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REPORT

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Behaviour of pelagic larvae of four coral-reef fish species in the ocean and an atoll lagoon

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Abstract In-situ behaviour of settlement-stage larvae (10–30 mm) of four coral-reef fishes – *Acanthurus triostegus*, *Chromis viridis*, *Neoniphon argenteus* and *Pterelectris* sp. – differed between lagoon and ocean at Rangiroa Atoll, Tuamotu Islands, French Polynesia. Divers released 130 larvae individually in midwater, and recorded larval swimming speed, depth and direction. All species swam faster than average currents, and *C. viridis* swam faster in the lagoon than in the ocean. Vertical distribution behaviour of all species differed between ocean and lagoon, generally by larvae swimming deeper in the ocean. Nearly all individual larvae swam directionally. Within a species, distribution of average bearings of individual larvae was not directional, nor did it differ between ocean and lagoon. Larvae detected predators 3–6 m away, and stopped or changed depth or direction to avoid them. We therefore reject the 'simplifying assumptions' that reef-fish larvae are passive or that their behaviour is independent of location. Behavioural flexibility of settlement-stage reef-fish larvae has implications for dispersal, retention and population connectivity. This constitutes the first report of larval reef-fish behaviour in the open ocean. However, in the ocean, many larvae descended rapidly below safe diving depth, and adult remoras interfered, making in-situ study of larval behaviour difficult.

Key words Larva · Behaviour · Coral reef · Fish · Dispersal · Retention · Connectivity

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Introduction

During the pelagic larval portion of their life history, coral-reef fishes may encounter different habitats and conditions prior to returning to settle in reef environments (Leis 1991). At present, most workers make a 'simplifying assumption' (e.g. Roberts 1997) that either these larvae are passive drifters with the ambient currents, or at best that behaviour does not alter among locations or environments. This assumption, nearly always made in the absence of any direct evidence, has important implications for how we view dispersal, connectivity among populations on different reefs, and the processes by which larvae find and settle on a reef. Further, these simplifying assumptions are frequently made in order to model dispersal and connectivity where the goal may be either theoretical or heuristic (e.g. Williams et al. 1984; Doherty et al. 1985) or for application to management purposes (e.g. James et al. 1990; Roberts 1997).

Recent studies have shown an unexpectedly high level of self-recruitment in two reef-fish populations (Jones et al. 1999; Swearer et al. 1999). It seems likely that non-passive behaviour by larvae contributes to such self-recruitment, and, if so, this clearly violates the simplifying assumptions of recent models. Therefore, it is important to determine whether reef-fish larvae are passive, and, if not, to what extent their behaviour might differ both among species and among habitats.

Late-stage reef-fish larvae have recently been shown by both laboratory and field methods to be strong swimmers (Stobutzki and Bellwood 1994, 1997, 1998; Leis et al. 1996; Leis and Carson-Ewart 1997, 1998, 1999; Leis and Stobutzki 1999), and, as a result, some researchers decline to make the ultimate 'simplifying assumption' of passivity (e.g. Hare and Cowen 1996). Models of dispersal are now beginning to take larval behaviour into account, and show how influential behaviour can be to the model predictions (Wolanski et al. 1997; Porch 1998; Armsworth 2000). However, at present, too little is known about larval behaviour to

provide modellers with appropriate, adequate input. Aspects of behaviour that might affect transport and the question of passive drift, such as depth selection and swimming direction, are poorly understood (Leis at al. 1996; Leis and Carson-Ewart 1999). Further, models have so far assumed that larval behaviour does not vary among different environments, but this assumption remains essentially untested.

To gain insight into these issues, particularly possible differences in behaviour between locations, we made in-situ observations of behaviour of late-stage larvae of four species of reef fishes in two contrasting pelagic environments: an atoll lagoon, and the open ocean that surrounds the atoll. We worked at Rangiroa Atoll, Tuamotu Islands, French Polynesia, where a very large (ca. 1,610 km^2) reef-enclosed lagoon of about 35 m maximum depth (20 m average) is found adjacent to open ocean conditions (Ricard 1985). These two environments differ greatly in not only depth but also water clarity, light regime, turbulence, presence of other species and probably feeding conditions. However, both are environments encountered by the same species, and often the same individual, during the pelagic larval phase (Leis 1991).

Because we were particularly interested in aspects of behaviour that are intimately involved with dispersal and connectivity, we collected data on swimming behaviour, especially speed, depth and direction. However, we also made unplanned observations on how the larvae responded when confronted with much larger, potentially predatory, adult fishes in the pelagic environment. Herein, we report on the swimming behaviour of the larvae of these four species in ocean and lagoon, and how it differs from the 'simplifying assumption' (=hypothesis) of passivity. Further, we test the hypothesis that swimming behaviour does not differ between the two environments, and we reject both these hypotheses. Because predation is thought to play a major role in regulating survival of pelagic larvae and, therefore, in recruitment (Chambers and Trippel 1997), and because direct knowledge of predation on pelagic larvae is extremely limited, we further report on our unplanned observations of the interactions of larvae with predators.

Previous in-situ observations of larval behaviour were made inside coral-reef lagoons, or over the continental shelf on the Great Barrier Reef where depths did not exceed 40 m. Many reef-fish larvae undertake some or all of their pelagic phase in true oceanic conditions, so this study also assessed the practicality of making in-situ behavioural observations on fish larvae in the ocean. Other than a few observations of swimming speed (Leis and Carson-Ewart 1997), this constitutes the first report of behaviour of larval coral-reef fishes in oceanic conditions.

Methods

The study areas were at Rangiroa Atoll, Tuamotu Islands, French Polynesia, in the central south Pacific Ocean (14°57′S, 147°14′W; Fig. 1A). In the lagoon, we worked 0.8–1.4 km south of the Service des Ressources Marines (SRM) aquaculture laboratory jetty on Avatoru Island on the north side of the atoll. The bottom was mostly sandy, but in places had scattered small coral heads with occasional coral pinnacles and low relief coral patches, and depth was about 21–25 m (Fig. 1B). In the open ocean, we worked 0.6–1.0 km north of the seaward reef's algal crest off the SRM laboratory. According to navigational charts, water depth in this location was over 300 m. In both lagoonal and oceanic locations, we were about 2.5 km east of the deep channel (Fig. 1B).

