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Planktonic larval duration and settlement marks on the otoliths of Mediterranean littoral fishes

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Abstract The planktonic larval duration (PLD) was estimated for 42 species of littoral fishes from the northwestern Mediterranean Sea. Daily increments and settlement marks on the otoliths (sagittae or lapilli) of new settlers and post-settlers were used to determine the larval stage duration. We also used PLD in the new settlers of some species to confirm the accuracy of the settlement marks in post-settlers. The duration of the planktonic larval stage ranges from 9 days in *Symphodus ocellatus* to 55 days in *Xyrichtis novacula* and 71 days in *Lipophrys trigloides*. Species in the same family did not display any clear tendency toward having similar PLDs. On the other hand, larval duration tended to be similar within a genus, with the exception of *Lipophrys*. Among conspecifics, the time spent in the plankton usually varied only by 2–7 days, except in *Aidablennius sphynx, Lipophrys trigloides*, *Coris julis* and *Thalassoma pavo*. No clear patterns were discernible in genera, with some species that settled in winter and other species that settled in summer, although we observed a certain tendency of individuals of closely related species (e.g. family Sparidae) to have a shorter larval duration in the warmer part of the year than in the colder part of the year. Settlement marks have been observed on the otoliths of all the species studied, and the PLDs in new settlers are an appropriate means of validating settlement marks. A rapid decrease in increment width over settlement (type Ia) is the most common type of mark (66.7% of the total species studied).

Introduction

Most marine fishes have complex life histories that include a pelagic larval stage. The influence of larval stage duration on dispersal and larval mortality is an important factor in species ecology (e.g. Bailey et al. 1995), and can influence not only specific biogeography but also settlement rates and patterns of recruitment to the adult population, with the resulting effects on community structure (Doherty 1991; Leis 1991; Victor and Wellington 2000).

The discovery of daily incremental marks and settlement marks on the otoliths of many fishes (Panella 1971; Brothers et al. 1983; Wilson and McCormick 1997, 1999) has furnished a means of ageing fishes on a daily basis and thus determining the amount of time they have spent in the plankton prior to settlement. Settlement marks have been used in various studies to detect life-history events, and in recent years have proved to be extremely useful in establishing when larvae settle to the bottom (Wilson and McCormick 1997, 1999). Daily increments and settlement marks also make it possible to perform back-calculations, providing interesting insights into settlement patterns in fishes (Danilowicz 1997; Vigliola et al. 2000).

Larval duration has been shown to vary considerably among species, from a few days to several months, without any clear patterns within a family or in a given geographic area (e.g. Brothers and McFarland 1981; Brothers et al. 1983; Victor 1986a,b; Fowler 1989; Wellington and Victor 1989, 1992; Victor and Wellington 2000). However, the different features characterising settlement marks that indicate the end of the larval stage on the otolith do present certain patterns among the species that have been studied. Settlement marks that take the form of an abrupt change in the width and appearance of bands at settlement are more common than settlement marks that take the form of a gradual alteration in the width of daily increments (Wilson and McCormick 1999).

Most studies on the planktonic larval duration (PLD) in fishes have been carried out in tropical regions; studies in temperate seas have been less common (Wellington and Victor 1989, 1992, and references therein). Studies of this kind are practically non-existent for the Medi-

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terranean Sea, and larval stage duration is known for only a very few species, e.g. *Diplodus puntazzo*, *D. sargus* and *D. vulgaris* (Vigliola et al. 2000); *Coryphaena hippurus* (Morales-Nin et al. 1999); and *Merluccius merluccius* (Arneri and Morales-Nin 2000). The littoral zone in the Mediterranean is inhabited by some 300 species, nearly 100 of which normally dwell at depths of < 50 m, primarily fishes in the families Sparidae, Labridae, Blenniidae and Gobiidae (Whitehead et al. 1986). In most of these species settlement occurs at depths of only a few metres in well-defined habitats, typically in spring and summer (García-Rubiés and Macpherson 1995; Harmelin-Vivien et al. 1995; Macpherson and Zika 1999).

The object of the present study was to estimate larval duration in 42 common species in the littoral zone in the western Mediterranean. This information will be particularly useful for increasing our knowledge of the ecology of littoral-dwelling Mediterranean fishes and for comparison with findings reported for other geographic areas with a view to drawing general conclusions from the patterns observed.

