

FROM THE OCEAN TO A REEF HABITAT: HOW DO THE LARVAE OF CORAL REEF FISHES FIND THEIR WAY HOME? A STATE OF ART ON THE LATEST ADVANCES

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PERCEPTION OF INFORMATION
CORAL REEF FISH
LARVAL SETTLEMENT
HABITAT SELECTION
CORAL REEF DEGRADATION

ABSTRACT. – As it is unlikely that successful settlement is solely a matter of chance (i.e. to find a suitable habitat), one of the greatest challenges facing the fish larvae is how to locate the relatively rare patches of coral reef habitat on which they settle and ultimately reside as adults. The answer must lie partly in the sensory modalities of fishes at settlement. Habitat selection is only possible if fish larvae could detect some environmental cues to select a suitable reef habitat at settlement. The present review aims at providing the latest works dealing with information perception in coral reef fish larvae at settlement. Two decades ago, it was generally assumed that larval behaviors and sensory abilities at settlement were considered too feeble to significantly affect dispersal outcomes. Several recent studies showed that recognition of suitable reef habitats by fish larvae at settlement is based on a combination of visual, chemical and acoustic cues. The first part of our review shows the main advances in the knowledge of visual, chemical and acoustic cues used by fish larvae to detect an island, a reef, a micro-habitat, a conspecific or some predators. The second part of our review deals with the effect of imprinting and/or innate capabilities. The third part focuses on the different cues used at different scales and underlines some contradictory results about the distance of transmission and detection of chemical and acoustic cues in coral reefs. Finally, as global and regional environmental changes have stressed coral reefs to such an extent that they are either destroyed or in decline, the fourth part presents the effects of both anthropogenic and environmental stressors on information perception and response capacities in coral reef fish larvae. If polluted seawater disrupts the larval abilities to find a suitable reef habitat, fish larvae may spend more time in the planktonic environment, resulting in increased energetic costs and predation risk, and consequently a lower larval settlement. We hypothesise that as the stability of fish communities is dependent, in part, on the stability of social interactions, the disruption of "larvae-habitat relationships" can have major consequences for larval settlement into adult population with further repercussions for the ecosystem as a whole. Overall, larval settlement of coral reef fish is an excellent example of the complexity of interactions between an organism and its environment as without perceiving environmental cues, fish larva would have very little chance of selecting a suitable reef habitat. Moreover, understanding the relationship between reef state and settlement potential will allow management planning for the maintenance of coral reefs that are increasingly degraded.

INTRODUCTION

Animals constantly make decisions: they choose mates, select a place to live or forage, and they decide whether to engage in activities which expose them to risk of predation. These decisions necessitate the perception of some environmental cues in order to optimize the social interactions (Cassier *et al.* 2000). Thus, results of simple decisions based on the perception of some cues may influence an individual's life span, a species' population biology,

and community structure (Blumstein & Bouskila 1996). While there is a lot of information about decision-making in breeding, foraging and habitat selection, little is known on habitat selection for fish species at settlement, especially in coral reefs (Lecchini *et al.* 2015).

The life cycle of most coral reef fish species includes a planktonic larval phase which usually lasts from three to six weeks, followed by a sedentary reef phase for the juveniles and adults (Leis & McCormick 2002). During the pelagic phase, the larvae may move far from their

native reef due to currents and/or their swimming abilities. Then larvae return to the reef (natal or not) to continue their development into juveniles, then to adults. At the end of its pelagic phase, a species-specific change in morphology and physiology, called metamorphosis, occurs during which fish lose many of the characteristics that enhance survival in the pelagic environment and develop other features suited to their new reef environment (transformation from larval to juvenile stage – McCormick *et al.* 2002). Moreover, a fish larva must choose a suitable reef habitat to settle, habitat that will facilitate post-settlement survival and growth (Doherty 2002). As fish larvae are subjected to strong selective pressures to choose the suitable reef habitat, many fish species show specific preference of habitat at settlement based on the presence/absence of specific substrates, conspecifics, predators and competitors for food and space (Doherty 2002). After several weeks or months in the settlement habitat, juveniles move into the adult population and become sexually mature (Lecchini & Galzin 2003).

As it is unlikely that successful settlement is solely a matter of chance (i.e. to find a suitable habitat), one of the greatest challenges faced by the fish larvae is how to locate the relatively rare patches of coral reef habitat on which they will settle and ultimately reside as adults (Myrberg & Fuiman 2002). The answer must lie partly in the sensory modalities of fishes at settlement. Habitat selection is only possible if fish larvae could detect some environmental cues to select the suitable habitat at settlement. Since 2000s, studies have highlighted the role of larval sensory and swimming mechanisms in habitat selection, including the detection of visual, chemical and sound cues from conspecifics, habitats, or predators (see next paragraphs). Thus, the perception of information by coral reef fish larvae resulting in successful settlement is a key process in population biology, shaping the characteristic texture of populations, communities and ecosystems in space and time.

The present review aims at providing the results of recent works dealing with information perception in coral reef fish larvae at settlement without going back to the historical background that is provided by the five excellent previous reviews (Kingsford *et al.* 2002, Myrberg & Fuiman 2002, Montgomery *et al.* 2006, Arvedlund & Kavanagh 2009, Leis *et al.* 2011). We tried to answer some of the questions raised by these syntheses using the latest works in the topic. In the first part, we present the main advances in the knowledge of visual, chemical and acoustic cues used by coral reef fish larvae at settlement. The second part deals with the effect of imprinting and/or innate capabilities. The third part focuses on the different cues used at different scales. Lastly, the fourth part presents the effects of both anthropogenic and environmental changes on information perception and response capacities in coral reef fish larvae.

