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Effect of pelagic larval growth and size-at-hatching on post-settlement survivorship in two temperate labrid fish of the genus *Symphodus*

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ABSTRACT: The characteristics of fish larvae affect settlement and recruitment survival. We examined the effects of the variation in the early life characteristics (pelagic larval growth, pelagic larval duration, size-at-hatching and size-at-settlement) on post-settlement survival in 2 littoral species of the genus *Symphodus* (*S. roissali* and *S. ocellatus*) in the NW Mediterranean over 2 yr. We used otoliths to back-calculate growth rates and other early life traits exhibited by individuals at settlement and 2 mo after settlement. Size-at-hatching clearly affected the post-settlement survival of the 2 species. Juvenile survivors of *S. roissali* and *S. ocellatus* were mostly larger at hatching than settlers, and recently settled individuals were susceptible to size-selective mortality. Our study, however, showed that other larval traits (pelagic larval duration, larval otolith growth, size-at-age, size-at-settlement) were not always consistent with the growth–mortality hypothesis.

KEY WORDS: Size selection · Post-settlement mortality · Larval growth · Early larval traits · Labridae · Otoliths

INTRODUCTION

One of the main objectives of research on fish populations is to identify the factors that determine the number of new individuals recruited to the adult stage each year (year-class strength) (e.g. Doherty & Fowler 1994, Caley et al. 1996, Macpherson et al. 1997, Caselle 1999). In some species, mortality rates in juvenile stages are size-selective, and small fish have a lower survivorship than larger ones of the same age, which gives cause to the ‘growth–predation theory’ or the ‘bigger is better concept’ (Anderson 1988, Bailey & Houde 1989, Leggett & DeBlois 1994). This is usually explained because, when mortality is size-dependent, fast-growing larvae and settlers are exposed to predators for a shorter period than those that grow more slowly. These processes have been studied by analysing some early life traits (e.g. growth rate, larval duration, size-at-hatching, size-at-settlement). Individuals with rapid growth (e.g. Meekan & Fortier 1996, Hare & Cowen 1997, Searcy & Sponaugle 2000, 2001, Shima & Findlay 2002) and/or with a larger size-at-hatching (Vigliola & Meekan 2002) have a higher survivorship than those with a lower growth rate and/or smaller size-at-hatching. Consequently, those that grow more quickly contribute more efficiently to the year-class strength and recruitment success (Bergenius et al. 2002, Wilson & Meekan 2002). However, other studies have questioned the generality of ‘the growth–predation theory’ (Litvak & Leggett 1992, Pepin et al. 1992) and others have shown that the intensity of size-selective mortality may vary from year to year (Meekan & Fortier 1996).

In spite of the interest in elucidating the effect of early life traits on fish settlement, few studies have examined these processes (e.g. Meekan & Fortier 1996, Hare & Cowen 1997, Searcy & Sponaugle 2001, Shima & Findlay 2002, Vigliola & Meekan 2002, Wilson & Meekan 2002). Here, we examined the effects of variation in the early life characteristics (pelagic larval

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growth, pelagic larval duration, size-at-hatching and size-at-settlement) on post-settlement survival in 2 littoral species of the genus *Symphodus* (*S. roissali* and *S. ocellatus*) in the NW Mediterranean over 2 yr. We hypothesise that if 'the growth–predation theory' is applicable to these species, then we will observe that post-settlement survivorship is significantly dependent on their early life characteristics.

MATERIALS AND METHODS

Study species. *Symphodus roissali* and *S. ocellatus* are small species (<15 cm) that are quite common at shallow depths (0 to 15 m) on rocky bottoms and in seagrass beds in the Mediterranean Sea (e.g. Harmelin-Vivien & Francour 1992, Macpherson et al. 2002). Spawning takes place in nests built and defended by the dominant males (Van den Berghe 1990, Raventos 2004). In *S. roissali* mating activity begins at the end of March and ends in mid-June, while in *S. ocellatus* it runs from late May to early July. Settlement in these 2 species occurs always on branching algae, at depths shallower than 8 m (García-Rubies & Macpherson 1995), when individuals have attained a size of around 5 to 7 mm (Raventos & Macpherson 2001). Planktonic larval duration (PLD) is short in both species, lasting 11 to 14 d in *S. roissali* and 8 to 11 d in *S. ocellatus* (Raventos & Macpherson 2001), and larvae are retained nearshore (Sabatés et al. 2003).

