In situ observation of settlement behaviour in larvae of coral reef fishes at night

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The swimming behaviour of 534 coral reef fish larvae from 27 species was explored at Moorea Island (French Polynesia) while they searched for a suitable settlement habitat, on the first night of their lagoon life. Most larvae swam actively (74%) and avoided the bottom (77%). A significant relationship was highlighted between the vertical position of larvae in the water column and the distance they travelled from lagoon entrance to settlement habitat: larvae swimming close to the surface settled farther away on the reef than bottom-dwelling larvae.

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In coastal ecosystems, most marine organisms have a bipartite life history: adults are benthic, mostly sedentary and produce larvae that are pelagic and potentially very mobile. These two stages are coupled by a fairly discrete process called 'settlement' whereby larvae choose a coastal habitat and enter the juvenile population. Numerous studies have examined the patterns of habitat use in settling marine larvae and many coral reef fish species are known to be very selective about where they settle (Doherty, 2002; Leis, 2006). A lack of understanding, however, remains about the proximate behavioural mechanisms underlying the settlement process (*e.g.* responses to cues and swimming abilities). Since settling fish larvae, in particular coral reef species, have efficient sensory systems and swim actively (Leis, 2006), such behavioural processes are potentially very important.

The swimming behaviour of late-stage fish larvae (speed and orientation) has been investigated in swimming chambers (Stobutzki & Bellwood, 1994) or observed *in situ* (Leis *et al.*, 1996). None of these studies, however, report direct observations of wild specimens. Instead, they used reared larvae or late-stage

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larvae captured in light traps and subsequently released into the ocean or experimental device. In addition, while many species are known to settle in greater numbers at night (Dufour & Galzin, 1993), only one study examines the behaviour of fish larvae *in situ* at night, and its observations are confined to the latest parts of the settlement process (Holbrook & Schmitt, 1996). The present study reports the vertical positioning and swimming activity of fish larvae observed *in situ*, throughout the settlement phase, on their first night in the lagoon. Relationships are then drawn between their behaviour and their settlement patterns.

The study was conducted on Moorea Island, French Polynesia (17°30′ S; 149°5′ W), where larvae enter the lagoon by 'surfing' above the reef crest at night, predominantly around new moon (Dufour & Galzin, 1993). Larvae were followed at night, during 2 h periods three times a week (Sundays, Tuesdays and Thursdays) in July, August and December 2001 and January 2002. Observation times were shifted within 2000–0500 hours to avoid the brightest moonlight, and no observations were carried out around full moon.

An observer positioned behind the reef crest and equipped with a submersible light waited for larvae crossing the crest. When a larva was spotted, it was followed for at least 2 min or until it settled onto the reef. If the larva was lost before 2 min of tracking, it was discarded. Because Moorea Lagoon is mostly shallow (depth <3 m), tracking was performed by swimming with a snorkel. During observations, larvae were identified to the lowest possible taxonomic level and their swimming activity (active or passive) and vertical position in the water column (surface, middle or bottom) were recorded. Moorea's lagoon was partitioned into 14 zones, from reef crest to shore (Lecchini, 2005), and when a larva was followed until it settled, its settlement zone was also recorded.

Active swimming was defined as conspicuous body undulation and fin movements. Passive larvae were either drifting in the current, usually positioned head down, 45° from the horizontal, with little to no fin movement, or they were lying on the substratum. Larvae that were passive, actually moved over the reef because the water flows from the reef crest to the coast. Vertical position was defined as 'surface' for the 300 mm below the surface, 'bottom' for the 300 mm above the substratum, and 'middle' for the water column in between. When a larva displayed multiple behaviours during a single observation, only the most common was recorded (*e.g.* a larva passive 10% of the time and active for the remaining 90% would have been recorded as active). This approach was adopted because all observed larvae displayed very consistent behaviour. For example, *en route* to their settlement habitat, active larvae swam constantly except for very brief stops, whereas passive larvae did not swim at all except possibly at the end of their ingress into the lagoon.

A total of 534 larvae belonging to 27 species from 14 families were successfully followed (Table I). No intraspecies variability was observed within the qualitative framework used: all larvae in each of the 27 species displayed similar swimming activity and depth. Thus, species and not individuals were considered for further analyses to avoid over-representing more frequently observed species. At the family level, only Pomacentridae displayed species-specific traits even though several families with more than one species were observed (Table I).

