FULL PAPER

Temporal variability of settlement in Carapidae larvae at Rangiroa atoll

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Abstract Carapidae (or pearlfish) are eel-like fishes living inside different invertebrates, such as holothurians, sea stars or bivalves. In some Polynesian areas where they live in sympatry, several species (*Carapus homei*, *Carapus mourlani*, *Carapus boraborensis* and *Encheliophis gracilis*) are able to inhabit the same host species. The heterospecific infestation rate is very rare, suggesting that the four species can compete for their hosts. Some differences in settlement period, breeding period and in pelagic larval duration (PLD) could allow better characterisation of the life history of each species.

More than 700 larvae were collected during an entire year on the Rangiroa atoll (French Polynesia). Each species was identified; their settlement pattern was examined and their PLD was deduced from otolith (sagittae) increments. In the four collected species, the settlement pattern differed: *C. homei* and *C. mourlani* settle on the reef during the entire year, and show an asynchronous and diffuse breeding cycle. *C. boraborensis* and *E. gracilis* have a shorter settlement period which could be compatible with breeding synchronisation. As most reef fishes, Carapidae larvae mainly settle during moonless nights. Moreover, each species presents some plasticity, allowing it to settle on the reef under suitable conditions.

Keywords Settlement pattern · Biotic and abiotic factors · Otolith · Symbiote

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Introduction

Carapidae, known as pearlfish, are a highly specialised family of shallow to moderately deep-dwelling fish which principally occur in tropical seas (Markle and Olney 1990). Although some species are free-living (*Pyramodon*, *Snyderidia*, *Echiodon*, *Eurypleuron*), others (*Carapus* and *Encheliophis* species) are able to enter, live and remain inside different hosts such as sea stars

and sea cucumbers (Trott 1970; Parmentier et al. 1999; Parmentier et al. 2000) where they are usually found in coelomic cavity or respiratory trees (Smith 1964; Trott 1970; Meyer-Rochow 1977; Gustato et al. 1979; Vandenspiegel and Jangoux 1989). *Carapus* species are commensal, and use their host as a shelter (Strasburg 1961; Trott and Trott 1972; VandenSpiegel and Jangoux 1989; Parmentier et al. 2000; Parmentier and Vandewalle 2003). *Encheliophis* species are parasitic which primarily feed on the host gonads (Parmentier and Vandewalle 2003; Parmentier and Das 2004). In some Polynesian areas where they live in sympatry, *Carapus boraborensis*, *Carapus homei*, *Carapus mourlani* and *Encheliophis gracilis* can inhabit the same holothurian species (*Bohadschia argus* and *Thelenota ananas*). However, the heterospecific infestation rate remains extremely weak. Parmentier and Vandewalle (2005) have reported less than 1% of heterospecific infestation while 83% of 257 holothurians collected were occupied by one or several specimens of the same species. In this same area, *C. mourlani* is also able to live inside the body cavity of different sea stars species (Meyer-Rochow 1977, 1979).

Like most reef fishes (Victor 1991), fishes of the Carapini tribe (*Carapus* and *Encheliophis*) have a complex life history divided into two stages (Fig. 1). The benthic stage concerns juvenile and adult living in the lagoon; the pelagic stage involves larvae living in the open ocean. Adults lay elliptical eggs which are then swept away to the ocean. After hatching, Carapidae present two larval stages: the vexillifer and the tenuis, respectively (Parmentier and Vandewalle 2003; Parmentier et al. 2004a). At the end of the tenuis stage (Fig. 1), larvae settle on the reef and may enter a benthic host for the first time (Smith 1964; Smith and Tyler 1969; Smith et al. 1981). In its host, the tenuis undergoes a metamorphosis during which its length is reduced by 60%, reaching to the juvenile stage (Parmentier et al. 2004a, b). Vexillifer and tenuis forms were poorly known, and have often incorrectly been considered two different species (Padoa 1947). Recently, Parmentier et al. (2002) were able to distinguish the Carapini tenuis of French Polynesia on the basis of a combination of pigmentation, meristic, morphological, dental and otolith (sagittae) features. This first step was necessary to go deeper in the knowledge of the way of life of this particular group. Different aspects of this life history remain however unknown, e.g. the reproductive behaviour. Prior to study it, it is of course important to know the appropriate periods.