Larvae were captured in a fine mesh fyke net, placed overnight in a hoa, or shallow (< 1 m) reef-flat channel leading from ocean to lagoon on the northern atoll rim (Fig. 1; Dufour 1994). The larvae were of settlement stage, and were protected by a specially designed cod-end (Dufour et al. 1996) until the net was emptied in the morning. Larvae were placed in large containers of seawater, sorted at the SRM, placed in 15-l covered buckets, and then transported to the study sites by boat. As all larvae were captured in the hoa net, we assume they had spent their pelagic phase in the open ocean, and were attempting to enter the lagoon via the hoa in order to settle there. Thus, they may be expected to be adapted to both oceanic and lagoonal pelagic conditions.

In the field, we used an in-situ methodology for making behavioural observations on fish larvae (Leis et al. 1996; Leis and Carson-Ewart 1997, 1998, 1999). Briefly, a larva is released by a pair of SCUBA divers at a study site. The direction of release is randomized. The divers follow 1–2 m behind the larva, and record depth and swimming direction every 30 s. A plankton-net flow meter measures distance travelled. This provides data on swimming speed, direction and depth and allows a three-dimensional trajectory of the larva to be determined. The papers cited above address the features, advantages and limitations of the methodology, and the reasons for believing that the presence of the divers does not overly bias the data obtained. Larvae are released at a standard depth of 5 m, and are not followed deeper than 18–20 m for safety reasons. A total of 130 larvae were released in this study. For a variety of reasons, all three types of data were not always obtained. Data from 11 larvae observed during a preliminary study in June 1996 are included, but most data were from May 1998.

Our goal was to follow each individual larva for 600 s. However, this was realized for only 33 larvae for several reasons, the most important of which involved depth, loss and predation. Larvae that swam deeper than 18 m were abandoned because of our diving protocol: 48 of the larvae swam to > 18 m. Some larvae were lost by the observer, usually because they ascended faster than was safe to follow. Four larvae were eaten by fishes that were attracted to the divers.

The four species studied here differ in adult size, morphology, habitat and ecology and also in the larval size, morphology and age at settlement. They are from two orders (Beryciformes and Perciformes), and the three perciform species are from three suborders: in short, none is closely related. They were chosen on the basis of: availability; suitability for in-situ observation; not being closely related or morphologically similar; varied size at settlement; and varied adult habitats. All had fully developed fins at the time of settlement. The settlement-stage fishes we studied all had some larval morphological specializations, and all were yet to undergo the morphological transition of metamorphosis to a juvenile form. Therefore, they conform to the definition of larva used by Leis and Carson-Ewart (2000), and we refer to them all as larvae. Sizes of all fishes are reported as standard length.

Convict surgeonfish, or Manini: *Acanthurus triostegus*, family Acanthuridae (for adults, see Randall et al. 1997): *A. triostegus* hatches from a pelagic egg, and is 22–29 mm and 44–83 days old at settlement (Randall 1961; McCormick 1999). At settlement, larvae have a silvery head and abdomen, may have faint, narrow black bars, but are otherwise transparent (Fig. 2), and undergo an extensive metamorphosis (Randall 1961; McCormick 1999). We released 36 *A. triostegus* larvae for observation.

Blue–green chromis: *Chromis viridis*, family Pomacentridae. (for adults, see Randall et al. 1997): *C. viridis* hatches from a demersal egg, and at settlement is 7–10 mm and 18–29 days old (Thresher

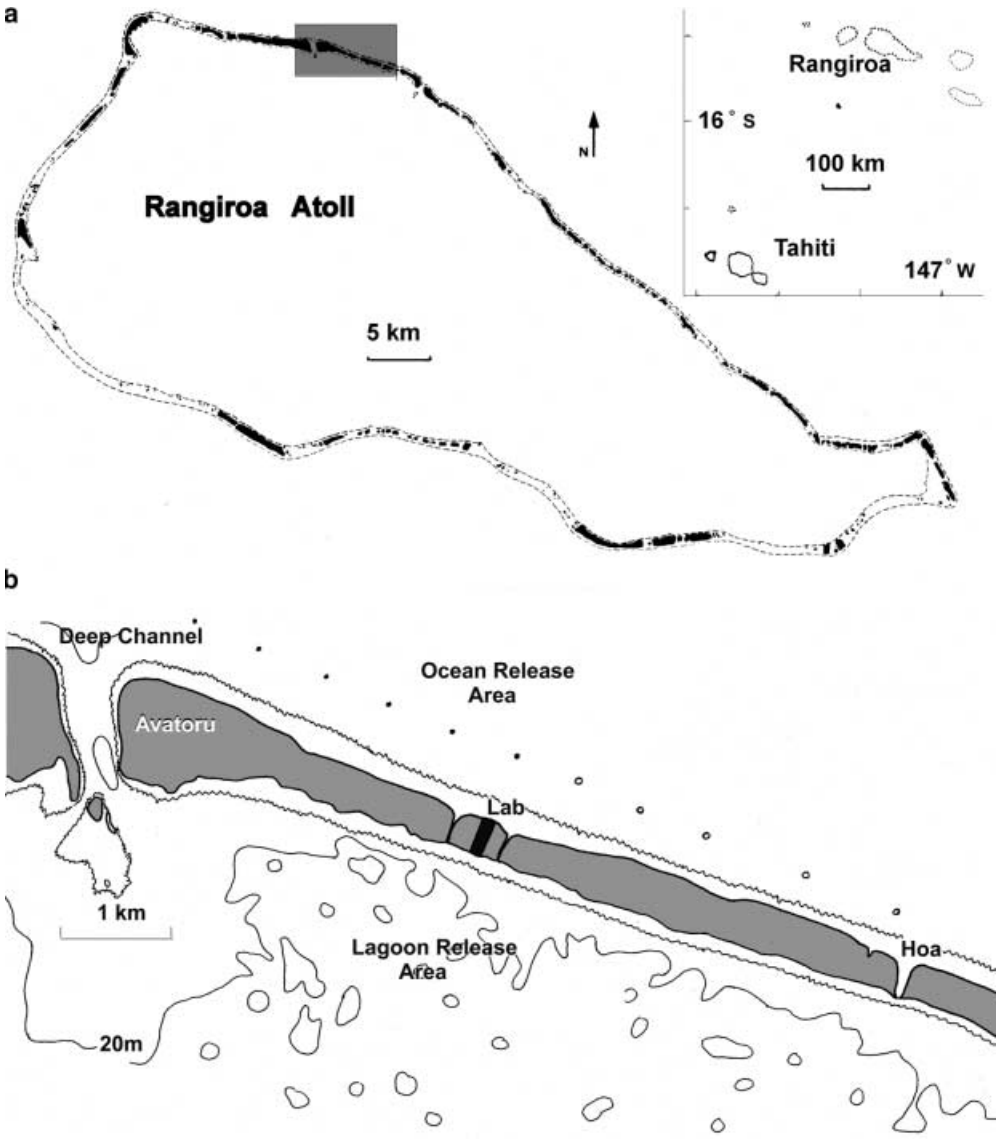

Fig. 1 Rangiroa Atoll, Tuamotu Islands, showing study locations. **A** Rangiroa Atoll. *Shaded area* is enlarged in **B**. *Inset* shows location of Rangiroa relative to Tahiti. Based on Ricard (1985). **B** Study areas. *Jagged line* is reef edge; *shaded areas* are land. *Dots* in ocean represent depths: *solid dots* are >300 m, *open dots* are 250–300 m; 20-m contour shown in lagoon: greatest depth in mapped lagoon area is 25 m. All depths taken from French navigational charts. In lagoon release area, patch reefs are only 1–2 m higher than surrounding soft bottom. *Hoa* is where larvae were captured by fyke net. North is to top of figure

