



# Effects of post-settlement mortality on size and parasite load in juvenile *Diplodus vulgaris* and *D. sargus* in the Mediterranean

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**ABSTRACT:** This study explored how mortality processes influence life history traits of recently settled juvenile fishes (*Diplodus vulgaris* and *D. sargus*) in the Mediterranean. Mortality was estimated by measuring the decrease in abundance of a cohort from settlement to 4 mo post-settlement. Growth and parasite load were simultaneously measured over time to determine those phenotypes more susceptible to mortality. *Diplodus* spp. juvenile mortality was between 71 and 81 % over the 4 mo period. A decrease in the coefficient of variation in size over time suggests that mortality may influence growth of both *Diplodus* species. A decrease in parasite abundance of both *Diplodus* species 60 d after settlement suggests that fish with higher parasite loads may have been more susceptible to mortality. Overall, mortality did not act randomly in *D. vulgaris* and *D. sargus* cohorts, as the variance in both size and parasite abundance of recently settled juveniles was not comparable to that of the adult population; only larger, parasite-free individuals survived.

**KEY WORDS:** Mortality processes · Selection · Parasites · Growth · Life history

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## INTRODUCTION

A fundamental goal in population ecology is to understand the processes that influence individuals to survive to reproduction (Kingsolver et al. 2001). Predation is often considered an important causal factor in structuring terrestrial and aquatic populations, as it can be a major selective force in the evolution of organism structure and function (e.g. life history traits, morphology, sexual dimorphism, activity times and habitat use; reviewed by Fenberg & Roy 2008). The critical period of high mortality for marine species (fish and invertebrates) that have a bipartite life cycle with a planktonic larval stage occurs during the transition of pelagic larvae from the open ocean to a benthic habitat (i.e. settlement phase; reviewed by Werner 1988). The small size of recently settled post-larvae/juveniles renders them susceptible to a wide range of predators, and predation is among the dominant factors influencing juvenile survival of marine species (e.g. Almany &

Webster 2006, Lecchini et al. 2007, Allen 2008). Indeed, mortality is assumed to be greatest at the time of settlement or soon thereafter: between 30 and 90 % of juveniles are removed by predation within the first weeks after settlement (e.g. Doherty 2002, Almany & Webster 2006, Allen 2008). In some species, losses may be as great as 60 % during the first night of settlement on a reef (Doherty et al. 2004). Furthermore, high predation mortality during settlement is not restricted to marine species; amphibians suffer elevated mortality rates from predation when moving from aquatic larval habitats to terrestrial adult habitats (Arnold & Wassersug 1978).

In general, these examples suggest that life stage transitions may result in high mortality as relatively naïve individuals enter new habitats and encounter a suite of more experienced and opportunistic predators. Although life stage transitions account for only a small proportion of a species' total life span, small changes in the way in which mortality acts may have profound

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effects on the number of individuals reaching the adult phase, as well as the phenotypes of those individuals (e.g. Stearns 1992, Kingsolver et al. 2001, Fenberg & Roy 2008). It is of particular interest to determine whether post-settlement mortality acts indiscriminately during life stage transitions, or in other words, whether all recently settled juveniles have a similar chance of being removed from the population, or whether a particular phenotype is more susceptible. The majority of the literature on selective mortality of marine species during the first post-settlement months has emphasised body size, condition or larval growth history without considering other aspects (e.g. Sogard 1997, Vigliola & Meekan 2002, Hoey & McCormick 2004, Meekan et al. 2006, Gagliano et al. 2007, Allen 2008).

In this study, a cohort of both *Diplodus sargus* (Linnaeus, 1758) and *D. vulgaris* (Saint-Hilaire, 1817) (coastal marine sparid fishes abundant in the Mediterranean Sea) were monitored from settlement for 4 mo, when juveniles are known to move to adult habitats. The term 'cohort' refers to individuals that settle over a short period of time (within 1 d) in the same settlement habitat (Planes et al. 1999). Mortality was estimated by measuring the decrease in population size of the cohort. Growth and parasite infection were simultaneously measured to gain insights into those phenotypes more susceptible to mortality.