TABLE I. Swimming behaviour: for each species, the number of larvae followed (n), their swimming activity (active or passive) and depth (surface, middle and bottom) are given. Settlement site: for seven species in this study, data on the settlement site of n′ larvae were recorded and compared with those determined by a concurrent capture–mark–recapture study that defined the nomenclature (Lecchini, 2005). Settlement zones are numbered from reef crest (1) to shore (14). When the same species was observed in several zones, n′ contains the number of settlers in each zone respectively

	Swimming behaviour			Settlement site		
Family	n	Activity	Depth	n′	Zone	Zone*
Species						
Acanthuridae						
Acanthurus lineatus	15	Active	Surface			
Acanthurus nigricauda	55	Active	Surface			13
Acanthurus triostegus	58	Active	Surface	2	14	14
Ctenochaetus striatus	40	Active	Surface	2,1	4,8	4,8
Naso unicornis	20	Active	Middle			
Zebrasoma veliferum	10	Active	Surface			
Apogonidae						
Apogon exostigma	36	Active	Bottom	5	1	1
Apogon franeatus	15	Active	Bottom			1
Apogon novemfasciatus	10	Active	Bottom			1
Aulostomidae						
Aulostomus chinensis	10	Passive	Middle			
Balistidae						
Rhinecanthus aculeatus	5	Passive	Surface			14
Belonidae						
Platybelone sp.	20	Active	Surface			
Chaetodontidae						
Chaetodon lunula	3	Passive	Surface			
Holocentridae						
Myripristis adusta	1	Passive	Middle			6
Lutjanidae						
Lutjanus fulviflamma	13	Active	Middle	2	6	13
Lutjanus fulvus	9	Active	Middle			13
Mullidae						
Mulloides flavolineatus	10	Active	Middle	2	6	14
Parupeneus barberinus	15	Active	Middle			
Muraenidae						
Gymnothorax spp.	16	Active	Middle			2
Pomacanthidae						
Centropyge flavissimus	17	Active	Surface			3
Pomacentridae						
Chromis viridis	8	Passive	Surface	2	12	12,13
Chrysiptera leucopoma	45	Active	Surface			3
Stegastes albifasciatus	24	Active	Middle			13
Stegastes nigricans	37	Active	Bottom	2	2	1,2,(4)
Scorpaenidae						
Scorpaenodes guamensis	4	Passive	Bottom			2

TABLE I. Continued

Family	Swimming behaviour			Settlement site		
	n	Activity	Depth	n'	Zone	Zone*
Scorpaenodes parvipinnis	3	Passive	Bottom			2
Synodontidae						
Synodus binotatus	5	Active	Middle			

*, From Lecchini (2005).

Active swimming was the more common swimming behaviour, observed in 20 of 27 species (74%). The vertical positions ratio was 11:10:6 for surface, midwater and bottom, which suggests bottom avoidance. Statistical tests failed to reveal a significant relationship between swimming activity and vertical position (Fisher's exact test, $P > 0.05$). For example, all Acanthuridae, Lutjanidae and Mullidae were active, but most Acanthuridae swam near the surface while all Lutjanidae and Mullidae swam at midwater.

Settlement sites could be determined for only 18 of the 534 larvae of this study. In most cases (14 out of 18), however, they were in agreement with a concurrent study which used a different technique (capture–mark–recapture) to determine the settlement sites of 229 other specimen (Lecchini, 2005). Therefore, settlement habitat data of those 229 larvae were used to compare against the swimming behaviour of larvae in the present study. Both studies were conducted at the same time and location, on specimens of similar age, and used the same nomenclature (14 reef zones).

No significant relationship between swimming activity and settlement site was detected (Fisher's exact test, $P > 0.05$). In contrast, the relationship between vertical position and settlement site was significant (Pearson's χ^2 test, $P < 0.01$; Fisher's exact test, $P < 0.01$). Indeed, species that swam near the bottom settled closer to the lagoon entrance (Fig. 1). For example, *Stegastes nigricans* (Lacepède, 1802) swam near the bottom and settled on the reef crest, while *Chromis viridis* (Cuvier, 1830) swam closer to the surface and settled on
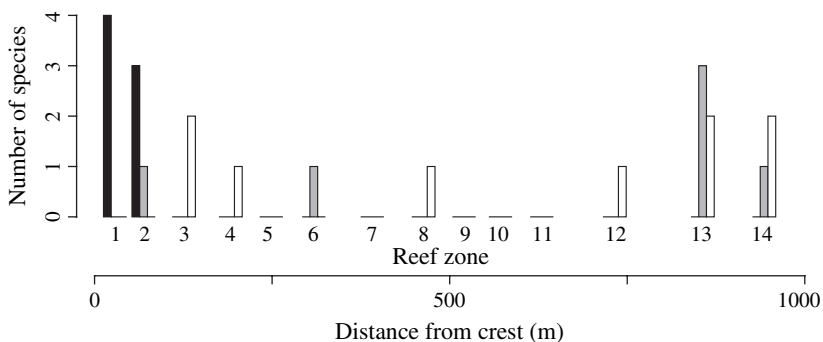

FIG. 1. Number of species per vertical position for each settlement zone: surface (□), middle (▨) and bottom (■). Zones are numbered from reef crest (1) to shore (14).

the fringing reef, farther from the crest. This result is particularly interesting since it suggests species-specific decisions about when to leave the water column and search the bottom for a suitable habitat.