et al. 1989; Wellington and Victor 1989). At settlement, larvae are silvery laterally (Fig. 2) and scaled, and undergo metamorphosis that includes colour change and loss of the head spination. We released 51 *C. viridis* larvae for observation. The closely related *C. atripectoralis* occurs at Rangiroa, but is much less common (R. Galzin and V. Dufour, personal communication). We assumed that all our observations were on *C. viridis*.

Clearfin squirrelfish: *Neoniphon argenteus*, family Holocentridae (for adults, see Randall and Heemstra 1986; Myers 1989): spawning mode of holocentrids is unknown, but eggs are probably pelagic (Leis and Carson-Ewart 2000). Pelagic duration of *N. argenteus* is unknown, but in the closely related *N. sammara* it is 40–59 days (Lefèvre and Lecomte-Finiger 1995). *N. argenteus* larvae are 28–32 mm at settlement (five hoa-net specimens), are scaled (Fig. 2) and undergo metamorphosis including colour change and loss of the elaborate head spination. We released 29 *N. argenteus* larvae for observation.

Dartfish: *Ptereleotris* sp., family Microdesmidae (for adults, see Randall and Hoese 1985; Randall et al. 1997): eggs of *Ptereleotris* spp. are probably demersal (Leis and Carson-Ewart 2000). Settlement size varies from 13–30 mm, depending on species (Randall and Hoese 1985 ; Leis et al. 1998). *P. evides* has a pelagic period of 40–55 days (McCormick and Makey 1997). At settlement, larvae are clear, transparent and lack scales (Fig. 2), and undergo metamorphosis including acquisition of scales and pigment, and alterations of body proportions (McCormick and Makey 1997; Leis and Carson-Ewart 2000). We were uncertain which of the four local *Ptereleotris* species (*P. evides*, *P. heteroptera*, *P. microlepis* or *P. monoptera*; Randall and Hoese 1985) we studied. The only available voucher specimen was either *P. heteroptera* or *P. microlepis*. Our specimens were unlikely to be *P. evides* (which settles at 13–16 mm) because of their size (ca. 25–30 mm). Larvae captured entering the lagoon from the ocean were unlikely to be *P. microlepis* because it apparently completes its larval phase inside lagoons (Leis et al. 1998, unpublished data). Thus, we think it most likely that we studied either *P. heteroptera* or *P. monoptera*, probably the former, based on the single voucher specimen. We released 14 *Ptereleotris* larvae for observation.

Behaviour of the four species differed somewhat on release, ranging from rapid upward to rapid downward swimming. While these initial behaviours were underway, the data diver was getting into position behind the observer diver, and, therefore, the first depth record often differed from the nominal 5-m release depth.

It is desirable to compare larval swimming speeds with ambient current speeds. Unfortunately, current speeds are apparently unreported at Rangiroa Atoll, except in the deep channel where average speed was 3–4 knots (Ricard 1985). We did not have access to current meters, but made very rough current speed estimates

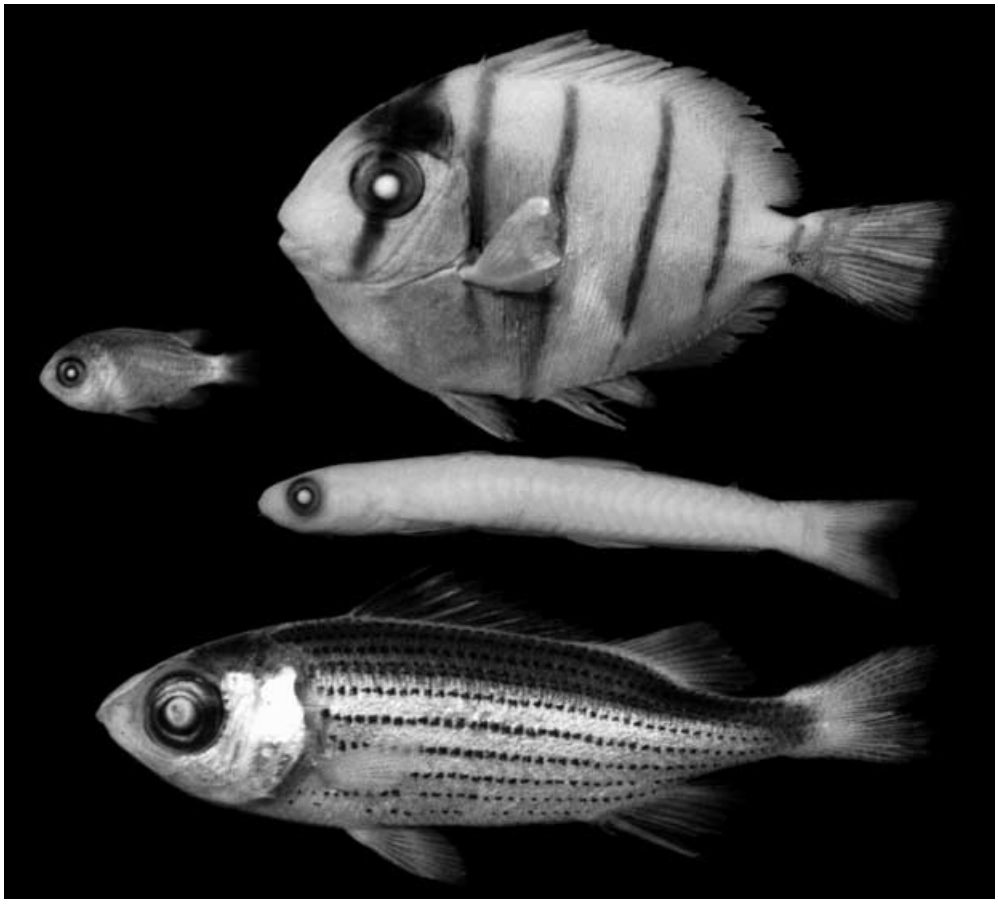

Fig. 2 Settlement-stage larvae of species used in this study (shown to scale). All were captured in fyke net in hoa shown in Fig. 1. *Clockwise from top*: *Acanthurus triostegus* (24.5 mm), *Ptereleotris* sp. (24.5 mm), *Neoniphon argenteus* (31.0 mm) and *Chromis viridis* (8.5 mm)

from how far the divers drifted in midwater while observing the larvae. GPS positions were taken at the start and end of each dive which lasted, on average, about 60 min.

