

NOTE

Fish larvae prefer coral over algal water cues: implications of coral reef degradation

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ABSTRACT: Many marine reef fishes have pelagic larval stages that develop in offshore waters. These larvae face the great challenge of relocating to patchily distributed reef environments in a vast oceanic matrix. We explored how chemical cues emitted from coral versus algal reefs attract fish larvae at Rangiroa Atoll (French Polynesia). Experiments with 2-channel choice chambers showed that during the recruitment stage, 7 of the 10 fish species studied preferred water from reefs dominated by coral compared to reefs dominated by algae (e.g. *Aulostomus chinensis*, *Chromis viridis*, *Ptereleotris microlepis*, and *Sargocentron spiniferum*). Only *Zebrasoma veliferum* preferred water from reefs dominated by algae. Overall, olfactory cues could play an important role in directing pelagic larval stage fishes to a suitable reef on which they can settle.

KEY WORDS: Sensory mechanisms · Habitat selection · Chemical cues

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INTRODUCTION

The replenishment and persistence of most coral reef fish species depends on larvae finding suitable adult habitat at the end of their pelagic dispersive stage (Leis et al. 2011). Researchers continue to be surprised by the sensory and swimming capabilities of fish larvae (e.g. Gerlach et al. 2007, Munday et al. 2009, Huijbers et al. 2012). The majority of fishes can swim either at hatching or soon thereafter. They also have the potential to use chemical or sound cues to control their position within the water column, increasing the probability that they will be transported to suitable reefs (for review, see Leis et al. 2011). Once a larva has located a reef, a suitable micro-habitat on which to settle must be found. Recent studies have highlighted the role of larval sensory mechanisms in patch identification and patch selection at smaller scales, including the detection of

visual, chemical and sound cues from conspecifics or micro-habitats (among patches separated by centimetres to metres within a single reef; for review, see Arvedlund & Kavanagh 2009). For example, Huijbers et al. (2008) showed that settling fish larvae were capable of olfactory discrimination and preferred the odour of their home reef (mangroves and seagrass beds versus coral reefs). Such small-scale behavioural responses resulting in patchy distributions can have strong effects on the subsequent growth and survival of individuals and can also reinforce or ameliorate spatial heterogeneity in environmental features (Leis et al. 2011).

While evidence is mounting that larval reef fish are active participants in the process of dispersal and recruitment (Arvedlund & Kavanagh 2009), the sensory and behavioural mechanisms by which larvae disperse and return from their oceanic phase to appropriate recruitment habitat remain unknown,

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especially in the context of habitat degradation (for exceptions, see Munday et al. 2009, McCormick et al. 2010). We aimed to test the preference of fish larvae for coral versus algal water cues at Rangiroa atoll (French Polynesia). Many reefs in French Polynesia have changed from coral to algal dominated states, and the abundance and species richness of dominant corals, sea urchins, parrotfishes, and surgeonfishes that provide either direct chemical cues or indirect auditory cues vary according to reef state (coral versus algal dominance; Adjeroud et al. 2005). Therefore, the potential of French Polynesian reefs to attract larvae may have decreased, with profound consequences on the number of larvae arriving, potentially disconnecting the recruitment potential of an island from the availability of larvae in the surrounding water column.

Specifically, we aimed to test the *a priori* prediction that larval fish will orientate themselves toward water from reefs dominated by coral compared to water from reefs dominated by algae. We discuss our results in the light of 3 hypotheses: larval fish are attracted to the chemical cues from (1) conspecifics or (2) coral habitat, and (3) the efficiency of conspecific cues could vary according to the environment in which they are emitted.

MATERIALS AND METHODS

Study areas

The present study was conducted on the north coast of Rangiroa atoll, French Polynesia. We selected 2 distinct morphological reefs that are considered as nursery areas for coral reef fish (Lecchini et al. 2012): Fringing Reef (which are areas along the submerged reef flat without any emergent land) and the inner reef flat of Motu (emerged coral cays). We sampled 2 alternate states in each of the 2 reefs: coral state (live coral cover, mean \pm SD: $27 \pm 2.3\%$; versus algal cover: $5 \pm 0.6\%$) and algal state (live coral cover: $3 \pm 0.5\%$, versus algal cover: $24 \pm 3.1\%$). Each algal or coral reef measured 310×105 m, and the depth ranged between 0 and 2 m. The 4 sampling sites had the same temperature (28°C) and salinity (36 psu).