The pelagic larval duration (PLD) corresponds to the period between hatching and settlement on the reef (Victor 1986). It is estimated on the basis of the increment number in otoliths (Panella 1971; Campana and Neilson 1985). In teleosts of the tropical seas, larval ring increments are generally considered to occur daily (Victor 1986). Depending on the species, the PLD varies between 9 and more than 100 days in coral reef fishes (Leis 1991). In the Carapini tribe, this daily

Fig. 1 Biologic cycle of the Carapini tribe (Carapidae)
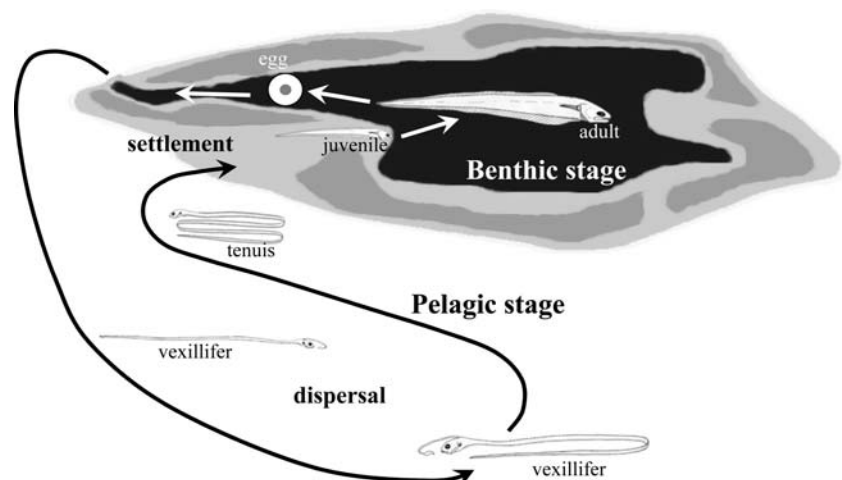
formation of the increments was validated by Parmentier et al. (2004a). The PLD can be influenced by various factors; larval growth rate is primarily dependent on food availability and temperature (McCormick and Molony 1992; Wellington and Victor 1992; McCormick 1994). Moreover, larval duration appears to be extremely variable among species as well as among species from different geographic areas. This plasticity mainly results from the ability of larvae to delay their settlement on the reef (Victor 1986).

Larval settlement occurs during certain periods of the year and could be influenced by several factors like season and lunar cycle (Robertson et al. 1990; Robertson 1992; Dufour et al. 1996; Sponaugle and Pinkard 2004). Generally speaking, larval settlement is maximal during the new moon and minimal close to the full moon (Robertson et al. 1990; Robertson 1992; Dufour et al. 1996; Sponaugle and Pinkard 2004). An adaptive hypothesis is usually used to explain this event: the majority of larvae settle on the reef during moonless nights to raise their survival possibilities by avoiding potential predators (Robertson et al. 1990).

The aim of this study is to obtain more information on the settlement periods and habits of the different carapid larvae living on the Rangiroa atoll in French Polynesia. These data should help to gain different kinds of information on the way of life of the different species, and notably how these species can cohabit. Moreover, the known PLD will allow to evaluate the reproduction periods in order to realise further studies on this part of the way of life.

Materials and methods

Sampling was carried out in a pass on the North coast of the Rangiroa atoll (French Polynesia) using fishing nets (2.20 m wide × 1 m high × 5 m long—1 mm mesh net), fixed on the reef crest, from Tropical Fish Tahiti firm. Two additional arms (1 m high × 10 m long) prolong the net, embracing the total width pass. A total of 716 larvae were obtained during the period from May 2004 to May 2005. However, fishing was not carried out every day (60% of the year). The different tenuis species were caught at night as

they settled on the reef crest and all specimens were stored in 70% ethanol.

Otolith extraction

The otoliths (sagittae) of 86 specimens belonging to different species were extracted in order to observe the increment number. Optical sections of sagittae were prepared by mounting and fixing otoliths on a glass slide in the thermoplastic polymer Crystal Bond®. A double polishing procedure was carried out with different grained sandpaper (600, 800 and 1,200 grain sizes) in order to obtain thin sections (10–40 μm) of the sagitta (Parmentier et al. 2002). The sections were observed with a polarising optical microscope (Leica DM1000) coupled with Canon PowerShot S50 camera. Daily growth increments were estimated by two different examiners. This also allowed estimation of the spawning periods using back-calculation.

One-way ANOVA followed by post hoc multiple comparison tests (Tukey test) was used to compare the PLD of the different species and to test the possibility to discriminate the species using the increment count.