Sampling protocol. Field sampling was performed along the shore off Blanes, Spain (41° 40′ 9″ N, 2° 47′ 9″ E, NW Mediterranean), at depths between 3 and 6 m over a 2 yr period (2001 and 2002). We collected individuals of the 2 species at settlement, 0 to 2 d after settlement, ca. 5 to 7 mm (the 'settlement' group) and juveniles, 60 to 70 d after settlement, ca. 3 to 4 cm (the 'juvenile' group). Settlement sampling was conducted daily from 1 April to 31 July in 2001 and 2002. These dates spanned the entire settlement periods for the 2 species in the area (Raventos & Macpherson 2005). Settlement of *Symphodus roissali* began in mid-April in 2001 and in mid-May in 2002 and ended in mid-June in both years, whereas settlement of *S. ocellatus* began at the end of June and ended in mid-July in both years. New settlers of *S. roissali* and *S. ocellatus* were collected using cores (400 cm^2 in cross-sectional surface area, 5 l volume) taken from drifting algal accumulations, where the new settlers were commonly observed (Raventos & Macpherson 2005).

Juveniles of the 2 species were collected by divers using hand-nets. These juveniles were sampled at the end of July (*Symphodus roissali*) and at the end of August (*S. ocellatus*). They were always found around branched algae, and were easily recorded and collected. To avoid sampling biases (Vigliola & Meekan 2002), we collected all individuals from algal patches situated ca. 300 m from the sampling area of new settlers. Algal patches (ca. 5 to 10 m^2) were haphazardly selected to conduct diving and sampling.

Otolith analysis. At the laboratory, all new settlers and juveniles were identified and measured to the nearest 0.01 mm, and the otoliths (lapilli) were extracted and mounted in an oil droplet on a microscope slide. Age readings were made, and the presence of settlement marks were determined using a light microscope connected to a digital camera and image analysis system, following the standard methodology described by various authors (e.g. Wellington & Victor 1992, Raventos & Macpherson 2001).

Eggs of both species were reared in aquaria to determine whether the first growth increment was laid down on the first day of the larval stage. This yielded both the date of formation of the first band (the same as the date of hatch) and the daily pattern of band deposition. Based on these experiments, band deposition was confirmed to take place daily from the first day of hatch. Settlement marks were always clear in these species and belonged to Type III, a gradual settlement mark with optical contrast between the pre- and post-settlement zones (Wilson & McCormick 1999, Raventos & Macpherson 2001).

Each otolith was read twice, and when the readings differed by more than 2 d, the otoliths were discarded (<5% discarded for each species, see also below). Ages of settlers and juvenile survivors were used to back-calculate the birthdate frequency distribution of each group. We analysed the otoliths along the longest radius from the centre to the edge, and recorded otolith width for each day during the pelagic larval period. This procedure was repeated 3 times to minimise measurement errors. We also recorded the size-at-hatching (the first increment), size-at-settlement and PLD.

A total of 204 individuals of *Symphodus roissali* and 202 *S. ocellatus* was used in the analyses (*S. roissali*, 137 individuals in 2001 [86 new settlers and 51 two-mo-old juveniles] and 67 individuals in 2002 [34 and 33, respectively]; *S. ocellatus*, 106 individuals in 2001 [55 and 51, respectively] and 96 individuals in 2002 [50 and 46, respectively]).

Data analysis. To avoid biases in back-calculating somatic growth (Vigliola et al. 2000), we based comparisons of early traits, growth rate and size on otolith measurements (Hare & Cowen 1997, Searcy & Sponaugle 2001).