A total of 10 fish species was captured at larval stage with crest nets (Lecchini et al. 2004) set up on the reef crest of Rangiroa in October and November 2007 (*Acanthurus triostegus*, *Aulostomus chinensis*, *Chromis viridis*, *Chrysiptera glauca*, *Chrysiptera leucopoma*, *Ctenochaetus striatus*, *Naso vlamingi*, *Ptereleotris microlepis*, *Sargocentron spiniferum*, and

Zebrasoma veliferum). Fish that were captured during the night were transferred and subsequently maintained in aquaria containing UV-sterilised and $50 \mu\text{m}$ filtered seawater. All experiments described below were conducted in the evening following larval capture (i.e. within 24 h of collection). Laboratory experiments were conducted under evenly distributed fluorescent tubes (i.e. neon lamps of 36 W).

Chemical detection abilities of fish larvae

The response of fish larvae to olfactory cues of coral versus algal reef water was tested in a 2-channel choice flume, as described by Gerlach et al. (2007). Each day, a total of 100 l (20 l combined from each of 5 sampling points) of water was collected by pumps within each coral or algal reef (Motu and Fringing Reef) and transported in tanks to the laboratory. The tanks were connected to the choice flume by pipes to create a constant gravity-driven flow (1 l min^{-1} per channel), and fish larvae were tested in the water collections within 24 h.

For each test, a single larva was placed into the centre of the downstream compartment of the choice flume for 1 min to acclimate (with a net prohibiting the larva from moving into the upstream channels). At the end of the acclimatisation period, the net was removed. The trial was finished when the larva stayed >15 s in an upstream channel (A or B) or after a 4 min period in which the larva made no choice (i.e. larva either still in the downstream compartment or still moving between the channels).

Using the protocol described above, we conducted 3 tests on each individual larva from a single cohort of 10 to 20 larvae per species. We determined the distribution of choice exhibited by a larva exposed to artificial seawater (fresh water to which aquarium sea-salt was added; temperature 28°C , salinity 36 ppt) in the 2 channels (the baseline distribution in the absence of manipulated chemical cues, as a 'control test'). We determined the distribution of choice exhibited by a larva exposed to coral reef water in one channel versus algal reef water in the other channel, with the test undertaken for each of the 2 reefs ('Fringing Reef test' and 'Motu test').

After each test, the flume chamber was emptied and rinsed with freshwater. The order of tests (Control, Fringing Reef, and Motu) was randomly alternated. To avoid exhausting the larva, the larva was maintained in an individual tank filled with artificial seawater for 60 min before being re-tested. For each fish species, a χ^2 test with a Bonferroni correction was

carried out separately for each reef to compare the observed distribution to a baseline distribution (i.e. number of larvae in the downstream compartment and in the Channels A or B when tanks were filled with artificial seawater).

RESULTS

During the tests, the fish behaviour was characterised as follows: Fish larvae swam from side to side during the acclimatisation period. When the net was removed, the fish larvae generally swam into the current and explored both of the upstream channels ('exploration phase') before they made a decision (i.e. stayed >15 s in one channel) or not (i.e. continued to swim between the downstream and upstream compartments). The exploration phase always lasted ≥ 48 s. If a fish larva stayed only in the downstream compartment without moving, the data was not used in the statistical analysis.

When the tanks were filled with artificial seawater, fish species either had a homogenous distribution between the 2 upstream channels (e.g. *Ctenochaetus striatus*, one channel: 9 larvae; other channel: 8 larvae; downstream compartment: 0 larva; $\chi^2_{0.05,1} = 0.06$, $p = 0.96$) or they did not make a decision (e.g. *Aulostomus chinensis*, downstream compartment: 14 larvae; one channel: 2 larvae; other channel: 2 larvae) (Fig. 1A). These results confirmed that the choices made by the larva were not because of external effects of the aquarium system.

When the tanks were filled with algal and coral seawater from Fringing Reef or Motu, only *Ctenochaetus striatus* and *Naso vlamingi* larvae did not show significant attraction ($\chi^2_{0.05,2} < 5.99$, $p > 0.05$). In contrast, the 8 other species tested used chemical cues to make definite choices between coral or algal reef waters (Fig. 1B,C). *Chromis viridis*, *Aulostomus chinensis*, *Ptereleotris microlepis*, and *Chrysiptera glauca* were significantly attracted to coral reef water from both reefs (for example, larval attraction of *C. viridis* to coral reef water of Motu $\chi^2_{0.05,2} = 30.5$, $p < 0.001$; larval attraction of *A. chinensis* to coral reef water of Fringing Reef $\chi^2_{0.05,2} = 16.0$, $p < 0.001$; larval attraction of *P. microlepis* to coral reef water of Motu $\chi^2_{0.05,2} = 17.3$, $p < 0.001$; larval attraction of *C. glauca* to coral reef water of Fringing Reef $\chi^2_{0.05,2} = 10.1$, $p = 0.005$). *A. triostegus* was only attracted to coral reef water from Motu ($\chi^2_{0.05,2} = 10.1$, $p = 0.005$), while *C. leucopoma* and *S. spiniferum* were only attracted to coral reef water from Fringing Reef ($\chi^2_{0.05,2} = 11.3$, $p = 0.004$; $\chi^2_{0.05,2} = 8.1$, $p = 0.01$; respec-