Morphological comparisons

The specimens were cleared and stained with alizarine red S according to Taylor and Van Dyke's method (Taylor and Van Dyke 1985). This method allows to distinguish the different species of Carapidae larvae based on a combination of features related to meristic, morphometric and morphologic data. However, the tenuis were not bleached with H_2O_2 to avoid breaking the melanophores which were used as discriminating feature (Parmentier et al. 2002). Morphometric measurements [total length, head length (HL)] were made with a Leica M10 binocular microscope coupled with a camera lucida.

Results

Larval settlement patterns and breeding cycles

Carapidae settle during the entire year, except in July during which no larvae were caught. Gener-

ally speaking, settlement starts in August, gradually increases until April when peak settlement (278 larvae) was reached, and decreases until June.

Settlement periods differ in time and in number from species to species, and reflect differences in breeding cycles. In Carapini, three settlement patterns can be distinguished (Fig. 2).

Carapus homei and *C. mourlani* present the same type of settlement pattern and appear to be the most abundant species, with 549 and 136 larvae, respectively. *C. homei* (Fig. 2a) settlement starts in August, gradually increases until April and decreases until June. The main settlement period of *C. mourlani* appears to be postponed for 1 month compared to *C. homei*. The first larvae were found in September and the colonisation peak occurs in May (Fig. 2b). Because they settle during the entire year, both species should possess a continuous gametogenesis cycle, reflecting an asynchronous and diffuse breeding cycle.

Only 11 *C. boraborensis* were collected. Its settlement is spread over 7 months with three main periods: September, December and April (Fig. 2c). The presence of these periods may imply the existence of a break after each settlement, and could reflect a breeding synchronisation.

Encheliophis gracilis (Fig. 2d) presents also a settlement pattern divided in three main periods: November, February and May. The majority of larvae settle on the reef in February (colonisation peak), except five specimens caught in November and May. It could also imply that breeding cycle is synchronised.
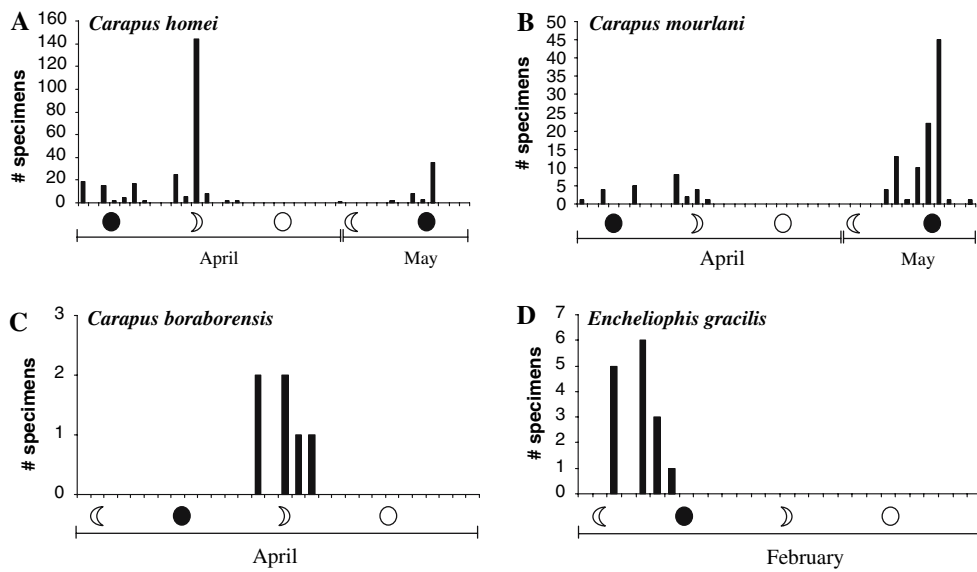
Larval settlement and lunar cycle

Carapidae settle on the reef between the last-quarter moon and the first-quarter moon, when lunar luminosity is lowest. Only 2% of 716 sampled larvae settle on the reef within 5 days of the full moon. In Fig. 3, the colonisation phase is illustrated for the period of the year (i.e. months) during which the settlement was the most abundant for each species.