Data on swimming directions were analyzed using circular statistics (Batschelet 1981; Zar 1996). We analyzed data only from individuals for which we obtained at least five bearings. Directed swimming means that the distribution of swimming bearings differed from a 'uniform' (=random) distribution at $p < 0.05$ in the Rayleigh's test for individual sets of bearings, or Watson's or Kuiper's test when comparing distributions of bearings between locations. Directions reported are in degrees magnetic: magnetic north is 11.5° east of true north at Rangiroa. Standard error is abbreviated to SE; range is abbreviated to Ra. Reference to t-test is Student's t-test.

We were able to observe reactions of larvae to predatory fishes. In the lagoon, large schools of planktivorous fishes (a jack *Decapterus* sp., a unicornfish *Naso* sp. and the fusilier *Pterocaesio tile*) were encountered. In the ocean, remoras (probably *Remora remora*), sometimes in groups of up to ten, but more often singly, and one large school of rainbow runners (*Elagatis bipinnulata*) were encountered.

Results

Swimming speed

Larvae swam at mean speeds ranging from 18.6–41.7 cm s^{-1} (Table 1), and some individuals of *A. triostegus* and *N. argenteus* were faster than 50 cm s^{-1}. In *C. viridis*, mean swimming speed was significantly greater in the lagoon than in the ocean by nearly 5 cm s^{-1} (Table 1), or 26%. Mean speed did not differ significantly between lagoon and ocean in *A. triostegus*, *N. argenteus* or *Ptereleotris* sp. In the first two, differences in mean speed between locations were small (2–3.5 cm s^{-1}) and variances of speeds within each location were large, so the lack of a significant difference was probably not a type II error. For *Ptereleotris* sp., the difference in speed between locations was relatively large (>7 cm s^{-1}, or 32%). If we had obtained observations on the same number of *Ptereleotris* larvae as in the more abundant species, such a difference between locations would have been significant. Therefore, we suspect a type II error, and regard this result as inconclusive due to the small number of observations. Average current speeds were in no case greater than average larval swimming speeds (Table 1).

Swimming depth

For all species, differences in vertical distribution were found between lagoon and atoll. In *A. triostegus*, three types of depth patterns were observed: swimming deep, ascent to surface, and swimming in midwater, usually oscillating (Table 2, Fig. 3) . The frequencies of these differed between ocean and lagoon ($p < 0.05$, G-test)

with more larvae swimming in midwater in the ocean and more at the surface in the lagoon. Overall, 19 of the 22 larvae that swam deep did so monotonically (Fig. 3), and most descended very rapidly. In the lagoon, 7 of the 11 larvae swimming deeper than 18 m were seen to settle or attempt to settle. The others were lost to sight soon after reaching 18 m.

Only two types of depth behaviour were present in *C. viridis* (Fig. 4, Table 2): swimming deep and swimming in midwater. A clear difference in swimming depth between lagoon and ocean was evident: larvae in the ocean descended rapidly to >18 m, whereas larvae in the lagoon descended more slowly, to about 10 m on average, and remained swimming in midwater (G-test, $p \ll 0.001$). Only one of the deep-swimming larvae did not descend monotonically, but in the ocean the descents were slower than those of *A. triostegus*.

In *N. argenteus*, there were only two types of depth patterns (ignoring the single larva lost in the lagoon when it swam to the surface): swimming downward rapidly to >18 m and swimming in midwater (Fig. 5, Table 2). The frequencies of these two behaviours differed between lagoon and ocean (G-test, $p < 0.025$), with more larvae swimming deep in the ocean, and more larvae swimming in midwater in the lagoon. Overall, all but one of the deep swimmers descended monotonically. One of the two deep swimmers in the lagoon was observed to settle on a small coral at about 25 m, but the other was lost to view.

Ptereleotris larvae demonstrated three depth patterns: swimming with oscillations to 18 m, swimming to or near the surface and remaining there and swimming in midwater in the upper portions of the water column with oscillations over large depth ranges (Fig. 6, Table 2). Although we made too few observations to allow rigorous analysis, it seems clear that larvae were more inclined to swim at or near the surface in the lagoon than in the ocean. In contrast to the other three species, all three *Ptereleotris* larvae that swam deep initially ascended.

Swimming direction

The large majority (64 of 68) of testable larvae had directional trajectories (Table 3). Only *C. viridis* larvae had a difference in the proportion of directional individuals between ocean and lagoon. *C. viridis* larvae in the ocean were less likely to swim directionally than those in the lagoon (17 of 17 directional in the lagoon, 10 of 13 directional in the ocean; G-test, $p < 0.05$). However, this difference in frequency is marginal and due to three ocean larvae for which minimal directional data were available. Further, its statistical significance is questionable due to a sample size (in this case, of non-directional individuals) smaller than normally considered suitable for the G-test. Only larvae with directional trajectories are considered below.

