ 1.199
	1995	0.044 $\pm$ 0.065	0.004 $\pm$ 0.008	0.777 $\pm$ 0.696	0.091 $\pm$ 0.042	0.356 $\pm$ 0.326
<i>D. vulgaris</i>	1993	5.917	2.750 $\pm$ 1.005	5.791 $\pm$ 0.178	0.683 $\pm$ 0.561	2.965 $\pm$ 1.771
	1994	3.251	0.307 $\pm$ 0.221	77.416 $\pm$ 42.779	1.886 $\pm$ 1.117	3.755 $\pm$ 4.162
	1995	3.535	nd	9.263 $\pm$ 9.205	0.739 $\pm$ 0.361	0.883 $\pm$ 0.773

were obtained depending on site and species. In Girona, the settlement of *Diplodus sargus* was significantly higher at protected stations, and in unprotected stations for *D. puntazzo* and *D. vulgaris* (Figs. 4 to 6). In Banyuls, the settlement of *D. sargus* was higher in protected stations in 1994 and lower in 1995, and always

higher in protected stations for *D. puntazzo*. In Marseille, *D. sargus* settled in higher number in unprotected stations, but no difference was observed for *D. puntazzo*. Thus, no obvious or consistent pattern in settlement intensity emerged with respect to the protection level of stations for the 3 species.

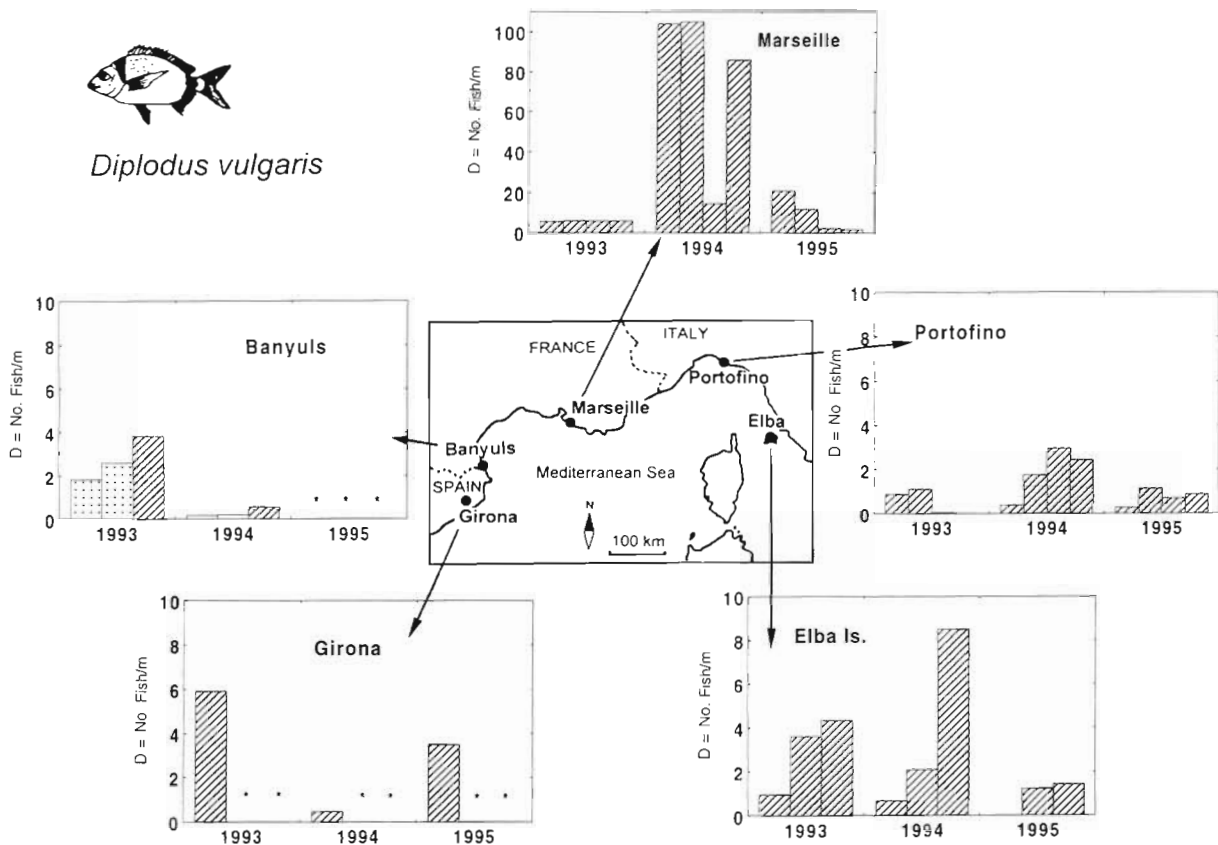


Fig. 6. *Diplodus vulgaris*. Settlement across the NW Mediterranean between 1993 and 1995 (ranking of stations is similar in each site each year with Stn 1 to the left). Hatched bars: stations located in unprotected zones, dotted bars: stations located in protected zones. \*Stations not surveyed. Note difference in scale for the unprotected Marseille stations