## MATERIALS AND METHODS

**Sampling strategy.** Two sampling sites were chosen along the Mediterranean coast in the southwest of France: Banyuls consists of 3 similar small bays (each 200 m wide), spaced 100 m apart along a rocky coast. St Marie consists of 3 similar artificial rocky jetties (each 5 m wide and 70 m long), each spaced 350 m apart and originally built to maintain the coastline's sandy beaches. Each jetty extends from the beach offshore to a depth of 2.5 m, with only sand between the jetties. As *Diplodus sargus* and *D. vulgaris* juveniles show very limited movement (only about 50 m around their shallow rocky settlement habitats) and avoid crossing unsuitable habitats such as sandy areas (Harmelin-Vivien et al. 1995, Planes et al. 1998), we assumed that fish did not move between bays or jetties. Moreover, visual underwater surveys showed that the bays and jetties were the only settlement habitats of *D. sargus* and *D. vulgaris* in the sampling area (Romans 2003). *D. vulgaris* were sampled at both sites, whereas *D. sargus* were only sampled at St Marie. Within each site, 3 different protocols were carried out at the 3 different bays or jetties.

**Settlement survey.** All *Diplodus* juveniles were removed daily from the central jetty at St Marie and

the central bay at Banyuls in order to estimate both daily settlement rates and to verify that juveniles do not move between jetties or bays. All *D. vulgaris* and *D. sargus* were monitored daily during the winter (22 November 2002 to 4 April 2003) and summer (1 May 1999 to 30 June 1999) seasons, respectively, to evaluate settlement patterns. Monitoring was conducted by underwater visual counting along the jetty or inside the bay (for more details about visual counting, see Harmelin-Vivien et al. 1985), and then all *Diplodus* were removed with small nets.

**Mortality.** The southernmost jetty and bay were used to estimate mortality of a single *Diplodus* cohort. Once a *Diplodus* cohort was identified on the first day of its settlement (defined as Day 0), mortality was estimated by measuring the decrease in population abundance of the cohort the following days after settlement: Days 7, 15, 30, 60 and 120. The survey consisted of 3 successive replicates of underwater visual counting along the jetty or inside the bay (Harmelin-Vivien et al. 1985).

**Growth and parasitism.** The northernmost jetty and bay were used to sample for growth and parasites over time. In total, 20 individuals were randomly sampled from the *Diplodus* cohort (using small hand nets with all precautions taken to ensure random collection; Romans 2003) at each sampling date (Day 0, 7, 15, 30, 60, 120). Growth corresponds to the change in standard length of 20 individuals compared to the previous sampling date measured using callipers. The variance in length among individuals was used to compute the coefficient of variation in size. Parasite abundance (total number of monogeneans on the gills, cestodes in the intestine and digeneans encysted in the muscles) and parasite prevalence (% of parasitised fish) were measured using the same 20 individuals.

**Statistics.** For all analyses, the *Diplodus sargus* cohort at St Marie and the 2 *D. vulgaris* cohorts at Banyuls and St Marie were treated as 3 species. Fully factorial 2-way analyses of variance (ANOVAs), with time and species as the 2 factors, were carried out on growth and parasitism. The assumptions of normality and heteroscedasticity were met by transforming the data ( $\log(x + 1)$ ).

## RESULTS

### Settlement survey

Daily settlement surveys showed peaks in settlement of *Diplodus* larvae: 50% of the total 172 *D. vulgaris* larvae that recruited at Banyuls between November and April settled on 10 December; 65% of the total 1741 *D. vulgaris* larvae that recruited at St Marie between

November and April settled on 13 December; and 82% of the total 280 *D. sargus* larvae that recruited at St Marie between May and June settled on 12 June (Fig. 1). The fish cohorts that settled during these peaks were selected for monitoring over 4 mo, and the date of each peak was defined as Day 0.

### Mortality

After 4 mo post-settlement, mortality of *Diplodus vulgaris* cohorts was 71.4 and 76.5% at Banyuls and St Marie, respectively (Fig. 2a,b). The decrease in