In no case was the distribution of the individual average directions for a species in either the ocean or the lagoon significantly different from a uniform distribution (Table 3), and this was also true if trajectories of

Table 1 In-situ swimming speed (cm s^{-1}) of larvae of four reef-fish species in lagoon of and in ocean near Rangiroa Atoll. *P* is for t-test comparing mean speed in the two locations. Current speeds were estimated from diver drift (see Methods). *Ra* Range

Species	Ocean			Lagoon			*P*
	n	Mean (SE)	Ra	*n*	Mean (SE)	Ra	
Acanthurus triostegus	12	39.5 (3.9)	8.7–56.3	14	41.7 (5.2)	11.4–65.3	0.74
Chromis viridis	17	18.6 (1.3)	10.5–30.7	19	23.4 (1.7)	9.1–32.8	0.04
Neoniphon argenteus	7	28.2 (7.0)	8.8–62.3	8	24.6 (6.1)	7.2–62.2	0.71
Ptereleotris sp.	4	29.8 (3.2)	23.6–37.8	7	22.1 (2.3)	11.0–28.3	0.13
Current speed	10	19 (4)	3–41	11	7 (2)	2–15	0.02

Table 2 Swimming depth patterns of larvae of four reef-fish species. Values are numbers of larvae except as labelled otherwise. See Figs. 3, 4, 5, 6 for vertical swimming trajectories. One *C. viridis* larva from each environment could not be readily assigned to a pattern because it was eaten or lost at <90 s and is omitted

Species	Environment (no. released)	Deep, >18 m (mean time in seconds ± SE to 18 m)	Deep, not reaching 18 m	Midwater	Surface
A. triostegus	Ocean (15)	9 (97 ± 29)	0	5	1
A. triostegus	Lagoon (19)	11 (120 ± 29)	2 lost at 12 m, 270 s, and 16 m, 420 s	1	5
C. viridis	Ocean (17)	16 (174 ± 15)	1–17.7 m, 600 s	0	0
C. viridis	Lagoon (19)	1 (90)	0	18	0
N. argenteus	Ocean (9)	6 (150 ± 27)	1 lost at 16 m, 99 s	2	0
N. argenteus	Lagoon (10)	2 (57 ± 45)	0	7	1
Ptereleotris	Ocean (4)	2 (300 ± 60)	1 eaten at 15 m, 242 s	0	1
Ptereleotris	Lagoon (8)	0	0	2	6

all four species were pooled. The mean of the average directions for all individual larvae in both ocean and lagoon was to the south (176° in lagoon and 214° in ocean), but as neither mean was significantly directional, this coincidence in direction is probably not meaningful.

With all species pooled, in both the lagoon and the ocean more larvae had a mean trajectory toward shore than away (22 of 37 in lagoon; 16 of 27 in ocean), but neither was significantly different from random (G-test, $p > 0.1$). Neither did this proportion differ between ocean and lagoon (G-test, $p > 0.1$). At the lagoonal study site, the nearest shoreline (Avatoru Island) was 500–1000 m to the north on the atoll rim, but of course all bearings in a lagoon are onshore eventually.

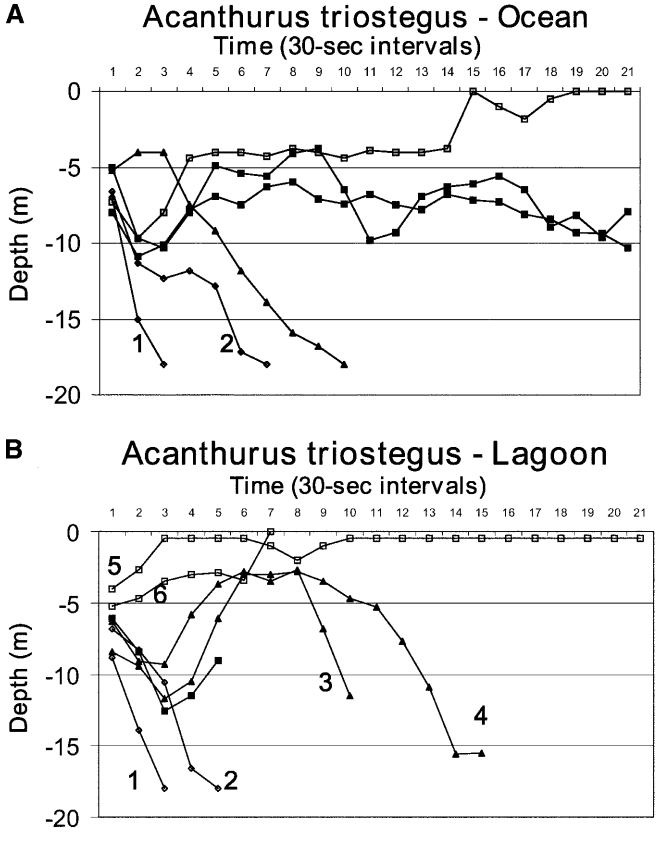

Fig. 3 Vertical swimming trajectories of individual *Acanthurus triostegus* larvae. **A** In ocean. One fish (▲) ascended initially but then descended steeply to 18 m. Between *lines 1* and *2* (◇), we omitted for clarity six trajectories that monotonically reached 18–20 m. Also omitted are trajectories of three larvae that were within same range as midwater trajectories shown (■), but that were lost after 150–300 s. Therefore, nine larvae swam deep (◇, ▲), five swam in midwater (■) and one swam at the surface (□). **B** In lagoon. Between *lines 1* and *2* (◇) we omitted for clarity nine other lines that monotonically reached 18–20 m: at least 7 of these 11 larvae attempted to settle on coral heads. Fish *3* and *4* (▲) initially ascended, but were lost descending rapidly, and are assumed to have reached 18 m. Between *lines 5* and *6* (□) we omitted for clarity three other lines that reached the surface at 90–210 s and continued there for 70–200 s before loss. Therefore, 13 larvae swam deep (◇, ▲), one swam in midwater before being lost at 120 s (■) and five swam at the surface (□)

In summary, individual larvae did not swim randomly, although they did not swim in any particular direction, nor did their trajectories or variation in them differ between ocean and lagoon.

Interactions with predators

Reactions to predators varied among larvae of different species (numbers refer to the number of times a behaviour was observed). *Acanthurus triostegus* attempted to use the observer diver as shelter (2), obviously not a natural response. *Chromis viridis* reacted in a variety of ways, including changing direction (5) or depth (3), and stopping (2), sometimes in combination. *Neoniphon argenteus* reacted with a change in direction (5), although once this was combined with a stop and change in posture. *Ptereleotris* sp. changed depth (3) or direction (2). The changes in direction ranged from 50–115°, except for one *N. argenteus*, where a complete circle was completed over 120 s, after which the larva resumed its