Carapus homei mainly settled on the reef during nights around the first-quarter moon (Fig. 3a) while numerous *C. mourlani* settled during nights close to the new moon (Fig. 3b). In *C. boraborensis*, settlement occurred around the first-quarter moon (Fig. 3c). However, these larvae also settled on the reef in September and December, during a period close to the new moon. *E. gracilis* settled on the reef between the last-quarter moon and the new moon (Fig. 3d). Moreover, the five specimens caught in Novem-
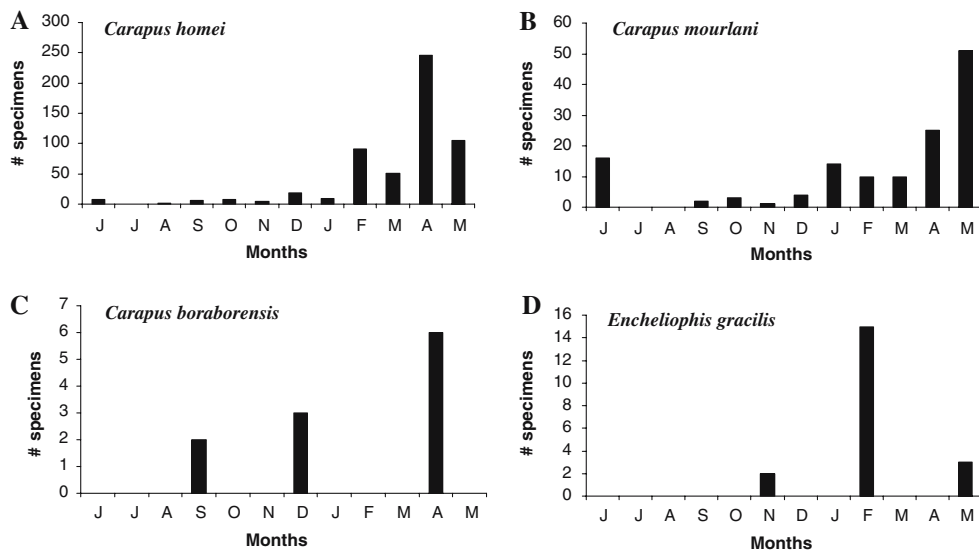
Fig. 2 Temporal settlement patterns of the four Carapini species

Fig. 3 Larval settlement depending on lunar cycle in the four Carapini species

ber and May (Fig. 2d) settled on the reef close to the new moon.

Interspecific and intraspecific variations in larval duration

Larval duration variations (ANOVA, $F_{3,69} = 25.41$, $p < 0.001$) were observed between the four Carapini species (Table 1). The *C. boraborensis* sagitta had the lowest number of increments, which clearly distinguished it from the other species (Tukey test, $p < 0.001$). The daily increments overlapped in *E. gracilis* and *C. mourlani* and did not allow separation of these species (Tukey test, $p > 0.05$). *C. homei* tenuis had the highest number of increments (Tukey test, $p < 0.01$).

Plasticity of larval duration was also observed within species, especially in species with high increment number. Daily growth increments in *E. gracilis* varied between 68 and 75, except in a specimen which had 92 increments (Table 2). In *C. mourlani*, the number of daily increments varied between 66 and 79, except in a specimen with 91 increments (Table 2). In *C. homei*, three

specimens had approximately 97 increments while the PLD average of the species was 81.8 (Table 2). Due to the higher number of increments, these individuals were excluded in the calculation of the PLD average because they were beyond the 99% confidence interval. The higher PLD of these fishes appears interesting, because it corresponds to older specimens. This hypothesis was clearly confirmed by their morphology: their body length and HL were longer (Table 2); their lower and upper jaws bore more teeth and they had more neural spines with eight (vs. three to six) in *C. mourlani* and seven (vs. three to six) in *E. gracilis*. Comparison between PLD, meristic and morphological data clearly showed that settlement of these specimens was delayed over a range of 15–20 days regarding to their congeners.

Moreover, the PLD plasticity observed in *C. homei* also appeared to be dependent on seasons ($t = 4.02$, $df = 53$, $p < 0.001$, Fig. 4). The number of increments varied on average from 86 to 90 (Table 3) during the dry season (May to October), during which the average ocean water temperatures was 26–28°C. On the other hand,

Table 1 Daily increment number (IN) of the four Carapini species

	C. homei (n = 58)	*C. mourlani* (n = 10)	*C. boraborensis* (n = 8)	*E. gracilis* (n = 10)
IN (mean ± s.d.)	82.6 ± 8.9	73 ± 7.4	50.2 ± 1.2	75.5 ± 8.5

Table 2 Daily increment number (IN) and head length (HL) in *C. homei*, *C. mourlani* and *E. gracilis* tenuis

	C. homei	*C. mourlani*	*E. gracilis*
IN (mean ± s.d.)	81.8 ± 8.5 (*n* = 55)	71 ± 4.1 (*n* = 9)	72.2 ± 3.1 (*n* = 9)
HL (mm)	5.2 ± 0.14 (*n* = 55)	5 ± 0.2 (*n* = 9)	4.4 ± 0.5 (*n* = 9)
IN (mean ± s.d.)	96.7 ± 2.9 (*n* = 3)	91 (*n* = 1)	92 (*n* = 1)
HL (mm)	5.5 ± 0.15 (*n* = 3)	5.4 (*n* = 1)	4.9 (*n* = 1)

the number of daily increments ranged from 73 to 83 (Table 3) during the humid season (from November to April), during which the average ocean water temperatures was 28–30°C.