tively). Lastly, *Z. veliferum* was the only species that was significantly attracted to algal reef water from Fringing Reef ($\chi^2_{0.05,2} = 10.0$, $p = 0.005$). *Acanthurus triostegus* was only attracted to coral reef water from Motu ($\chi^2_{0.05,2} = 10.1$, $p = 0.005$), while *Chrysiptera leucopoma* and *Sargocentron spiniferum* were only attracted to coral reef water from Fringing Reef ($\chi^2_{0.05,2} = 11.3$, $p = 0.004$, and $\chi^2_{0.05,2} = 8.1$, $p = 0.01$, respectively). Lastly, *Zebrasoma veliferum* was the only species that was significantly attracted to algal reef water from Fringing Reef ($\chi^2_{0.05,2} = 10.0$, $p = 0.005$).

DISCUSSION

Visual surveys were conducted at Rangiroa to estimate the abundance of recently settled or adult fish on the same coral and algal reefs described in the present paper (see also Lecchini et al. 2012). The surveys showed that *Ptereleotris microlepis*, *Aulostomus chinensis*, and *Chromis viridis* (whose larvae were attracted to coral reef water of both reefs) were only present as recent settlers and adults in the coral habitat at the 2 reefs (Fringing reef and Motu) and were absent from the algal habitat at these reefs. For these species, it could be hypothesised that the chemical cues from (1) conspecifics or (2) coral habitat may be responsible for larval attraction. For example, *C. viridis* settled always on live coral colonies of *Porites rus* occupied by conspecifics in French Polynesia islands (Lecchini et al. 2007). The chemical cues emitted by conspecifics or *P. rus* could favour the settlement of larvae on this habitat.

In contrast, recent settlers and adults of the other species whose larvae were only attracted to coral reef water (*Acanthurus triostegus*, *Chrysiptera glauca*, *C. leucopoma*, and *Sargocentron spiniferum*) were present in similar densities on both coral and algal reefs (Lecchini et al. 2012). For these species, the chemical cues from conspecifics were present in waters from both the coral and algal dominated reefs, yet larvae were only attracted by coral reef water. For these species, it could be hypothesised that either the chemical cues from coral habitat (and not from algal habitat) may be responsible for larval attraction (Hypothesis 2) or the efficiency of chemical cues from conspecifics varied according to the environment in which they were emitted (Hypothesis 3). Larval responses to the cues of conspecific adults might be influenced by the medium in which they are offered. For example, Fisher et al. (2006) showed that the alteration of the chemical environment could disrupt communication in freshwater fish. In coral reefs,