In order to know if fish that arrived early in the settlement period (first half) differ from those that arrived late (second half), we compared early larval traits between these 2 cohorts. No significant differences were found between the cohorts for otolith size-at-hatching, otolith growth rate, size-at-settlement or age-at-settlement (*t*-test, $p > 0.05$ in all cases). These results were observed in both years of study. Therefore all data were considered together.

Selective mortality on the basis of early traits for each species was examined by comparison of the growth trajectory of the cohort back-calculated from the otoliths from each group (settlers and juveniles).

Cochran's test was used to determine the optimal transformation to improve normality and homogeneity of variance of the data. Repeated MANOVAs (multivariate analyses of variance) were used to compare estimates of the growth trajectory and length-at-age of the 2 groups (Chambers & Miller 1995, Meekan & Fortier 1996). Wilks' λ was used as the test statistic (see also Searcy & Sponaugle 2001). The number of individuals in this design guaranteed its statistical power, since it complied with the constraints recommended by Maxwell & Delaney (1990) and Von Ende (1993). To determine whether there was selective mortality based on age-at-hatching, pelagic larval duration and size-at-settlement, we compared settler versus juvenile groups using standard ANOVA (analysis of variance) techniques (e.g. Searcy & Sponaugle 2001, Vigliola & Meekan 2002). Power tests to measure the adequacy of sample sizes on all non-significant ANOVA results were considered using the Pearson & Hartley method (Zar 1984).

RESULTS

The relationship between otolith length and body length was highly significant (least-squares-fit regression) for both species of *Symphodus*, indicating that otolith radii along their longest axes were good predictors of the standard length of fishes. The relationships were: for *S. roissali* fish length = 0.35 + 0.0058 (otolith radii) ($r^2 = 0.80$, $p < 0.001$, $n = 130$) and for *S. ocellatus* fish length = 0.38 + 0.0086 (otolith radii) ($r^2 = 0.75$, $p < 0.001$, $n = 93$).

The birthdate frequency distributions of settlers and juvenile survivors of both species overlap each other (Fig. 1), indicating that juvenile populations are formed by individuals arriving from the entire settlement period.

The growth of *Symphodus roissali* was initially fast until 3 d after hatching, after which it decreased rapidly until 6 to 7 d after hatching, increasing again thereafter (Fig. 2a,c). Juveniles (2 mo after hatching) of this species exhibited consistently faster growth and larger size-at-age than settlers only in 2001. At all ages, individuals in the juvenile group were larger than those that belonged to the settler group (Fig. 2a,b). These trends, however, did not differ significantly in 2002 (repeated-measures MANOVA,