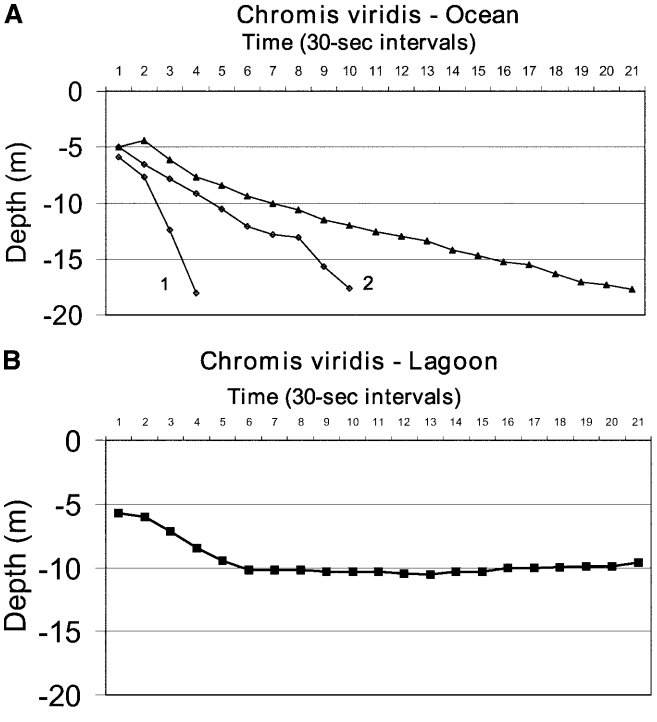

Fig. 4 Vertical swimming trajectories of *Chromis viridis* larvae. **A** In ocean. Trajectories of individual larvae are shown. Between *lines 1* and *2* (◇) we omitted for clarity 14 other trajectories that monotonically reached 18–20 m. One larva (▲) ascended briefly and then descended slowly: it was the only larva that did not reach 18 m by 300 s, although it was close to 18 m at 600 s. Therefore, 16 larvae (◇) swam deep rapidly and one (▲) swam deep but more slowly. **B** In lagoon. Shown is average trajectory based on 16 larvae followed for a full 600 s: standard errors for points range from 0.25–0.89 m. A similar trajectory of one larva abandoned at 12 m, 270 s, due to equipment problems is not included but is clearly midwater. Omitted is trajectory of the only larva to reach 18 m (in 90 s). Therefore, 18 larvae swam in midwater and one swam deep

previous course. In all the above cases, the larvae reacted when the predators were at distances visually estimated to be 3–6 m. Only in three cases of actual attack by predators did larvae react with rapid swimming or violent evasive manoeuvres at close quarters. In the other three attacks, the larvae were eaten without visible reaction, and we assume they did not see the predator.

Discussion

The larvae we observed were near the end of their pelagic period of 20–80 days, and our observations and conclusions apply only to this portion of the pelagic phase during the day. However, it is obvious that at this

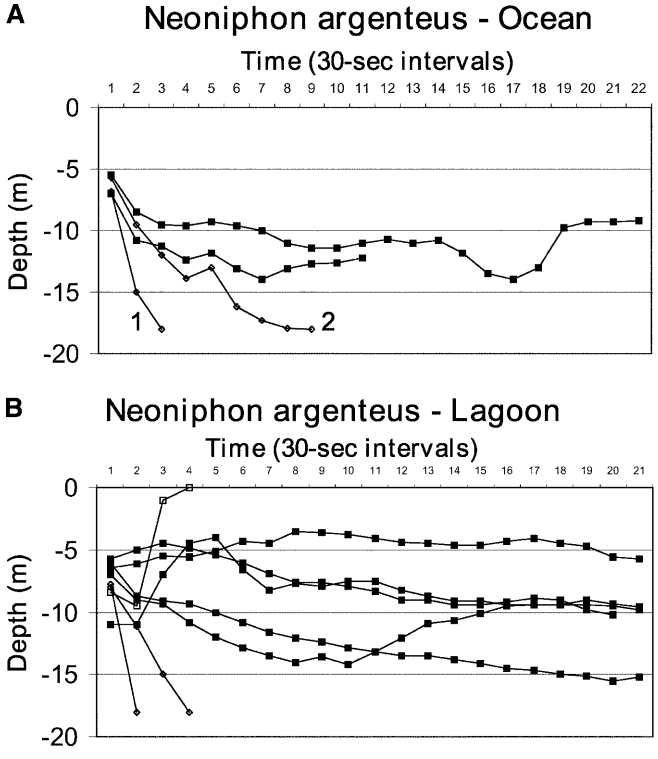

Fig. 5 Vertical swimming trajectories of individual *Neoniphon argenteus* larvae. **A** In ocean. Between *lines 1* and *2* (◇) we omitted for clarity four lines that reached 18 m, plus one larva lost at 16 m while descending rapidly. Shorter of the two midwater trajectories (■) terminated at 320 s when larva was eaten by a remora. Therefore, seven larvae (◇) swam deep and two (■) swam in midwater. **B** In lagoon. Not shown are trajectories of two fish lost in midwater (7 and 14 m) at 140 and 105 s, respectively. One fish (□) swam rapidly to the surface, where it was lost almost immediately. Therefore, two larvae (◇) swam deep, seven larvae (five ■, plus two lost) swam in midwater and one (□) swam to the surface

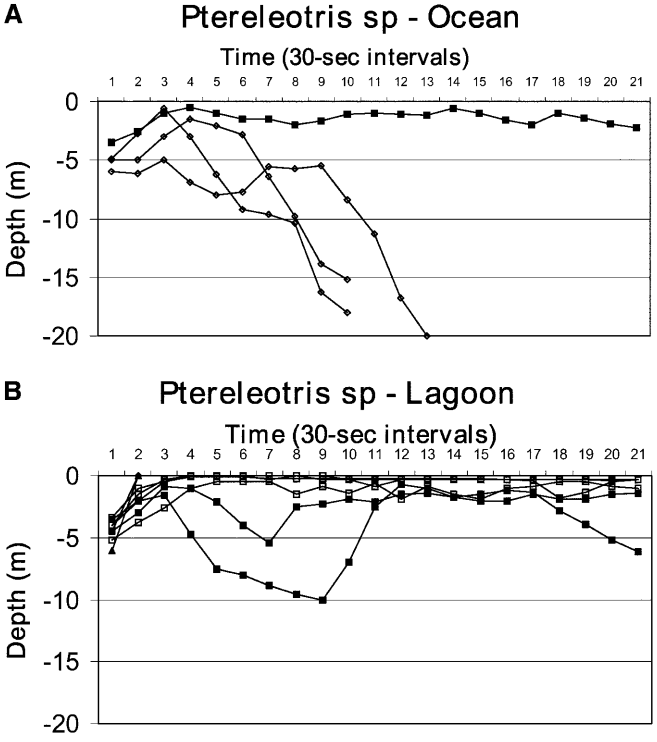

Fig. 6 Vertical swimming trajectories of individual *Ptereleotris* sp. larvae. **A** In ocean. Three larvae (◇) swam deep after an initial ascent. Two of these reached 18–20 m and third was eaten by a remora at 15.6 m while descending steeply. Other larva (■) oscillated over a narrow range of depths near the surface. Therefore, three larvae (◇) swam deep and one (■) swam at the surface. **B** In lagoon. Two larvae (▲) immediately swam to the surface where they were lost in less than 1 min. Four larvae (□) swam to or near the surface and remained there throughout rest of 600-s observation period. Two larvae (■) oscillated in midwater, although one spent about half of observation period near the surface. Therefore, six larvae (□, ▲) swam at or near the surface and two (■) swam in midwater