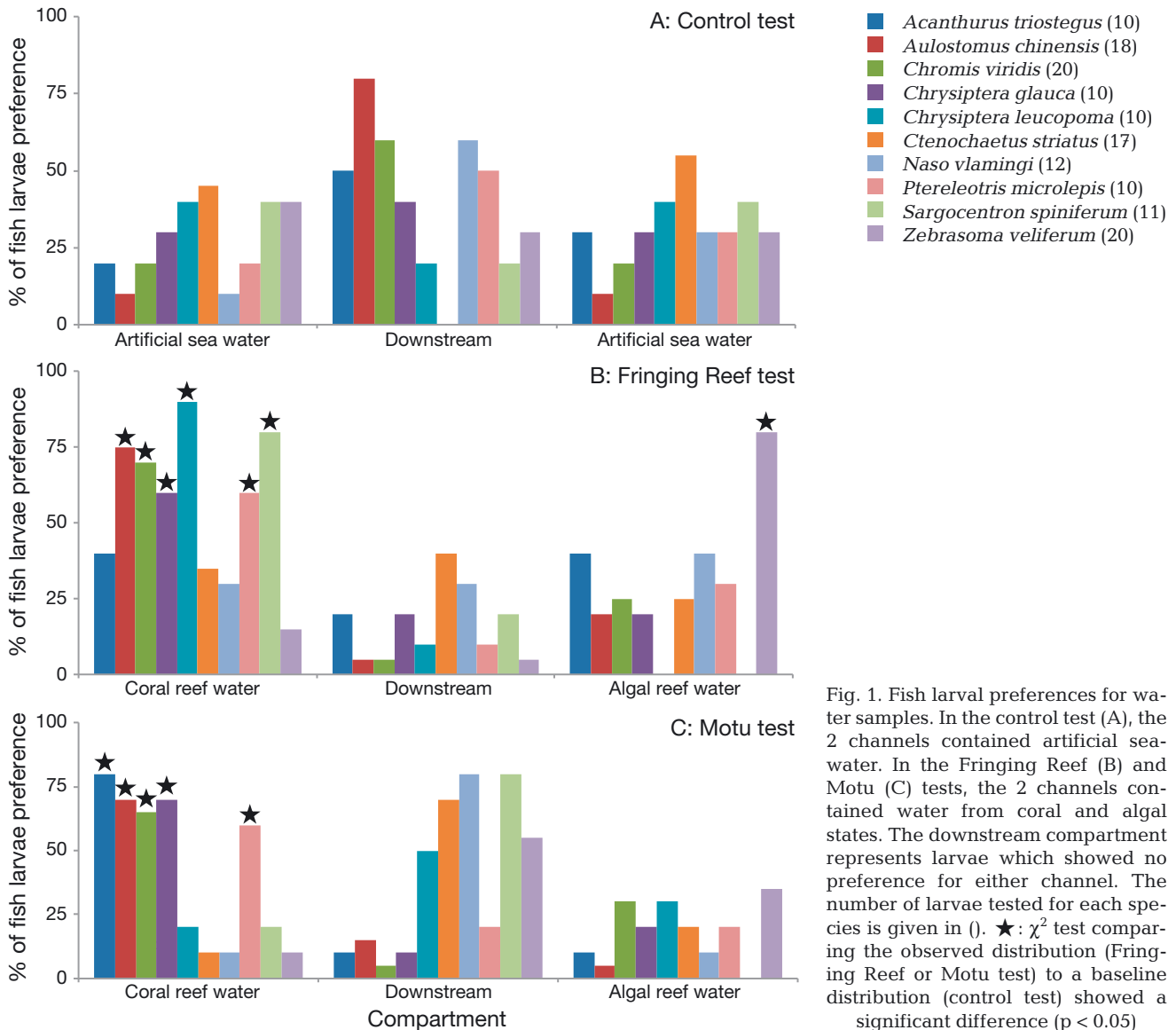


Fig. 1. Fish larval preferences for water samples. In the control test (A), the 2 channels contained artificial sea-water. In the Fringing Reef (B) and Motu (C) tests, the 2 channels contained water from coral and algal states. The downstream compartment represents larvae which showed no preference for either channel. The number of larvae tested for each species is given in (). ★: χ^2 test comparing the observed distribution (Fringing Reef or Motu test) to a baseline distribution (control test) showed a significant difference ($p < 0.05$)

Munday et al. (2009) showed that acidification of sea-water could disrupt the olfactory mechanism by which clownfish larvae discriminate between cues that may be used in locating suitable adult habitat. These 2 studies could thus support our hypothesis that the response of larval fish at Rangiroa would be weaker when conspecific cues are offered in algal dominated reefs versus coral dominated reefs. Indeed, the properties of the water (e.g. physical or chemical properties) on algal versus coral reefs should be different, and these differences in the water properties between reefs might influence the olfaction abilities of marine larvae to recognise the conspecific cues.

Lastly, the visual surveys showed that recent settlers and adults of *Zebrasoma veliferum* were mainly

present in the algal habitat at Fringing Reef. It is not surprising that *Z. veliferum* larvae were attracted by chemical cues of algal dominated habitat or conspecifics. Indeed, these larvae are herbivorous. Moreover, as densities of recent settlers and adults were much larger on algal reefs, then it would be expected that conspecific cues are found in lower concentrations in water collected from coral reefs.

Overall, although it is still not known how fish larvae find their way back to a particular habitat, our results suggests that fish larvae could respond to many different types of chemical cues associated with coral or algae directly or with conspecifics, whose presence changes in response to coral versus algal cover, and that the efficiency of these recruitment cues could vary according to the environment

in which they are emitted. These results raise the issue of coral reef degradation. Indeed, variation in the composition of marine communities has largely been attributed to factors affecting the recruitment of marine larvae (McCormick et al. 2010). Jones et al. (2004) showed that the decline in adult populations of coral reef fish in degraded habitat had more to do with recruitment failure than adult mortality. They also suggested that the rescue effect of recruitment might be completely ineffective in degraded habitat. Therefore, understanding the sensory mechanisms that determine how marine larvae respond to different stages of coral stress (coral versus algae) is a pressing issue as recent changes in tropical reefs from coral to algal domination are predicted to continue in the future.

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