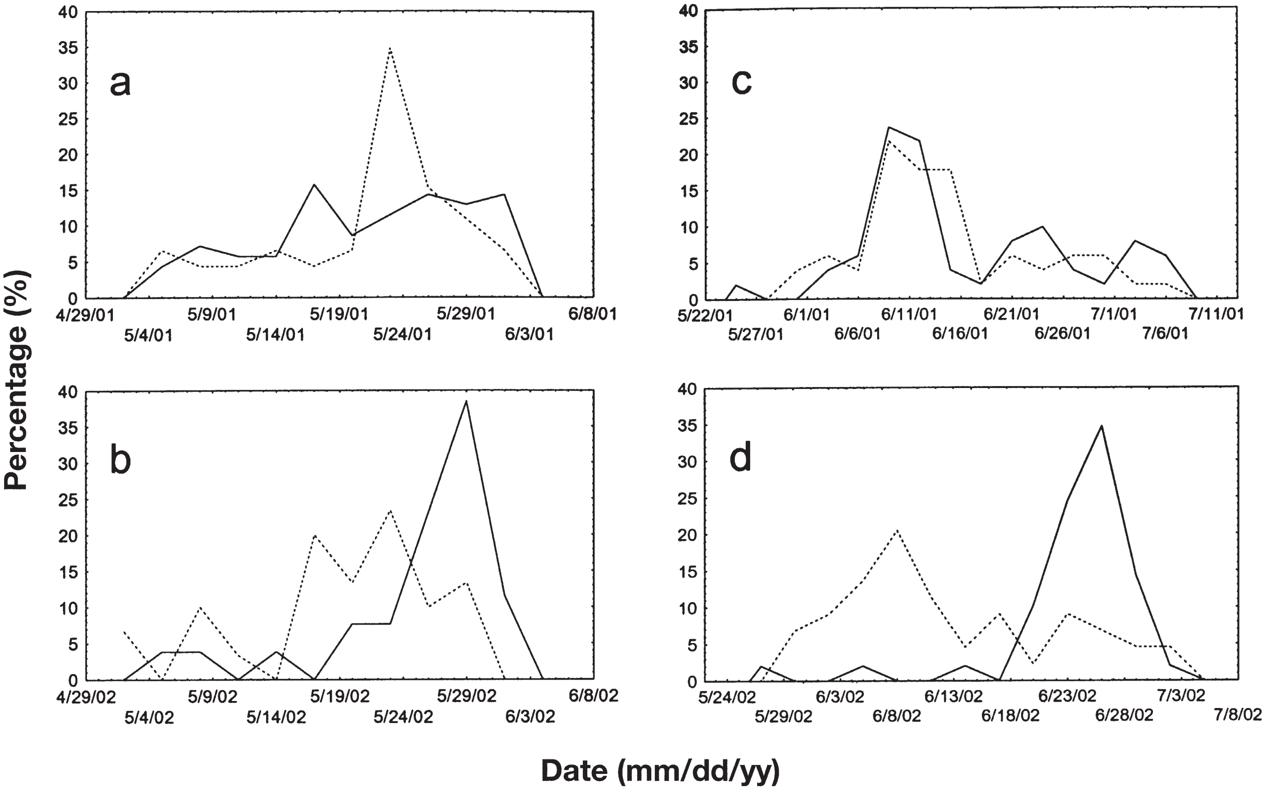

Fig. 1. (a,c) *Symphodus roissali* and (b,d) *S. ocellatus* birthdate frequency distributions (%) of settlers (solid line) and juveniles (dashed line)