### Relative importance of species

Settlement intensity varied among species as well as among stations, sites and years. In total, *Diplodus puntazzo* represented 4.2% of the total number of sparid settlers recorded, *D. sargus* 24.8% and *D. vulgaris* 71.0%. At all sites, *D. puntazzo* settled with the lowest intensity, representing from 2.8 to 5.4% of the total number of sparid recruits in 1994, and from 0.2 to 29.0% in 1995. *Diplodus sargus* and *D. vulgaris* were more abundant and dominated at different sites with time. Opposite trends were observed in the respective proportions of these 2 species in the western and in the eastern part of the NW Mediterranean. The proportion of *D. vulgaris* was higher in 1994 than in 1995 in Girona and Banyuls (64% vs 33%). Conversely, it was lower in 1994 than in 1995 in Marseille, Portofino and Elba (40% vs 78%). The reverse was observed for *D. sargus*, which represented 32% of all *Diplodus* settlers in 1994 and 38% in 1995 at the western sites and 55% in 1994 versus 13% in 1995 at the eastern sites.

### DISCUSSION

Many authors working on coral reef fishes have emphasized the variability in settlement and recruitment both in space and time, implying that recruitment of juveniles was largely a stochastic process (Doherty 1987, 1991, Doherty & Williams 1988, Sale 1991). However, some coherent patterns now suggest the involvement of deterministic processes (Victor 1983, 1986, Cowen 1985, Fowler et al. 1992). Our study showed that the settlement of sparids in the NW Mediterranean was highly variable in space and time, but presented some consistent patterns, probably related to hydroclimatic factors acting on several spatial and temporal scales.

Sparid settlement has typically been studied with beach seines or other devices which catch juveniles larger than 20 to 25 mm TL (Ranzi 1930, Quignard et al. 1984, Jug-Dujakovic 1988). Using visual censuses, we have demonstrated that settlement for the 3 *Diplodus* species studied here occurred at about 10 mm TL.



Table 6. *Diplodus* spp. Two-way ANOVA performed on transformed data using  $\log(D_m+1)$  comparing differences in mean settlement intensity of *D. sargus*, *D. puntazzo* and *D. vulgaris* between sites and years. \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ , ns:  $p > 0.05$ ). % variance: percentage of the total variance explained by each factor

Species	Factor	df	F	p	% variance
<i>D. sargus</i>	Site	4	4.455	**	31.5
	Year	1	7.964	**	14.1
	Site $\times$ Year	4	0.183	ns	1.3
<i>D. puntazzo</i>	Site	4	3.455	*	20.0
	Year	2	0.977	ns	2.9
	Site $\times$ Year	8	2.533	*	29.4
<i>D. vulgaris</i>	Site	3	30.358	***	61.2
	Year	1	4.169	ns	2.8
	Site $\times$ Year	3	1.181	***	22.5

This technique allowed us to determine the actual timing of settlement: May-June for *D. sargus*, October-November for *D. puntazzo*, and November to February for *D. vulgaris*. The 3 *Diplodus* species exhibited similar habitat requirements at settlement, but were segregated on a clear seasonal basis, with each species occupying the same nursery ground successively, except for a short overlap between *D. puntazzo* and the first pulse of *D. vulgaris* (Garcia-Rubies & Macpherson 1995, Harmelin-Vivien et al. 1995). The succession in settlement time could potentially circumvent competition between related species for food and shelter resources.

Small-scale spatio-temporal variability in settlement abundance of the 3 *Diplodus* species was high at all sites. Dates of arrival and peak abundance, and the maximum number of settling individuals varied greatly between stations within each site. The rank of stations changed from year to year and among species in most sites, except for a few stations which always harboured more individuals, such as Stn EL3UP. These data implied that microhabitat characteristics were not the only factor explaining small-scale variability in *Diplodus* settlement, whereas they could affect settlement patterns at that scale (Tolimieri 1995). Differ-

ences in settlement between stations could be partly attributed to the patchy distribution of pre-settling fish, as suggested by the 'larval patch' hypothesis developed to explain the spatial variability of recruitment patterns over scales of metres to kilometres (Cowen 1985, Victor 1986, Doherty & Williams 1988). At a small scale, time was more important than space for explaining the high variability in sparid settlement. In each site, year-to-year variations in settlement of the 3 *Diplodus* species were higher than variations between stations. Nevertheless, significant interactions between year and station indicated that, to accurately record temporal variation in settlement, different stations per site should be sampled.