Table 3 Summary of swimming directions of larvae of four reef-fish species in ocean near and lagoon of Rangiroa Atoll. Only larvae for which at least five bearings were available are included. *P* refers to Rayleigh's test. Values in last two columns include only larvae with directional trajectories and are based on individual average trajectories. *Ra* Range; *nt* not tested

Species	Environment (*n*)	Mean bearings per fish (Ra)	Number of directional fish (*P*)	Number of non-directional fish (*P*)	Number onshore/offshore	Mean of average bearings (*P*)
A. triostegus	Ocean (8)	12 (5–21)	7 (0.01–<0.001)	1 (>0.62)	5/2	250° (>0.88)
A. triostegus	Lagoon (7)	12 (6–21)	7 (<0.004–<0.001)	0	0/7	215° (0.11)
C. viridis	Ocean (13)	8 (5–21)	10 (0.04–<0.001)	3 (0.07–0.51)	5/5	126° (>0.90)
C. viridis	Lagoon (17)	20 (8–21)	17 (0.002–<0.001)	0	8/9	204° (0.65)
N. argenteus	Ocean (5)	11 (7–21)	5 (0.05–<0.001)	0	3/2	275° (0.32)
N. argenteus	Lagoon (7)	16 (5–21)	7 (<0.001)	0	3/4	142° (0.42)
Ptereleotris	Ocean (4)	13 (9–21)	4 (0.05–<0.001)	0	3/1	130° (nt)
Ptereleotris	Lagoon (6)	21 (21–22)	6 (0.05–<0.001)	0	4/2	84° (0.40)

stage the larvae are strong swimmers with considerable control over their depth and their swimming speed and direction. Differences among species in these characteristics show there was no meaningful 'generalized larval behaviour'. Perhaps most interesting was the difference in these behaviours between lagoonal and ocean environments.

Larvae can have the most control over their position and trajectory if they are 'effective' swimmers (sensu Leis and Stobutzki 1999): i.e. if they swim faster than average ambient current speeds (Armsworth 2000). Average swimming speeds of all four species were greater than or equal to current speeds in both environments (Table 1). In the lagoon, average speeds of all four species exceeded even the maximum current speed, and even the slowest individuals of all species exceeded average current speed. In the ocean, average speeds of *A. triostegus* were approximately equal to the maximum current speed estimate, and the fastest *N. argenteus* were much faster than the maximum current speed. Clearly, all four species were 'effective' swimmers at all times in Rangiroa Lagoon, and under most conditions in the ocean nearby. They would not, however, be expected to be effective swimmers in or near the deep passes. This is the first evidence that reef-fish larvae are effective swimmers in oceanic conditions.

Although nearly all the larvae swam directionally, average swimming directions of the larvae provided no indication that they knew the location of the atoll or were swimming in any particular direction in either ocean or lagoon. One would not expect larvae in the lagoon to swim in any particular direction if attempting to find a reef – reefs lie in every direction, and, indeed, in many cases, directly below on the lagoon floor. In contrast, in the ocean, swimming toward the atoll reef might be expected, although we did not find this. Attempts to detect any such swimming were hampered because most larvae swam downward so steeply that we were able to obtain few directional data on each individual, thus leading to either untestability or tests of low power. Although settlement-stage larvae of the four species were effective swimmers at Rangiroa Atoll, we have no evidence that they applied this ability in a non-random way to reach the Rangiroa reefs. However, other studies have concluded that settlement-stage reef-fish larvae swim in directions indicating they know where the nearest reef is located (Leis et al. 1996; Stobutzki and Bellwood 1998).

We detected within-species variation in swimming speed, depth and direction, and the degree of variation was not consistent among species. For example, in the lagoon, *A. triostegus* had three patterns of depth behaviour that varied widely, from rapid descent to swimming at the surface. In contrast, *C. viridis* effectively had only one vertical swimming pattern in the lagoon, and was so consistent that we could derive a meaningful average vertical swimming pattern for the species (Fig. 4B). Although *C. viridis* did not occupy only one depth, its relatively consistent behaviour would perhaps make modelling its dispersal in a lagoon easier, and presumably lead to more precise model predictions than would be the case for *A. triostegus*. Similarly, variation in swimming speed was high, with the range of values within a species about $\pm 50\%$ of the mean or more. In addition, mean swimming direction varied widely among individuals of a species.

Differences in speed, depth and direction between locations were also evident within species. In one species, there was a difference in swimming speed between the two environments: *C. viridis* swam about 26% faster in the lagoon than in the ocean. Possibly, this is related to its vertical distribution behaviour, as this species may simply swim faster when moving horizontally as it did in the lagoon, than when moving nearly vertically as it did in the ocean. In any case, considerations involving swimming during the pelagic period must take into account that *C. viridis* swims 26% faster in the lagoon than in the ocean. On the Great Barrier Reef (hereafter, GBR), settlement-stage larvae of the serranid *Plectropomus leopardus* and some *Chaetodon* spp. swim much faster in open water, or when swimming away from a nearby reef, than when swimming toward or over a reef (Leis and Carson-Ewart 1999, unpublished data), indicating that even greater behavioural flexibility is possible over finer spatial scales than we investigated at Rangiroa.

The most striking difference in behaviour between ocean and lagoon was in vertical distribution. All four species differed between ocean and lagoon in some aspect of their vertical distribution behaviour. In general, larvae swam deeper in the ocean than in the lagoon. This is not simply a physical restraint due to the shallow lagoon bottom, because even the deepest of our observations in the lagoon were 4–7 m off the bottom. Further, in the lagoon, the larvae usually maintained depths well above our 18-m dive limit. Several observations are pertinent in attempting to frame hypotheses about why larvae swim deeper in the ocean.

First, the distribution and quality of light in the two environments are very different. In the ocean, it is very dark below, whereas in the lagoon, even when the bottom is not visible (to a human diver), it is much brighter below due to reflection off the white sand bottom. This difference in upwelling light could conceivably stimulate larvae to swim deeper in the ocean.