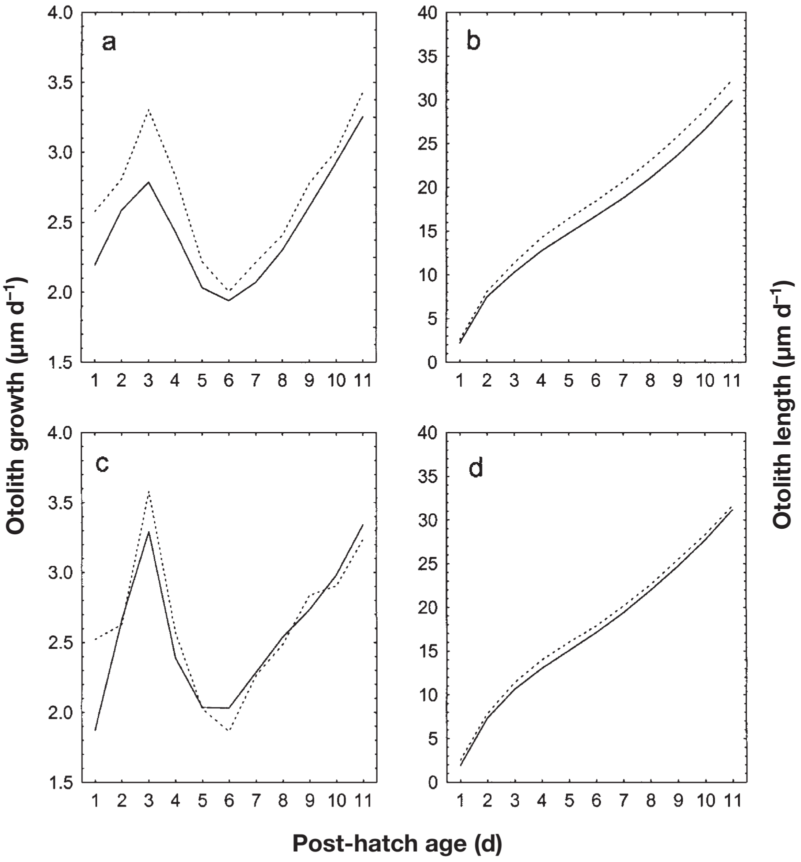

Fig. 2. *Symphodus roissali*. Mean larval otolith growth rate trajectories (µm d^{-1}) and length-at-age (µm) for settlers (solid line) and 1 mo old juveniles (dashed line). (a,b) Year 2001; (c,d) year 2002

Table 1. *Symphodus roissali* and *S. ocellatus*. Results of repeated-measures MANOVA comparisons of larval otolith length and growth of settlement group (Set) versus juvenile group (Surv) (2 mo after settlement)

	Measure	df	Wilks' λ	*F*	p	Trend
S. roissali						
2001	Length	10,108	0.825	20.12	0.0001	Set < Surv
	Growth		0.898	11.23	0.001	Set < Surv
2002	Length	11,57	0.87	1.90	0.174	–
	Growth		0.68	0.51	0.477	–
S. ocellatus						
2001	Length	8,98	0.909	0.15	0.697	–
	Growth		0.914	0.35	0.556	–
2002	Length	8,88	0.553	11.89	0.0009	Set > Surv
	Growth		0.507	33.30	0.0001	Set > Surv

Fig. 1, Table 1). Settlers in 2002 showed faster growth than juveniles only until Day 5 after hatching (Fig. 2c). Furthermore, size-at-age did not differ significantly between the 2 groups (Fig. 2d). PLD was not significantly different for juveniles (ANOVA, Table 2). In only a single year (2001) was the otolith size in the settlement group significantly higher than that in the juvenile group (ANOVA, $p < 0.001$, Table 2). In contrast, size-at-hatching was significantly higher for the juvenile group in the 2 years of sampling (ANOVA, $p < 0.001$, Table 2).

The initial growth trajectory for *Symphodus ocellatus* showed a similar pattern to that of *S. roissali*. Growth increased until Day 3 after hatching, decreased slowly until Days 6 to 7 and increased thereafter (Fig. 3a,c). However, no significant differences in larval otolith growth and size-at-age between settlers and juveniles were observed in 2001 (repeated-measures MANOVA, Fig. 3a,b, Table 1). In contrast, the results in 2002 showed significant differences in these 2 traits between settlers and juveniles. However, contrary to expected results, settlers grew faster and had larger size-at-age than juveniles (repeated-measures MANOVA, Fig. 3b,d, Table 1). In addition, no significant differences in size-at-hatching, PLD or size-at-settlement were observed in 2001 (ANOVA, Table 2). In contrast, in 2002, the width of the otolith band at hatching was significantly wider for juveniles than settlers (ANOVA, $p < 0.01$, Table 2), while the PLD was shorter for juveniles and length-at-settlement was significantly greater for settlers (ANOVA, $p < 0.001$, Table 2).

For both species, the power of the ANOVA, which usually falls below the desired power of 0.8 (Zar 1984), opens the possibility that non-significant differences could be attributable in some cases to sample size. However, given the small magnitude of the differences between mean values and the relatively small standard deviations characterising non-significant results (Table 2), larger sample sizes would be unlikely to change the significance of the tests.

PLD was negatively correlated with size-at-hatching and size-at-settlement in both species and in both years (regression coefficients were always significant, $p < 0.01$ in all cases, although explaining a

Table 2. *Symphodus roissali* and *S. ocellatus.* Data and results of ANOVA of early life-history traits of settlement group (Set) versus juvenile group (Juv). NS: not significant