At a large scale, *Diplodus* settlement was also highly variable, but differences between sites predominated over differences between years. The consistently higher settlement observed in Marseille and Girona may either be related to the topographic characteristics of the stations or reflect a real difference in regional influx of larvae. Tolimieri (1995) demonstrated that habitat did not influence recruitment variation on a large scale. As stations have been selected to present suitable microhabitats for sparid settlement, differences between sites were probably not related to habitat differences in this study. In some cases, the presence of suitable habitats does represent the main factor involved in differences between sites. The lack of sparid juveniles around certain islands in the Marseille area is explained by the absence of suitable habitats on abrupt coasts (Harmelin-Vivien et al. 1995). Cowen (1985) found that recruitment occurred consistently from year to year in areas with larval sources upstream, whereas in areas out of the typical larval flux, recruitment was highly variable and dependent upon anomalous flow events. Little is known of where *Diplodus* spp. spawn in the NW Mediterranean, except that spawning sites are probably located deeper on the continental shelf (Divanach 1985). The few sparid larvae sampled by Sabates (1990) and Sabates & Olivar (1996) were collected far from the coast, suggesting that dispersal by hydrographic processes during the pelagic life is important. Thus, information on spawn-

Table 7. *Diplodus sargus* and *Diplodus puntazzo*. Effect of protection level on settlement intensity of *D. sargus* and *D. puntazzo* in the NW Mediterranean. Data from Girona, Banyuls and Marseille were combined (mean number of fish per coastal metre  $\pm$  SD). n: number of stations; ns:  $p > 0.05$

Species	Year	n	Protected	n	Unprotected	Result
<i>D. sargus</i>	1994	7	2.599 $\pm$ 2.268	6	6.947 $\pm$ 6.649	ns
	1995	5	0.542 $\pm$ 0.362	6	3.598 $\pm$ 2.894	ns
<i>D. puntazzo</i>	1993	7	0.426 $\pm$ 0.444	6	0.558 $\pm$ 0.340	ns
	1994	7	0.174 $\pm$ 0.076	6	0.285 $\pm$ 0.420	ns
	1995	4	0.006 $\pm$ 0.007	6	0.538 $\pm$ 0.655	ns

ing grounds and local coastal circulation would be necessary to understand the spatial variability of sparid settlement in the Mediterranean. Finally, our analysis failed to find any effect of protection level on the intensity of settlement of the 3 species. Fishing pressure does not obviously influence the intensity of juvenile fish settlement into benthic habitats, contrary to what has been demonstrated for adult populations. It is now well-known that protection measures have increased fish diversity and abundance and individual size of adult fish populations in Mediterranean marine reserves (Bell 1983, Garcia-Rubies & Zabala 1990, Francour 1994, Dufour et al. 1995, Harmelin et al. 1995).

Some coherent temporal patterns were also observed at a large scale. Interannual differences in the date of maximum abundance were similar at all sites. The settlement of *Diplodus sargus* and *D. vulgaris* peaked earlier in 1994 than in 1993, and the peak abundance of *D. puntazzo* occurred earlier in 1995 than in the 2 preceding years. Differences in the timing of peaks of settlement may relate to variation in the date of adult reproduction or the duration of the pelagic life. Similar trends in year-to-year variability of settlement intensity were observed at a large spatial scale in 2 of the 3 species. The level of settlement of *D. sargus* was higher in 1994 than in 1995 at all 5 of the sites, which are spread along approximately 1000 km of coast line. This could not be related to habitat variability, as habitat characteristics of stations did not change from year to year. The consistency of interannual variation in settlement intensity of *D. sargus*, which settled in May-June, suggested the influence of strong large-scale deterministic processes operating over distances of hundreds of kilometres during that period. Individuals recorded at the different sites likely belonged to different local subpopulations, which certainly reproduced in different areas, as evidenced by a genetic study on *D. sargus* (Lenfant & Planes 1996). Nevertheless, the consistent feature of year-to-year variation observed in this species suggested that hydroclimatic conditions were stable and similar in the whole NW Mediterranean during larval life and the settlement period (end of spring to beginning of summer) and have influenced the various subpopulations in a similar way. In a study on temperate flatfishes, Henderson & Seaby (1994) demonstrated that temperature during the spawning and larval period may directly influence the abundance of juveniles. In *D. puntazzo* and *D. vulgaris* different trends in interannual variations in settlement intensity were observed among sites. The absence of a general pattern of year-to-year variation might be related to unstable conditions in coastal waters in late autumn and winter, the period of benthic settlement of these 2 species.

Settlement of the *Diplodus* species varied as much as 1 order of magnitude from year to year. In temperate commercial fishes, recruitment variability is largely attributed to survivorship during the egg and larval stages (Gulland 1982, Cushing 1988), when starvation and predation are major mortality factors (Leggett & Deblois 1994). The general pattern observed over the whole NW Mediterranean in interannual variations of *D. sargus* tends to confirm that settlement is controlled by factors operating at a large spatial scale occurring at the pelagic life-history stage. Favourable general hydroclimatological factors in 1994 may have enhanced the success of one or several of various processes, such as reproduction, egg fertilization, larval survivorship, food supply, and advection of larvae to settlement sites. To understand the differences in temporal variability of settlement among species would require correlation of the interannual fluctuations in settlement with differences in hydrological and climatological conditions over time.

The implications of this study are important not only for understanding the dynamics of sparid populations, but also in terms of management of these resources in the Mediterranean, which requires discrimination between the natural variability of settlement and changes due to anthropogenic disturbances of coastal waters. Our data showed consistent patterns both in space and time that implicate deterministic processes of sparid settlement in the Mediterranean at a large scale, which may differ from species to species in spite of high variability at a small-scale. Such natural variability may be still emphasized by a degradation of coastal habitats which constitute the nursery grounds of many littoral fishes, resulting in greater instability in the size of local fish populations.

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