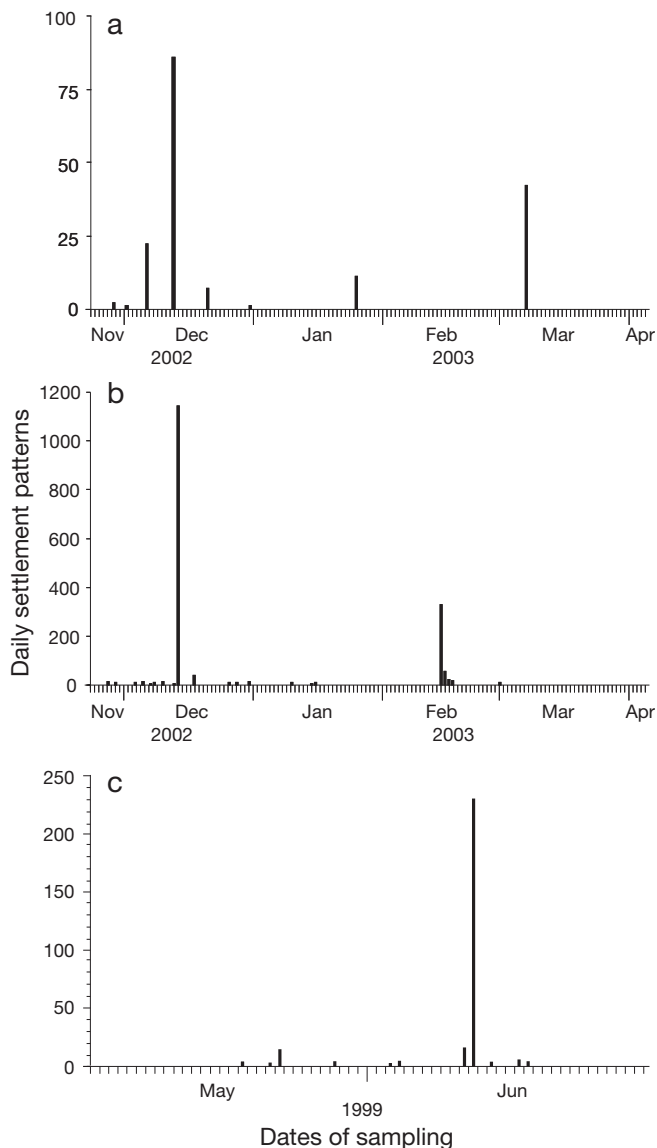


Fig. 1. *Diplodus vulgaris* and *D. sargus*. Daily settlement patterns of *D. vulgaris* in the winter season (22 November 2002 to 4 April 2003) at (a) Banyuls and (b) St Marie, and (c) of *D. sargus* in the summer season (1 May 1999 to 30 June 1999) at St Marie

cohort abundance over time followed an exponential model (Abundance = Initial abundance  $\times$  Exp $[-0.019 \times$  Days since settlement],  $r^2 = 0.79$ ,  $n = 120$ ,  $p < 0.001$  at Banyuls; Abundance = Initial abundance  $\times$  Exp $[-0.017 \times$  Days since settlement],  $r^2 = 0.87$ ,  $n = 120$ ,  $p < 0.001$  at St Marie). Mortality for the *D. sargus* cohort was 80.8% after 4 mo at St Marie (Fig. 2c). The cohort decrease across time followed an exponential model (Abundance = Initial abundance  $\times$  Exp $[-0.021 \times$  Days since settlement],  $r^2 = 0.91$ ,  $n = 120$ ,  $p = 0.007$ ).

### Growth

*Diplodus* recruits grew on average from 8.8–10.0 mm at settlement to 27.1–29.7 mm for *D. vulgaris* and to 57.0 mm for *D. sargus* after 4 mo (Table 1). Growth showed a significant difference with time and species (2-way ANOVA; time:  $F_{4,285} = 16889.64$ ,  $p < 0.001$ ; species:  $F_{2,285} = 9042.21$ ,  $p < 0.001$ ). The interaction between the 2 factors was also significant (Time  $\times$  Species:  $F_{8,285} = 1492.73$ ,  $p < 0.001$ ). The growth of *D. vulgaris* cohorts was different between the 2 sites (Student-Newman-Keuls post hoc tests;  $p < 0.001$ ), and *D. sargus* showed faster growth than *D. vulgaris* (Student-Newman-Keuls post hoc tests;  $p < 0.001$ ). The coefficient of variation (CV) in size of both *Diplodus* species decreased from settlement over 4 mo (Fig. 3a). This decrease was significantly correlated with time at St Marie for both *Diplodus* species (Spearman correlation test; *D. vulgaris*:  $r = -0.90$ ,  $p = 0.03$ ; *D. sargus*:  $r = -0.94$ ,  $p = 0.03$ ), but not for *D. vulgaris* at Banyuls ( $r = -0.78$ ,  $p = 0.07$ ).