Materials and methods

Study species and sampling procedure

PLD was estimated for 42 species belonging to 13 families collected in the north-western Mediterranean Sea. The families were (number of species in parentheses): Apogonidae (1), Atherinidae (2), Blenniidae (7), Clinidae (1), Gadidae (1), Gobiesocidae (3), Gobiidae (1), Labridae (13), Pomacentridae (1), Scorpaenidae (1), Serranidae (1), Sparidae (7) and Tripterygiidae (3) (see Table 1).

Sampling was performed on the coast off Blanes, Spain (ca. 42°02′N; 3°13′E, NW Mediterranean), with a few additional samples in the adjacent areas, between March 1999 and June 2000. A minimum of three samples were carried out weekly during the settlement period for most of the species (spring–summer) and one or two samples weekly in autumn–winter (see García-Rubiés and Macpherson 1995; Harmelin-Vivien et al. 1995; Macpherson and Zika 1999; and authors' unpublished data, for settlement period identification). Samples were collected at depths between 0 and 20 m (occasionally down to 30 m) by SCUBA divers using hand nets. In the laboratory, fish were measured within 1 h of capture, and the otoliths (sagittae and lapilli) were removed and preserved in 96% ethanol. Whenever possible, newly settled individuals of the different species were collected. New settlers were easily identifiable by their morphology, pigmentation pattern and meristic characters, following the works of Padoa (1956) and Russell (1976), as well as from personal observations obtained during the frequent samples carried out in the present work. New settlers usually changed their planktonic characters a few hours (e.g. *Aidablennius sphynx*, *Lipophrys trigloides*) or a maximum of 1–2 days (e.g. *Diplodus annularis*, *Oblada melanura*, *Symphodus roissali*) after settlement, facilitating their differentiation from older post-settlers. For those specimens, total increment counts equalled the time spent in the plankton. In the case of post-settlement specimens of those same species, we tried to identify a reference mark (e.g. a hiatus in increment formation or an abrupt change in increment width) on the otolith that was associated with settlement, using methodology similar to that described by other workers (e.g. Brothers and McFarland 1981; Brothers et al. 1983; Victor 1986a; Wilson and McCormick 1997, 1999). The size of newly settled individuals ranged from 5 to 20 mm, depending on the species (Table 1), and the size of post-settlers was in all cases < 43 mm.

Determination of larval stage duration

Otoliths were mounted on microscope slides using Eukitt as mounting medium. After mounting the otoliths were polished to expose all the daily increments within the same plane. Readings were made and increment widths measured using a light microscope connected to a digital camera and image analysis system.

One pair of otoliths consisting of a lapillus and a sagitta from each specimen were mounted and analysed. If the counts obtained for the first pair agreed, the other pair was not used. In certain species, only one of the otoliths was used, since clarity and definition varies both among and within species. The otolith in which increments were most easily visible are shown for each species in Table 1.

Pre-settlement increments were defined as those occurring from the centre of the otolith out to the settlement mark. Subdaily increments (i.e. faint increments occurring between dark, well-defined increments) were found on the otoliths of some species. Victor (1986a) and Wellington and Victor (1989) described bifurcation of increments (multiplication of increments in different focal planes) and the assumptions made in interpretation. The same criteria for interpreting which increments were daily growth increments were applied in all cases. As a general rule, the larger increments, fewer in number, were considered to have been accreted daily.

As previous authors have pointed out (e.g. Wellington and Victor 1992; Wilson and McCormick 1999; Vigliola et al. 2000), for the data reported here we can assume that the increments formed during the larval stage are daily. However, as Brothers et al. (1983) note, the time of initiation of daily increments in our study species is not known. Thus, our counts could slightly over- or underestimate the length of larval life, depending upon the exact timing of growth-increment initiation. At least for one species, *Symphodus roissali*, we have observed in larvae reared in the laboratory that the increment deposition started the first day of hatching (authors' unpublished data).

Determination of settlement mark type

The transition-centred method described by Wilson and McCormick (1997) was used in this study to identify settlement marks. This method involved centring the increment width profile for each individual on the first increment in the settlement mark rather than on the first larval increment. The mean width of the ten increments before and after the mark was calculated for the larger individuals from each species collected. Settlement mark type was classified according to Wilson and McCormick (1999):

Type I:

> an abrupt settlement mark characterised by a sharp decrease in increment width across the settlement mark; in type Ia the settlement transition was completed within one increment; in type Ib the settlement transition consisted of two or three increments.