Since no information was available on the behaviour of settling reef fish larvae, a bold approach was chosen to collect a large amount of data. The potential artefacts caused by the introduction of visible light, however, must be discussed before interpreting the results.

As a first step, larvae conspicuously affected by light (*e.g.* staying close to the light source or fleeing the light beam) were not recorded. These reactions to light were highly species specific (*i.e.* for each species, almost all individuals were affected or none seemed affected). Hence, no individuals of the species eventually presented here were discarded, and the results for them are not affected. Nonetheless, many animals freeze when exposed to light at night, and such behaviours would have been recorded as passive in the study. Though this potential artefact cannot be ruled out, the results hold even when passive individuals are discarded (*i.e.* the relationship between vertical position and settlement location is still significant). Furthermore, followed larvae were more visible to predators because they were illuminated, yet predation attempts were rarely observed. When they were, the larva was usually lost because it was eaten or burst away to avoid the predator. Their behaviour was therefore assessed only before the encounter of predators, when larvae were not yet affected.

Coral reef fish larvae settle in successive peaks, as larval patches reach the reef (Dufour & Galzin, 1993). Hence, when a larva was followed, several individuals from the same patch were probably swimming around or had settled hours to minutes before. When it was possible to follow a larva until it settled, conspecifics that colonized the reef on the same night (characteristic morphological traits are often displayed during the night of settlement) were repeatedly observed near the settlement site of the tracked specimen. Furthermore, settlement sites observed in the study and those determined by Lecchini (2005) using a completely different method (capture–mark–recapture) were similar. This suggested that tracked larvae exhibited natural, unbiased behaviour and settled into their usual habitat.

Overall, following fish larvae at night using a visible light probably introduced some artefacts. Other observation methods used to assess the behaviour of fish larvae (Stobutzki & Bellwood, 1994; Leis *et al.*, 1996), however, have also done so. Yet, they yielded results important for the understanding of the late larval phase of coral reef fishes.

In the present study, most larvae (74% of species recorded) swam actively which confirms that their behaviour is an important factor of the settlement process. Bottom avoidance could be interpreted as a way to avoid predation by benthic predators, in particular opportunistic species. Since predation is particularly high during the night of settlement (Doherty *et al.*, 2004; estimated mortality at 61%), any predation avoidance mechanism would be favoured by natural selection. Eventually, larvae swimming close to the bottom were shown to settle earlier than surface- and midwater-dwelling larvae. The first part of the relationship is well exemplified by apogonids, which quickly and actively descended towards the bottom immediately upon lagoon entry. They

swam for a while among coral rubble and finally settled among these debris. A simple explanation would be that larvae swimming on the bottom settled earlier simply because they encountered a potential habitat earlier. On the other hand, surface- and midwater-dwelling larvae could have descended to settle at any time during their ingress into the lagoon. Yet, most swam directly to areas 13 and 14, very close to the shore, which suggests that they searched for particular conditions met only in these areas. Two hypotheses can be proposed to explain the inverse relationship between swimming depth and settlement location: either larvae search for a specific settlement habitat and consequently adapt their vertical position, or vertical position is predetermined in a species-specific way and larvae obey a 'first-encounter first-stop' model. The latter situation is observed for many marine invertebrate larvae, even active ones, which appear to settle on the first encountered substratum and only afterwards may desert unfavourable environments (Abelson & Denny, 1997). On the other hand, Doherty *et al.* (1996) and Leis & Carson-Ewart (2002) demonstrated the existence of predefined habitats and of habitat selection prior to settlement for pomacentrids.

To conclude, observing fish larvae *in situ* with a submersible light may introduce some artefacts, but this simple method yielded completely novel data on the behaviour of wild coral reef fishes during their night of settlement. Such behavioural studies during the late larval stage, as well as throughout ontogeny, are needed because very little is known about the vertical distribution and swimming behaviour of these animals. These knowledge gaps currently hamper full understanding, modelling and prediction of the critical processes of dispersion, habitat selection and recruitment.

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