### Parasitism

The only parasites that were found in juveniles of both *Diplodus vulgaris* in the winter and *D. sargus* in the summer were encysted digeneans in muscle. The cysts were found at the base of the dorsal and caudal fins. Parasite abundance decreased significantly with time ( $F_{5,342} = 2.60$ ,  $p = 0.03$ ), and this decrease varied according to species ( $F_{2,342} = 8.58$ ,  $p < 0.001$ ). The interaction between the 2 factors was not significant ( $F_{10,342} = 0.84$ ,  $p = 0.56$ ). *D. vulgaris* at both sites was more parasitised than *D. sargus* (Student-Newman-Keuls post hoc tests;  $p < 0.001$ ; Table 1). The prevalence of *D. vulgaris* at both sites decreased from settlement over 4 mo (Fig. 3b), but not significantly (Banyuls:  $r = -0.77$ ,  $p = 0.10$ ; St Marie:  $r = -0.82$ ,  $p = 0.08$ ). In contrast, the prevalence of *D. sargus* showed a significant decrease over time ( $r = -0.82$ ,  $p = 0.03$ ; Fig. 3b).

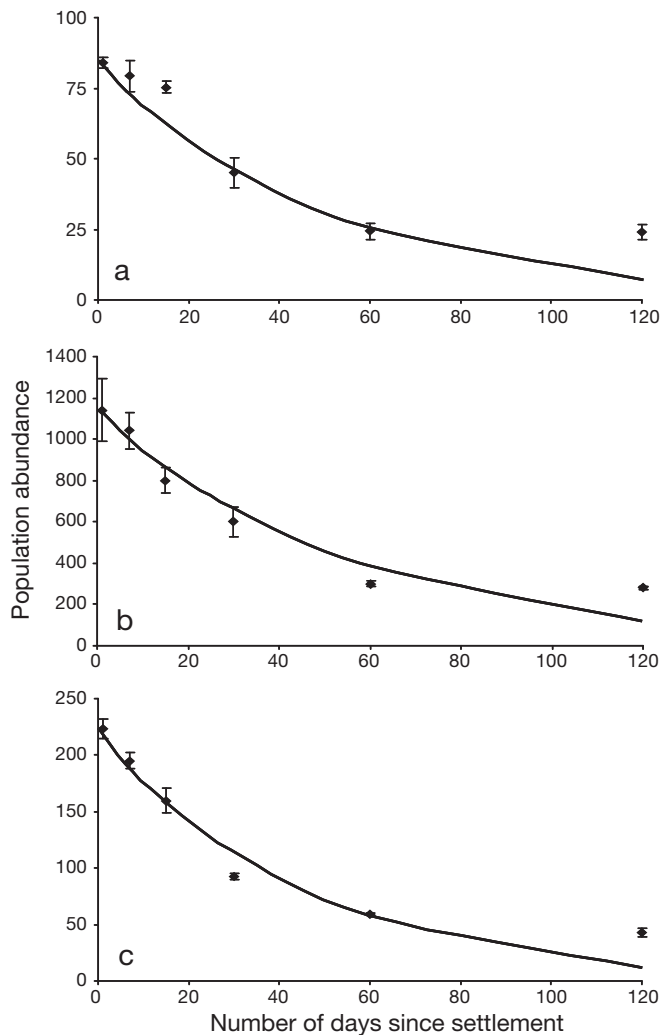


Fig. 2. *Diplodus vulgaris* and *D. sargus*. Decrease in population abundance over the first 4 mo post-settlement for (a) a *D. vulgaris* cohort arriving on 10 December 2002 at Banyuls; (b) a *D. vulgaris* cohort arriving on 13 December 2002 at St Marie; and (c) a *D. sargus* cohort arriving on 12 June 2003 at St Marie. Population decrease was monitored on the following days post-settlement: Days 0, 7, 15, 30, 60 and 120. Error bars represent the SE of 3 successive underwater visual counts along the jetty or inside the bay

## DISCUSSION

Our study examined patterns of survival and growth, as well as within-cohort variance in length and parasite load over a period of 4 mo post-settlement for 2 closely related reef fishes in the Mediterranean. Mortality of *Diplodus* juveniles in each cohort was high (between 71 and 81%; Fig. 2), and mortality did not seem to act randomly in *D. vulgaris* and *D. sargus* cohorts.

As the present work is based on surveys of the same cohort through time, before interpreting the results, we must be sure that fish surveyed belong to the same cohort (i.e. no overlap between successive settlement pulses and no emigration of individuals out of the surveyed areas). At settlement, *Diplodus* larvae are transparent and ~8 to 10 mm total length. Planes et al. (1998, 1999) showed that from the first post-settlement day, they quickly develop juvenile pigmentation patterns. This allows us to distinguish between *Diplodus* individuals on the first day of settlement and older conspecifics (i.e. larvae arriving on the second pulse being clearly identifiable from those from the first pulse). Thus, after the *D. vulgaris* cohort on 10 December and the *D. sargus* cohort on 12 June, the next significant settlement pulse did not occur before 1 mo (Fig. 1). This absence of overlap between successive settlement pulses allowed us to identify and easily follow one larval cohort during several months.