Group	n	Size-at-hatching (µm)		Pelagic larval duration (d)		Otolith length-at-settlement (µm)	
		Mean (SD)	ANOVA	Mean (SD)	ANOVA	Mean (SD)	ANOVA
S. roissali							
2001							
Set	86	1.94 (0.64)	0.0006	12.57 (1.73)	NS	35.11 (4.19)	0.00004
Juv	51	2.34 (0.56)		12.78 (1.55)		39.11 (3.96)	
2002							
Set	34	1.66 (0.82)	0.0007	12.20 (1.49)	NS	36.29 (3.28)	NS
Juv	33	2.37 (0.46)		12.76 (1.25)		37.14 (3.13)	
S. ocellatus							
2001							
Set	55	1.62 (0.54)	NS	10.30 (1.09)	NS	37.13 (3.05)	NS
Juv	51	1.66 (0.44)		10.20 (0.89)		37.25 (4.10)	
2002							
Set	50	1.46 (0.56)	0.004	10.53 (1.12)	0.0001	35.47 (3.12)	0.02
Juv	46	1.75 (0.39)		9.36 (0.92)		33.92 (3.26)	

low percentage of the variance, r^2 ranging between 0.04 and 0.16). However, size-at-hatching was never related to size-at-settlement ($r^2 < 0.01$ and $p > 0.5$ in all cases).

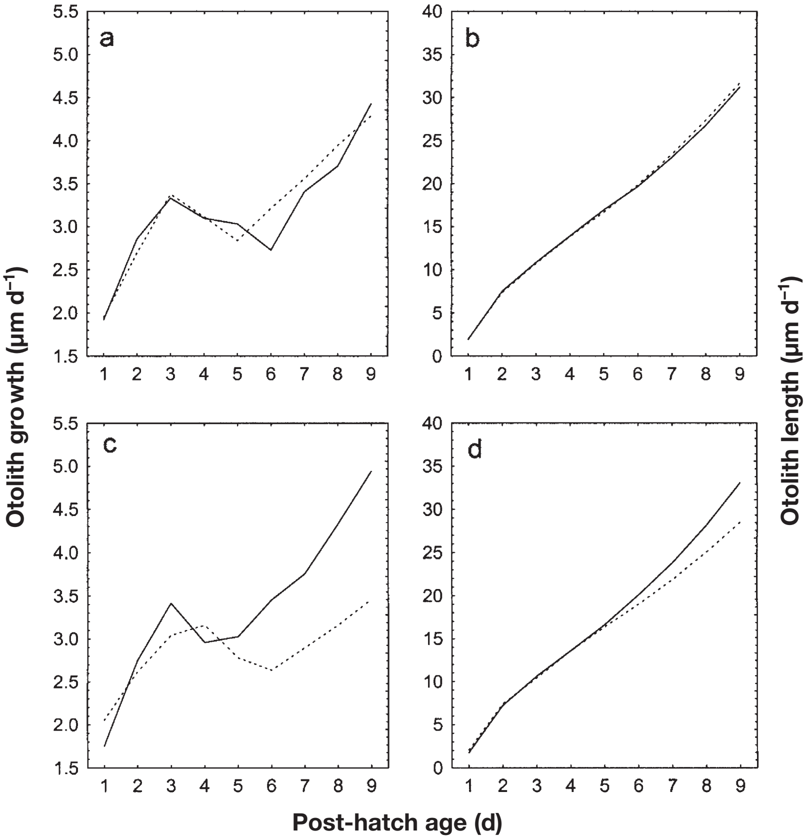

Fig. 3. *Symphodus ocellatus*. Mean larval otolith growth rate trajectories (µm d^{-1}) and length-at-age (µm) for settlers (solid line) and 1 mo old juveniles (dashed line). (a,b) Year 2001; (c,d) year 2002

DISCUSSION

Size-at-hatching usually affects the post-settlement survival of *Symphodus roissali* and *S. ocellatus.* Juvenile survivors of these 2 species showed larger sizes-at-hatching than settlers, and generally revealed that recently settled individuals are susceptible to size-selective mortality. Our results, however, showed that other larval traits (pelagic larval duration, larval otolith growth, size-at-age, size-at-settlement) were not always related to size-at-hatching, nor were they consistent with the growth–mortality hypothesis of Anderson (1988). Although most of these traits are correlated each other (Sogard 1997, Searcy & Sponaugle 2001, Shima & Findlay 2002, Vigliola & Meekan 2002), our results indicated that only size-at-hatching predicted the presence of selective mortality. The absence of a clear pattern in the comparison of growth trajectories and related indices (planktonic larval duration and size-at-settlement) between settlers and juveniles indicates that the intensity of size-selective mortality may also vary from year to year, as reported for *Gadus morhua* (Meekan & Fortier 1996).