Type II:

> a zonal settlement mark with a wide transition zone where post-settlement increments were wider than pre-settlement increments.

Type III:

> a gradual settlement mark with gradually decreasing increment width; optical contrast between the pre- and post-settlement zones was the main indicator of the settlement mark.

Results

Planktonic larval duration

On the whole, increment clarity and definition were better on the lapilli, and thus readings on the lapillus

Table 1 Larval phase duration (PLD) and settlement mark types of 40 species of Mediterranean littoral fishes. The larval durations are based on otoliths (*S* sagittae; *L* lapilli) from individuals newly settled, and on settlement marks of otoliths from post-settler individuals. The total length (*TL*, in cm) of the individuals newly settled, the mean days of larval duration, the range values (*in parentheses*) and the number of individuals (*n*) are included. Settlement-mark types are from Wilson and McCormick (1999), see "Materials and methods – Determination of settlement mark type" for further explanations. The existence of subdaily increments (*SdI*), the type of spawning (*TS*; *B* benthic; *P* pelagic) and the settlement season (*SS*; *W* winter; *Sp* spring; *S* summer) are also given

Species	PLD based on newly settled individuals			PLD based on settlement marks		Mark type	SdI	Otol.	TS	SS
	n	Mean days (range)	Mean TL (cm) (range)	*n*	Mean days (range)					
Apogonidae										
Apogon imberbis				8	22 (19–23)	Ia	No	L	B	S
Atherinidae										
Atherina boyeri	3	11 (10–12)	0.5 (0.5–0.6)	14	10.5 (9–12)	Ia	Yes	S	B	Sp-S
Atherina hepsetus				24	11.8 (10–15)	Ia	Yes	S	B	W
Bleniidae										
Aidablennius sphynx	8	41.6 (35–45)	1.7 (1.5–1.8)	3	42 (41–43)	Ia	No	S	B	S
Coryphoblennius galerita				2	26.5 (26–27)	Ia	No	S	B	S
Lipophrys adriaticus				2	24	Ia	No	L	B	S
Lipophrys canevai				3	31 (30–32)	Ia	No	S	B	S
Lipophrys trigloides	3	50 (40–68)	2.0 (1.9–2.0)	12	52 (37–71)	Ia	No	S	B	Sp-S
Parablennius incognitus	1	24	1.6	9	23.8 (22–25)	Ia	Yes	L	B	S
Parablennius sanguinolentus				1	34	Ia	No	S	B	S
Clinidae										
Clinitrachus argentatus				4	26.5 (26–27)	Ia	No	S	B	Sp-S
Gadidae										
Gaidropsarus meditterraneus				1	43	Ia	No	L	P	W
Gobiesocidae										
Apletodon dentatus	2	14.5 (14–15)	0.7	1	15	Ia	No	L	B	W
Gouania wildenowi				1	17	Ia	No	L	B	Sp
Lepadogaster candollei				1	13	Ia	No	L	B	S
Gobiidae										
Gobius bucchichi				10	19.4 (18–20)	Ia	No	L	B	S
Labridae										
Coris julis	2	28.5 (27–30)	1.6	21	28.9 (21–34)	II	No	S	P	S
Ctenolabrus rupestris	1	20	1.1	11	21.5 (19–23)	Ia	No	L	P	S
Labrus viridis				1	34	Ia	No	L	B	Sp
Symphodus cinereus				3	11.7 (11–13)	III	No	L	B	S
Symphodus doderleini				3	12.7 (12–14)	III	No	L	B	S
Symphodus mediterraneus				9	13.4 (12–15)	III	No	L	B	S
Symphodus melops				2	15	III	No	L	B	Sp
Symphodus ocellatus	1	12	0.8	22	10.0 (9–13)	III	No	L	B	S
Symphodus roissali	6	13.8 (13–14)	0.7	100	12.8 (10–15)	III	No	L	B	S
Symphodus rostratus				2	13.5 (13–14)	III	No	L	B	S
Symphodus tinca				4	10.5 (10–11)	III	No	L	B	S
Thalassoma pavo				11	43.9 (38–49)	II	No	L	P	S
Xyrichtis novacula				1	55	II	No	S	P	W
Pomacentridae										
Chromis chromis	9	18.1 (17–19)	1.1 (0.9–1.1)	8	18.1 (18–19)	Ia	No	L	B	S
Scorpaenidae										
Scorpaena porcus				1	29	Ia	No	L	P	Sp
Serranidae										
Serranus cabrilla				3	26	Ib	No	L	P	Sp
Sparidae										
Boops boops	4	16.5 (16–18)	1.2 (1.2–1.3)	10	16.7 (16–18)	Ia	No	L	P	S
Diplodus annularis	1	17	0.9	14	18 (16–21)	Ia	Yes	S	P	S
Diplodus cervinus				1	17	Ia	Yes	L	P	S
Oblada melanura	13	16.3 (14–18)	1.0 (0.9–1.1)	12	15.8 (14–17)	Ib	Yes	L	P	S
Pagrus pagrus				1	38	Ia	No	L	P	W
Sarpa salpa				11	31.2 (29–35)	Ib	No	L	P	Sp
Spondyliosoma cantharus				2	38	Ia	No	S	B	Sp
Tripterygiidae										
Trypterygion delaisi				3	17.7 (17–18)	Ia	No	L	B	S
Trypterygion melanurus				6	17.0 (15–18)	Ia	No	L	B	S
Trypterygion tripteronutus	1	17	1.4	4	17.3 (17–18)	Ia	No	L	B	S