The most difficult problem, when following mortality, is to distinguish between mortality and emigration of individuals out of the survey areas. Several studies showed that *Diplodus* juveniles had a limited migration (about 50 m around the settlement habitat) and did not cross unsuitable habitats such as sandy areas (Harmelin-Vivien et al. 1995, Planes et al. 1998, 1999). Romans (2003) monitored *D. vulgaris* and *D. sargus* daily during the winter and summer seasons, respectively. He showed that no *Diplodus* juvenile was observed between jetties or bays, and that bays and jetties were the only settlement habitats of *Diplodus* in

Table 1. *Diplodus vulgaris* and *D. sargus*. Mean ( $\pm$ SE) of size and digenean parasite abundance examined to determine the causes of mortality of *D. vulgaris* and *D. sargus* at 2 sites in the Mediterranean Sea during the first 4 mo post-settlement. Parameters are given on the first day of settlement (Day 0) and then days after settlement. na: data not available

Day	Standard length (mm) (n = 20)			Parasite abundance (ind. fish <sup>-1</sup> ) (n = 20)		
	<i>D. vulgaris</i> Banyuls	<i>D. vulgaris</i> St Marie	<i>D. sargus</i> St Marie	<i>D. vulgaris</i> Banyuls	<i>D. vulgaris</i> St Marie	<i>D. sargus</i> St Marie
0	8.96 ( $\pm$ 0.53)	8.85 ( $\pm$ 0.53)	10.00 ( $\pm$ 0.01)	7	13	4
7	9.43 ( $\pm$ 0.54)	9.68 ( $\pm$ 0.52)	11.8 ( $\pm$ 0.10)	10	6	4
15	13.13 ( $\pm$ 0.52)	12.75 ( $\pm$ 0.54)	15.69 ( $\pm$ 0.11)	6	9	1
30	16.18 ( $\pm$ 0.62)	15.22 ( $\pm$ 0.76)	25.29 ( $\pm$ 0.21)	5	4	0
60	20.13 ( $\pm$ 0.83)	19.86 ( $\pm$ 0.60)	35.87 ( $\pm$ 0.30)	4	4	0
120	29.72 ( $\pm$ 0.92)	27.06 ( $\pm$ 0.82)	57.02 ( $\pm$ 0.23)	na	na	0

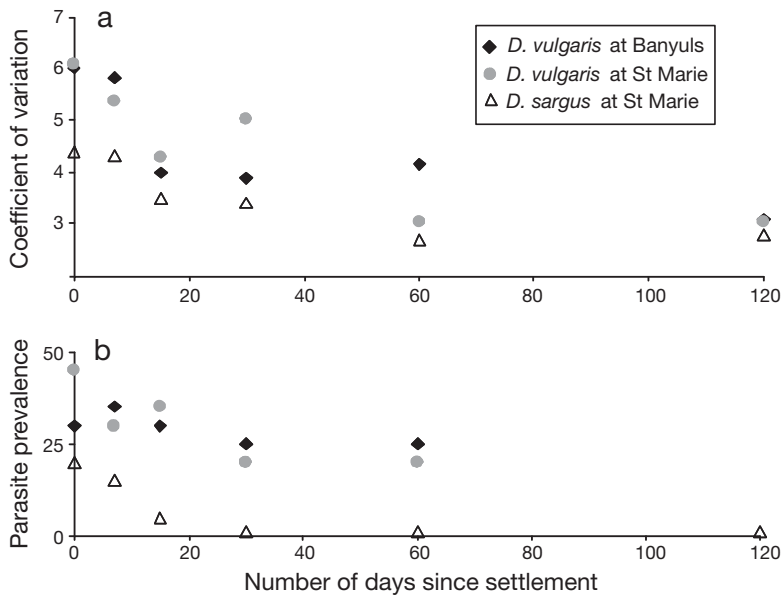


Fig. 3. *Diplodus vulgaris* and *D. sargus*. Evolution in (a) the coefficient of variation of size and (b) parasite prevalence (% of parasitised fish) of both *Diplodus* species at both sampling sites over the first 4 mo post-settlement

the sampling areas (Banyuls and St Marie). This habitat restriction during the first post-settlement months made the fish easy to count in settlement habitats, and we assumed that fish did not move between bays or jetties.