This selective mortality has been observed in other newly settled fishes. Individuals of *Pomatomus saltatrix* with faster growth have a higher probability of survival (Hare & Cowen 1997). In addition, the feeding conditions of juvenile *Stegastes partitus* affect their survivorship (Booth & Hixon 1999). Surviving juveniles of 2 coral reef species, *Thalassoma bifasciatum* and *Halichoeres bivittatus*, suffer size-selective mortality during early post-settlement (Searcy & Sponaugle 2001). Fast-growing larvae of *Paralabrax clathratus* experience enhanced survival during the first days after settlement relative to larvae with slower growth (Shima & Findlay 2002). Individuals of *Neopomacentrus filamentosus* that survive intense selective mortality after settlement are the largest members of the cohort at hatching and grow faster during planktonic life (Vigliola & Meekan 2002). Other studies, both in marine (e.g. Rosenberg & Haugen 1982, Crecco et al. 1983, Hovenkamp 1992, McCormick & Molony 1992, Suthers et al. 1992) and in freshwater fishes (e.g. Rice et al. 1987, Titus & Mosegaard 1991, Ludsin & de Vries 1997) report a similar pattern.

Furthermore, these studies emphasise the size advantages that allowed post-settlers to survive the settlement period, when mortality caused by predation is intense (Macpherson et al. 1997, Caselle 1999, Schmitt & Holbrook 1999). However, our results showed that these size advantages were not always applicable in the 2 species of *Symphodus*. The differences observed in size-at-hatching were not clearly reflected in the other indices. Therefore, we conclude that in our case the 'bigger is better' hypothesis (Miller et al. 1988) is not applicable, and that larval quality (measured as size-at-hatching) is the best indicator of juvenile viability.

The absence of a consistent trend for selective mortality on the basis of all larval traits has been reported for other species (Searcy & Sponaugle 2001). Most studies that have analysed size-selective mortality were performed in species that settle in shoals of distinct sizes, with moderately long planktonic periods (usually >3 wk) (see references above). The 2 species of *Symphodus* have a very short planktonic larval duration (PLD = 9 to 12 d), they settle individually into branching algae, which are used for hiding (Raventos & Macpherson 2005), and remain motionless until they leave the algae when they reach a size of ca. 2 to 3 cm (>40 d old), when predation pressure is presumably low (Macpherson et al. 1997, Caselle 1999). Although larvae and new settlers of *Symphodus* suffer predation by numerous species (e.g. shrimps, crabs, cannibalism, other fishes, authors' pers. obs.), the short PLD and hiding behaviour could diminish the advantages of rapid larval growth (McCormick 1998, Shima & Findlay 2002).

The effect of size-at-hatching in the posterior size-selective mortality emphasises the importance of larval condition in the early life of these species (McCormick 1998, Searcy & Sponaugle 2001). The relationship between larval size-at-hatching and the size of the eggs (Chambers 1997, Coleman & Galvani 1998) is influenced by maternal size and condition (Chambers et al. 1989, Marteinsdottir & Steinarsson 1998, Ouellet et al. 2001). As several authors have pointed out (Ludsin & de Vries 1997, Vigliola & Meekan 2002, McCormick 2003), the condition of parental stocks, through the maternal effect on larval size-at-hatching, could have a considerable effect on settlement and recruitment. Unfortunately, the potential relationships between maternal and larval conditions are unknown for *Symphodus roissali* and *S. ocellatus*, and future research is needed on these aspects (see also Bergenius et al. 2002, Wilson & Meekan 2002).

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