Discussion

Carapus boraborensis, *C. mourlani*, *C. homei* and *E. gracilis* can inhabit the same host species (VandenSpiegel and Jangoux 1989; Markle and Olney 1990). However, infestation is considered to be monospecific when several conspecifics are observed in the same host (Parmentier and Vandewalle 2005), suggesting that the four species compete for their hosts. Differences in the life history of each species could therefore diminish or avoid competition.
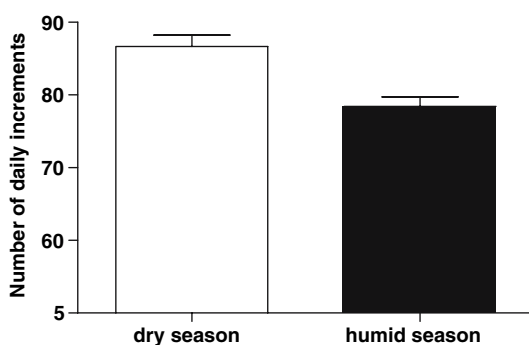
Settlement periods

The settlement pattern of Rangiroa fishes are divided into two groups (Lo-Yat 2002): the non-frequent and the frequent settling fishes. Carapini are in the second group. The latter group is also divided in two groups: the first has a higher larval flux at the beginning of the year (January to April) and the second has a higher larval flux at

Fig. 4 Larval duration variation in *C. homei* tenuis depending on seasons

the end of the year (September to December). Carapini are in the first group. Generally speaking, the pattern settlement of Carapini recorded during this study corresponds to this one of Lo-Yat (2002) during 1996 and 1997: it occurs during all the year but the larval flux is higher from February to May. However, settlement pattern and/or larval duration varies from species to species (Fig. 2), highlighting different strategies. Interspecific competition for host might be the most important factor influencing the temporal variability of settlement observed in the four Carapini species.

Carapus mourlani are able to enter into holothurian hosts (Markle and Olney 1990). However, in some areas where the four Carapini live in sympatry, *C. mourlani* shifts hosts and inhabits asterian hosts, such as *Culcita novaeguineae* (Meyer-Rochow 1977; Parmentier and Das 2004). Its ability to live inside other hosts enables it to diminish competition for habitat. In this case, the pattern of settlement in *C. mourlani* could be considered as representative of the norm.

In French Polynesia, *C. homei* and *C. boraborensis* are usually found at the same depth, in the same waters and are both commensal of the same sea cucumber species, *B. argus*. The ability to enter the same host seems at the origin of competition between these species, for which larvae appear to be able to devour each other (Parmentier and Das 2004; Parmentier and Vandewalle 2005). Differences in settlement periods could be factor limiting competition or improving fitness: *C. homei* have an asynchronous breeding cycle and produce numerous larvae during the entire year, whereas *C. boraborensis* have a synchronous breeding cycle and produce a smaller number of larvae during certain periods of the year. It is admitted here that the net has the same efficiency for both species. Three aspects of their way of life could be at the origin of these differences.

Table 3 Daily increment number (IN) in *C. homei* tenuis according to the seasons

Humid season				
Months	May	June	September	
IN (mean ± s.d.)	85.5 ± 8.2 (*n* = 15)	88.2 ± 4.2 (*n* = 4)	89.5 ± 7.6 (*n* = 4)	
Dry season				
Months	December	January	February	April
IN (mean ± s.d.)	81.7 ± 1.9 (*n* = 8)	81 ± 12.3 (*n* = 3)	82.8 ± 7.2 (*n* = 10)	72.5 ± 4.1 (*n* = 11)

1. The hypothesis dealing with the synchronisation in *C. boraborensis* is reinforced by the observation of emaciated males during breeding periods. The emaciation seems result from the search for several sexual partners in various hosts, the average sex ratio being of 3 females:1 male (Parmentier and Vandewalle 2005). The males cannot accomplish their reproductive behaviour continuously, leading to seasonality.