Mortality was influenced by size (Fig. 3a). Indeed, the complete spectrum of variability in size of recently settled juveniles at settlement was not transferred through to the *Diplodus* cohorts 4 mo later, suggesting that, contrary to expectations of random fish mortality, surviving fish show less variation in size (e.g. Vigliola & Meekan 2002, Hoey & McCormick 2004, Gagliano et al. 2007). Mortality processes can thus operate in a size-selective manner, with viability selection acting either on larger or smaller fish sizes in *Diplodus* cohorts. Meekan et al. (2006) showed that selective mortality acted to preferentially remove fish that were slow-growing in *Spratelloides gracilis* cohorts ('bigger is better' template, reviewed by Sogard 1997). Examples of viability selection acting on smaller fish sizes have also been reported, typically in response to selective predation on larger fish by non-gape-limited predators, such as birds or humans (Fenberg & Roy 2008). Our sampling protocol was not able to determine if viability selection acted either on larger or smaller fish sizes; only the back calculation of size from otoliths allows the direction of size-selective mortality to be identified (e.g. Vigliola & Meekan 2002, Vigliola et al. 2007). Nevertheless, our sampling protocol highlighted that the timing and strength of size selection varied according to location and *Diplodus* species

(Fig. 3a), with the strongest size selection present in the cohort with the highest initial density (*D. vulgaris* at St Marie). The non-significant decrease in the coefficient of variation in length for *D. vulgaris* at Banyuls could thus be explained by a low initial density (172 *D. vulgaris* larvae at Banyuls compared to 1741 *D. vulgaris* larvae at St Marie). These results may therefore be consistent with density-dependent mortality selecting against individual variation (Vigliola et al. 2007). However, processes other than selective mortality could also result in a decrease in the coefficient of variation in length of fish over time (e.g. compensatory growth, size-dependent emigration; Arendt 1997, Carlson et al. 2004, Gagliano & McCormick 2007).

The most significant result, in terms of process-driven analysis, is certainly that parasite abundance of both *Diplodus* species at both sites decreased significantly with time (Table 1), and prevalence decreased significantly with time for *D. sargus* at St Marie (Fig. 3b). Many parasites adversely affect their hosts or modify host behaviour to increase the host's vulnerability to

predation in order to enhance the parasite's transmission to the definitive hosts (e.g. Combes 1995, Sasal et al. 2000, Bourque et al. 2006). In the case of the digenean metacercarian cyst found in *D. vulgaris* and *D. sargus*, the only transmission pathway after *Diplodus* is via their predation (Combes 1995). These digenean cysts were located at the basal section of dorsal and caudal fins, the most important fins for swimming performance in fish. Therefore, digeneans may have evolved to reduce the swimming capability of their intermediate host in order to increase predation by the final host. Alternatively, reduced swimming capacity of fish would diminish their foraging ability and reduce their condition. Regardless of the mechanism, selective mortality appears to be acting on parasite load. However, the influence of parasitism on mortality must be treated with caution, as less than 50% of *Diplodus* juveniles were infected with parasites at settlement and the abundance of parasites on infected individuals was low (1 to 13 fish<sup>-1</sup>; Table 1).

## CONCLUSIONS

Selective mortality appears to be acting on both fish size and parasite infection. If mortality of recently settled juveniles was random with respect to fish size and parasite load, the complete spectrum of variability of these phenotypes would be transferred through to the adult population of *Diplodus* species, which is contrary to our findings. The conclusions of this study should

nevertheless be treated with caution, as selection pressures are often context-dependent and are likely to fluctuate both in time and space due to variation in biotic and abiotic factors (Carlson & Quinn 2007). For example, the coefficient of variation in size significantly decreased with time for *D. vulgaris* at St Marie, but not at Banyuls. Holmes & McCormick (2006) showed that the extent to which mortality was size selective immediately after settlement can differ among locations separated only by hundreds of metres. The conflicting results in our study suggest that mortality at settlement is not always acting on fish with a small body size and/or high parasite load, and that mortality depends on conditions into which individuals settle (Gagliano & McCormick 2007). Therefore, future studies on other species exploring the spatio-temporal variability of these processes should test the hypotheses outlined here in terms of size- and parasitism-selective mortality of marine species.

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