were easier to make because of the nearly complete absence of changes in the growth plane on those otoliths in the species examined in this study. Readings were performed using lapilli in 30 species and using sagittae in 12 species (Table 1). Subdaily increments were not uncommon, and were observed on the otoliths of 6 of the 42 species considered (Table 1).

The duration of the planktonic larval stage of the littoral-dwelling Mediterranean fishes studied ranged from 9 days in *Symphodus ocellatus* to 55 days in *Xyrichtis novacula* and 71 days in *Lipophrys trigloides*. Species in the same family did not display any tendency to have similar PLDs. However, larval duration did tend to be similar within a genus, with the exception of *Lipophrys*, in which *L. trigloides* had a mean larval stage lasting 51.6 days compared with 24.3 days for the other two species studied in that genus (*L. canevae* and *L. adriaticus*). Among conspecifics, the time spent in the plankton usually varied by only 2–7 days, except in *L. trigloides* (range = 37–71 days), *Coris julis* (range = 21–34 days) and *Thalassoma pavo* (range = 38–49 days) (Table 1).

No clear patterns were discernible in genera that contained some species that settled in winter and others that settled in summer. In the family Blenniidae, *L. trigloides* had a longer PLD in the early months of settlement (April–May, mean = 67.5 days, SD = 1.9, $n = 7$) than at the end of settlement (June–July, mean = 41 days, SD = 2, $n = 8$) (Mann–Whitney test, $P = 0.001$), although considering the low number of individuals examined a certain amount of caution is recommended in the interpretation of this pattern. The mean PLD of this species (51.6 days) was also longer than the PLDs of the other species in the same genus (*L. canevae*: 31 days; *L. adriaticus*: 24 days) and in that same family that settled in summer (e.g. *Parablennius incognitus*: 23.8 days; Mann–Whitney test, $P = 0.0002$), with the exception of *Aidablennius sphynx* (41.7 days; Mann–Whitney test, $P = 0.5$). For the family Sparidae, the PLD was longer for *Pagrus pagrus*, *Sarpa salpa* and *Spondyliosoma cantharus* (38, 31.2 and 38 days, respectively), which settled in winter–spring, than in *Boops boops* (16.6 days), *Diplodus annularis* (18.8 days), *Diplodus cervinus* (17 days) and *Oblada melanura* (15.6 days), which settled in summer. However, in the two species in the genus *Atherina*, the PLD was similar in both the species with a winter (*A. hepsetus*: 11.8 days) and a spring–summer settlement period (*A. boyeri*: 10.7 days).