2. Another difference of both species concerns the PLD. The latter involves that the larval developmental state is different at the time of settlement. *C. boraborensis*, with the smallest number of otolith increments is also the species with the weakest dentition in buccal and pharyngeal jaws and the shortest HL and body length. The *C. homei* tenuis has the longest HL and body length with the most developed dentition and the highest number of larval increments (Parmentier et al. 2002; this study). The shortest *C. boraborensis* larvae could help them to avoid predators, the latter being preferentially attracted by the longer larvae entering at the same period. From this point of view, the lesser development in *C. boraborensis* could be considered as an adaptative response.

3. Two other aspects might explain the case of *C. boraborensis*: *C. boraborensis* is the only species for which tenuis can cohabit with adults. Adults could protect or, at least, not eat tenuis of their own species (Parmentier 2003). *C. boraborensis* is also able to enter in *T. ananas*, in which no *C. homei* were never found (Parmentier et al. 2002; Parmentier and Vandewalle 2005). This ability could constitute an advantage in avoiding competition with *C. homei*.

Encheliophis gracilis is a parasitic species which primarily feeds on the holothurian's gonads (Parmentier and Vandewalle 2003; Parmentier and Das 2004). The breeding period is very short and is spread over 6 months (Fig. 2d), and could correspond to a breeding synchronisation. Moreover, the main larval settlement period might correspond to gonadal maturation of *T. ananas* and *Holothuria scabra*, which occurs during January and February (Conand 1993). Therefore, their settlement on the reef during this specific period could enable the larvae to benefit from food immediately after metamorphosis. However, additional studies on the holothurian breeding cycles are needed to ascertain this hypothesis.

Larval duration plasticity in Carapidae

In Teleostei of tropical seas, daily growth increments seem correspond to the PLD (Wilson and McCormick 1999). Leis (1991) showed that PLD varied between 9 and more than 100 days, depending on the coral reef fish species; Carapini larvae therefore remain pelagic for an extended period (Table 1). If PLD appear to be genetically determined (Planes 1993; Planes et al. 1998a, b; Jones et al. 2005), each individual seems also able to undergo behavioural and physiological modifications in order to adapt environmental variations and settle during the most suitable periods (Wellington and Victor 1992; McCormick 1994). This intraspecific variability of the larval duration has already been observed in the field and in the laboratory (Victor 1986; McCormick 1999; Parmentier et al. 2004a). *Acanthurus triostegus* (Acanthuridae) larvae caught during settlement and put back in a pelagic environment delay their metamorphosis (McCormick 1999). *C. homei* larvae are able to delay their metamorphosis for

at least 21 days if they do not encounter optimal conditions for their metamorphosis (Parmentier et al. 2004a).

In this study, PLD plasticity was observed in Carapidae larvae. The PLD could be influenced by different factors, such as ocean water temperatures, food availability or currents (strength and/or direction), whereas the settlement seems largely under the influence of the lunar cycle.

Carapus homei larvae showed variation of PLD (Fig. 4) which was on average 90 days during the dry season (May to September), and 80 days during the humid season (December to April). Because a positive correlation exists between temperature and larval growth (McCormick and Molony 1995; Green and Fisher 2004), *C. homei* larvae could have a shorter PLD during the humid season.

Numerous works have shown that reef fish populations are genetically constrained and relatively closed (Planes 1993; Planes et al. 1998a, b; Jones et al. 2005). However, because of the potential for transport of propagules by currents, larval dispersal could also be dependent on patterns of water movement. Local populations of reef fish would then be expected to be replenished by larvae derived from elsewhere (Williams 1982; Roberts 1997). It is interesting to note that some *C. mourlani*, *C. homei* and *E. gracilis* larvae show longer larval duration than their conspecifics and that back-calculation shows that their spawning period does not correspond to those of other larvae at the same site. This is consistent with the possibility of larval drift from one reef to another. Moreover, Carapidae larvae are long (up to 230 mm for *C. homei* and *C. mourlani*) and serpentine, with large swimbladder, which improves flotation (Govoni et al. 1984) and the ability to drift over long distances (Montgomery et al. 2001). Oceanic currents could have an influence over the drift of reef fish larvae, and could explain how larvae are able to travel considerable distances from the reef during their pelagic stage.

This paper has highlighted the settlement pattern in four Carapini species. It shows differences in the behaviours and gives a better understanding of their ecological niche. Moreover, settlement dates and PLD will also permit

to encircle the reproduction period in order to study deeper this behaviour.

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