Secondly, the bottom was often visible to the divers in the lagoon from depths considerably less than 18 m, and possibly to the larvae, and it was never visible in the ocean. If the larvae can perceive the bottom as well as the divers can (a reasonable assumption, but one not yet tested, J. Shand, personal communication), this could influence their vertical distribution behaviour: for example, a larva might either continue a descent to settle on a reef it had seen, or alternatively continue swimming horizontally if the bottom did not appear suitable for settlement. In the ocean, larvae may swim deep in an attempt to gain a view of the bottom, but it is also possible that larvae in the ocean find shallow reefs by

descent to a relatively deep bottom followed by up-slope migration (Sancho et al. 1997). In other words, larvae may descend until the bottom becomes visible and they can assess if it provides suitable settlement habitat. Behaviour of *A. triostegus* tends to support this idea. In the lagoon, the *A. triostegus* larvae that swam deep and were not lost were seen to settle or attempt to settle onto coral, whereas the other common pattern for this species in the lagoon was to swim at the surface. Neither *C. viridis* nor *Ptereleotris* larvae swam near the bottom in the lagoon, and only two *N. argenteus* larvae did so (one settled), so perhaps these species generally judged the lagoon-floor reefs not suitable for settlement or simply did not see the bottom.

Thirdly, if larvae were selecting vertical position on the basis of illumination levels – a commonly cited mechanism – they would select deeper depths in the ocean due to higher turbidity in the lagoon. Whatever stimulates this difference in behaviour between the two environments, the result is that larvae experience different conditions of light, currents, food, predators and perhaps temperature in the lagoon compared to in the ocean. As all of these factors have been implicated in influencing dispersal, growth and survival during the pelagic phase (Chambers and Trippel 1997), such differences have important implications for inter-reef connectivity and recruitment. As an example, realistic models of dispersal take into account vertical differences in horizontal current trajectories, so it is important to place larvae in the correct depth stratum and to know how this differs among locations.

We found few differences in swimming direction between the two environments. Only one proved to be possibly significant: a higher proportion of *C. viridis* larvae swam directionally in the lagoon than in the ocean. None of the other measures of swimming direction, including swimming toward or away from the reef, differed between locations for any species. It is difficult to assess the significance of this result. Low numbers of observations per individual in the ocean and limited numbers of individuals observed decreased our ability to detect any differences that may have been present. However, it is possible that larval behaviour in the ocean differs from that over the GBR continental shelf, where differences in swimming direction among locations have been detected (Leis et al. 1996, unpublished data). For example, in the ocean, descent to a preferred depth greater than we could follow may precede directional swimming relative to a reef. This was our first attempt to examine larval behaviour in the ocean, and only further oceanic work will clarify the situation.

No larvae were eaten or attacked in the lagoon, but four were eaten in the ocean and two more attacked unsuccessfully. This is probably because the oceanic predator species were initially attracted to the divers, and once the predators were close, the larvae were noticed and attacked. In contrast, the lagoonal predator species made no attempt to closely approach the divers, and we had no indication that they noticed the larvae we were following. It must be noted that our observations on predation in the two environments are not quantitatively or even relatively meaningful because of the presence of the divers and because the two environments contained different predator species with obviously different behaviours relative to the divers.

Our observations do indicate, however, that the larvae reacted in a way that reduced their chances of being detected by the predator: by stopping, by changing depth or by changing direction. Larvae seem alert to the threat of predation, can detect larger fishes at a distance of several metres, a distance great enough that it is unlikely they would have been seen, and can react in ways that reduce their chances of coming close enough to the predators to be seen and attacked. Settlement-stage larvae behave in a way that seems effective in avoiding predators: not a surprising conclusion, but one that indicates the behavioural sophistication of the larvae (Leis and Carson-Ewart 1998).

Because the larvae reacted to the predatory fishes several metres away, we assume that they detected these fishes visually, as did the divers. However, we cannot rule out detection by other means. In the ocean, larvae reacted when the predators were 3–6 m away although the predators were visible to the divers at much greater distances. In the more turbid lagoon, the predator schools would first be seen by the divers at smaller distances (5–10 m), but the larvae would react to them at distances similar to those in the ocean, i.e. 3–5 m. Regardless of the stimuli, the larvae reacted at distances much greater than those reported in laboratory studies of fish larvae of similar size (e.g. Higgs and Fuiman 1998; Poling and Fuiman 1999). In fact, the reaction distances we observed were much greater than the dimensions of the containers used in those laboratory studies. The cited investigators suggest that larvae avoid predators by dodging at the last moment, when the predator is too close to react effectively. This may be an effective last-ditch defence, but our in-situ observations combined with the lab results imply that fish larvae may have a layered defence. One set of behaviours operates at distance to take advantage of the small size and low visibility of the larvae to decrease the likelihood of being detected by the predator, and the other set of behaviours operates at small separation distances if the first set fails and the larva is detected by the predator. This implies considerable behavioural sophistication by the larvae, but no more than many adult fishes possess.

One goal of the present study was to evaluate the practicality of the in-situ methodology of observing larval-fish behaviour in the open ocean. Although we had no problems with sharks once we learned to avoid the vicinity of the deep channel, and although larvae could be followed in oceanic conditions, the tendency of larvae to descend rapidly to > 18 m severely limited both the duration of the dives and the amount of data we could obtain. Where larvae tend to sound, limitations are imposed on the types of data that can be obtained, and, therefore, on the kinds of questions that can be

investigated using in-situ methodology. Another problem that we encountered much more frequently in the ocean than in the lagoon, or, indeed, in GBR waters, was the remora. These pelagic fish are attracted to divers, and often attempt to attach to them. Remoras make a nuisance of themselves by distracting the divers and the larvae, and at times by attacking or eating the larvae we were observing, all resulting in the acquisition of less data per dive. Therefore, in the ocean, the in-situ methodology was more difficult to apply and less productive than in lagoonal waters.

Observations of settlement-stage larvae of four species of coral-reef fishes in an atoll lagoon and in the nearby ocean show that neither of the 'simplifying assumptions' of passive behaviour or of uniform behaviour in different environments is supportable. Further, behaviour differs among species, and may also differ among individuals of the same species. Larvae do behave differently in the ocean compared to in the lagoon. We made observations only during the day: it is likely that behaviour at night differs from that during the day. In short, there is no overall 'larval behaviour pattern'. None of this should be surprising, as reef-fish larvae at settlement are well developed and some species are relatively large (Leis and Carson-Ewart 2000). Behaviour of settlement-stage larvae varies among and within species, between locations and environments, and probably on a diel basis. This is essential knowledge for those who would understand or realistically model larval dispersal or retention and connectivity of fish populations on different reefs, but it will considerably complicate their tasks.

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