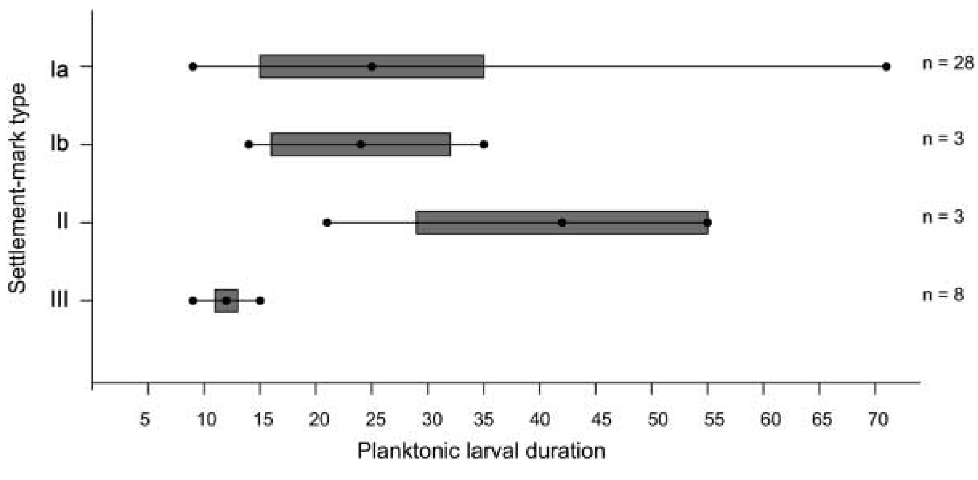
Determination of settlement mark type

Settlement marks were observed on the otoliths of all study species (Table 1), although they were never observed in new settler individuals. New settlers were an appropriate means of confirming settlement marks, since the number of increments before the settlement mark on the otoliths of newly settled individuals was the same as the number of increments before the settlement mark on the otoliths of post-settlers in all the species for which this comparison was possible (Table 1). Settlement mark type was not always clear in all specimens from the same species; therefore, the mark type in those species with only one or a few specimens examined should be confirmed with additional material.

Type Ia was the most common type of mark (67.7% of the total study species), followed by type III (19% of the total of study species) (Table 1; Fig. 1). Settlement mark type Ia appeared in 12 of the 13 families considered here, whereas settlement mark types II and III were restricted to the family Labridae, type III being found exclusively in the genus *Symphodus*.

Settlement marks types Ia and II appeared on the otoliths of species spanning nearly the entire range of larval durations (9–71 days and 21–55 days, respectively), and type III was restricted to species having relatively short PLDs (9–15 days). Type Ib appeared in intermediate PLDs (14–35 days) (Fig. 1).

Fig. 1 Relationship between planktonic larval duration, in days, and settlement mark type, see "Materials and methods – Determination of settlement mark type" and Wilson and McCormick (1999) for the definition of each type category, for Mediterranean littoral species (*shaded box* standard deviation for each group of species; *error bars* range; *n* number of species within each mark type)



A discontinuity in the deposition pattern of the increments appeared on the otoliths of some specimens of *Coris julis* and *Thalassoma pavo* and also on the single specimen of *Xyrichtis novacula* studied. The discontinuity arose from deposition of narrower daily increments before the settlement mark. That transition took place at around 3 weeks of planktonic life in *C. julis* and around 5 weeks in *T. pavo* and *X. novacula*.

Discussion

The presence of settlement marks on otoliths has proved to be valuable in determining larval duration in many species (Victor 1986a; Wilson and McCormick 1997). The similarity in the estimates of larval duration made from new settlers and from settlement marks on the otoliths of post-settlers agrees with the findings of other workers (Sponaugle and Cowen 1994; Wilson and McCormick 1997). Basically, all the settlement marks observed matched one of the types described by Wilson and McCormick (1999). Similar to our study, they reported that type Ia (abrupt settlement mark) was the most common mark in >40 tropical species.

The results of our study have shown larval duration to be highly variable in fishes dwelling in the littoral zone in the Mediterranean Sea. Planktonic larval duration for some species lasts somewhat more than a week (e.g. *Symphodus* spp.), while for other species it lasts up to nearly 2 months (e.g. *Lipophrys trigloides*, *Xyrichtis novacula*). Other researchers have reported similarly high levels of heterogeneity in other regions, which corroborates the extremely variable nature of this critical stage in the life history of fishes (e.g. Brothers et al. 1983; Victor 1986a).

Studies on larval duration have most often dealt with species in tropical regions, and less with species in temperate seas (Leis 1991). The variability observed by different workers has brought to light certain differences between families. Victor (1986a) studied larval duration in 100 species of the family Labridae off the Hawaiian Islands and in different tropical areas of the Pacific and western Atlantic, and found a range of 15–121 days (see also Victor and Wellington 2000). That same broad range has also been observed for the species of the family Labridae considered in this study, with long (38–55 days, *Thalassoma pavo* and *Xyrichtis novacula*), intermediate (21–34 days, *Coris julis*, *Ctenolabrus rupestris* and *Labrus viridis*), and short PLDs (9–15 days, *Symphodus* spp.). *T. pavo* had a similar PLD (38–49 days) to *T. bifasciatum* from Caribbean waters, ca. 45 days (Caselle 1999), although shorter than other representatives of the genus from the tropical eastern Pacific (Victor and Wellington 2000). The low number of species per family examined in this study prevents more extensive comparison with the dominant families in other regions. However, a comparison of species in the same genus in different geographical areas (e.g. *Chromis*) showed that the PLDs for the Mediterranean species (*C. chromis*) were similar (17–19 days) to those for *C. alta*, *C. insolata* and *C. retrofasciata* (18–19 days) in the Caribbean Sea and Central Pacific, whereas other species had much longer PLDs (35–37 days), e.g. *C. lineata* and *C. punctipinnis* (Wellington and Victor 1989; Victor and Wellington 2000).

Vigliola et al. (2000) reported that Mediterranean species of the genus *Diplodus*, with a winter settlement period (*D. vulgaris*), had slightly longer larval durations than species with a settlement period in warmer months of the year (*D. sargus*, spring–summer; *D. puntazzo*, autumn). For the sparids considered here, the PLD was longer for *Pagrus pagrus*, *Sarpa salpa* and *Spondyliosoma cantharus*, with a winter–spring settlement period (38, 29–35 and 38 days, respectively), than for *Boops boops* (16–18 days), *Diplodus annularis* (16–21 days) and *Oblada melanura* (14–18 days), with a summer settlement period. A similar pattern was observable for species in the genus *Lipophrys*: *L. trigloides* (spring) and *L. canevai* and *L. adriaticus* (summer). On the other hand, the two species in the genus *Atherina* did not exhibit that same pattern, both species spending a similar amount of time in the plankton, even though *A. hepsetus* has a winter settlement period and *A. boyeri* a spring–summer settlement period. Notwithstanding the exceptions, there did appear to be a certain tendency for individuals of closely related species to have a shorter larval duration in the warmer part of the year than in the colder part of the year, a feature that was probably linked to water temperature (McCormick and Molony 1995). Still, that pattern needs to be taken with considerable caution, because other important factors exist with a major influence on larval duration, such as food availability (McCormick and Molony 1992), facultatively delayed metamorphosis (e.g. Victor 1986b; Cowen 1991; McCormick 1999) and spatial larval distributions (see below).

The spatial distribution of larvae and the distance of larvae from the settlement areas, along with larval behaviour upon settlement to the bottom, may be related to larval duration (Brogan 1994; Leis and Carson-Ewart 1998). Some work on the larval distributions of the species considered in this study has been carried out in the western Mediterranean (e.g. Sabatés 1990, 1994; Olivar and Sabatés 1997). Certain labrid species (e.g. *Coris julis*) are commonly found several miles offshore, near the shelf break. Similar distribution patterns have been observed for species in the genus *Diplodus*, and for *Oblada melanura*, *Scorpaena porcus*, *Serranus cabrilla* and *Chromis chromis*. Conversely, other species have only been found close inshore, e.g. species in the families Tripterygiidae, Gobiesocidae, Blenniidae and Atherinidae, and in certain nesting labrid species, e.g. *Ctenolabrus rupestris* and *Symphodus* spp. (A. Sabatés, personal communication). The results presented here indicate that species with short PLDs (<2 weeks) tended to have inshore spatial distributions. Still, several species with relatively short larval durations (e.g. *Oblada melanura*, 14–18 days; *Chromis chromis*, 17–19 days) have larval distributions ranging from close inshore to several miles offshore. Furthermore, not all taxa with inshore distributions have very short PLDs, e.g. Blenniidae (> 22 days). These results suggest that there is no clear-cut relationship between spatial larval distributions and PLD (Victor and Wellington 2000).

Relationships between larval duration, larval behaviour and the morphological characteristics of new settlers lies outside the scope of the present paper, but some of the findings presented here, as well as the interesting results on delayed metamorphosis (see McCormick 1999, and references therein) suggest that there is a need for further studies on this critical stage in the life histories of fishes, in order to elucidate the different mechanisms used by species to optimise settlement and the recruitment to the adult population.

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