The sensory cues used by coral reef fish larvae at settlement... Fifteen years after

At the end of their pelagic phase, fish larvae undergo metamorphosis and choose settling habitats, based mainly on the presence or absence of conspecifics, as well as other species (Doherty 2002). Until two decades ago, it was generally assumed that larval behaviors and sensory abilities at settlement were considered too feeble to significantly affect dispersal outcomes (Williams *et al.* 1984). In fact, only three main studies have explored the sensory abilities of coral reef fish larvae at settlement before 2000s (Sweetman 1988, Booth 1992, Elliott *et al.* 1995). Since then, much evidence have demonstrated the developed behavioral and sensory abilities of larvae, rejecting the traditional paradigm that fish larvae could be regarded as passive plankton (Leis 2015). Today, we know that visual, olfactory and auditory senses are used by fish larvae to settle on their first reef habitat.

New insights on chemical cues

Coppock *et al.* (2013) used choice plumes to show that the presence of conspecifics and the coral species attract settlement-stage larvae of *Dascyllus melanurus*, *Chrysiptera paraseuna*, *Chaetodon octofasciatus*. Several recent studies have thus demonstrated that chemical cues are used by fish larvae to find a suitable reef habitat (*e.g.*, Atema *et al.* 2002, Lecchini *et al.* 2005a, b, 2013, Dixon *et al.* 2011, 2014a), to find conspecifics (*e.g.*, Lecchini *et al.* 2005a, b, 2007b), or to avoid predators (*e.g.*, Dixon *et al.* 2012). However, few studies have explored the relative importance of the different types of chemical cues (predator, conspecifics, vs. habitat). For example, Lecchini & Nakamura (2013) explored the effect of chemical cues at different spatial scales (reef patch vs. microhabitat or conspecifics) at Ishigaki Island (Japan). They showed with choice flume experiments that three of the eight fish species detected olfactory cues at large spatial scales (Exp. 1: reef patch), whereas six of the eight species detected olfactory cues at small spatial scales (Exp. 2: conspecifics). Moreover, when fish larvae had the choice between chemical cues of reef patch, coral habitat and conspecifics, they preferred the conspecific cues above other types of information for habitat selection. A multitude of other animals also use conspecific information more often than habitat information to find a suitable habitat (Stamps & Krishnan 2005). Conspecific attraction generally occurs when animals use social cues as positive proximate stimuli during decision-making, including foraging, movement, and settlement decisions (Danchin *et al.* 2004). Social aggregation of fish larvae with older conspecifics may be the result of individuals using conspecific “guides” to potentially find beneficial resources (availability of resources and low mortality; Ben-Tzvi *et al.* 2009). However, the importance of chemical cues

of conspecifics vs. predators has not been explored. Yet, some recent studies have tackled the question of chemical cues from the perspective of risk assessment. Vail & McCormick (2011) showed that *Pomacentrus nagasienkii* and *P. amboinensis* larvae (damselfishes) settled 24-43 % less to reefs with predator scent.

The relative effectiveness of chemical cues originated from the reef is dependent on the spatial scale, and the hydrological conditions at which fish larvae could detect each cue. No study has directly addressed this point. However, some studies have estimated the distance of detection of fish larvae. Paris *et al.* (2013a), using *in situ* techniques, showed that some pomacentrids and apogonids larvae changed speed and direction when placed in an odour plume, even at a distance of several kilometres from the reefs. Atema *et al.* (2002) estimated that the transmission distance of odour plume from a coral lagoon in the ocean could range between 1.6 to 3 km, using temperature measurements and visual observations of turbidity. Lecchini *et al.* (2014a) explored the distance of transmission of chemical cues emitted by live vs. dead coral reefs (High Pressure Liquid Chromatography analyses of water sampling stations at 0, 1 and 2 km away from the reef) at Ishigaki Island, Japan. The results highlighted that a live coral reef produced different and distinct molecules from a dead coral reef, and some of these molecules could be transported to a distance of at least 2 km from the reef with a 14-17-fold reduction in concentration. However, *Chromis viridis* larvae detected the chemical cues only at a distance of 1 km away from the live coral reef.

Overall, several recent studies have demonstrated that chemical cues are mainly used by fish larvae to find a suitable reef habitat and/or conspecifics, or to avoid predators. Three fruitful research avenues should be conducted in the future on the chemical cues at settlement: (1) Test the interaction, the hierarchy, and the relative importance of habitat, conspecifics and predator cues to understand the decision making dynamics when choosing a habitat for settlement. (2) Identify the distance of detection of chemical cues in different environments; and (3) Test the importance of chemical cues integrated with visual and acoustic cues. (4) Chemical cue orientation is normally assumed to involve swimming along chemical concentration gradients; however mixing processes in the ocean may break a chemical plume into smaller disconnected patches. Larvae which use chemical cues for orientation need to behaviorally overcome this problem using special ranging strategies (Vergassola *et al.* 2007). It will be interesting to examine how coral reef fish larvae behaviorally cope with this problem.

New insights on acoustic cues

Acoustic cues are crucial in most marine organisms for mating, feeding, orientation, territory defence and prey-predator detection (*e.g.*, Tolimieri *et al.* 2004, Mont-

gomery *et al.* 2006, Parmentier *et al.* 2010, Simpson *et al.* 2010). They have the advantage of propagation in all directions, are not stream-dependent as are the chemical cues, are effective independently on the light and turbidity, and propagate far beyond the visual cues. The underwater acoustic environment is characterized by loud and various noises (Cato 1992), including from abiotic (*e.g.*, surf, wind and waves) and biotic sources (*e.g.*, crustaceans, fishes and mammals). In coral reefs, sound level is known to be greater close to the reef due to a high density of sound sources (*e.g.*, breaking waves, snapping shrimps and vocalizing fishes), and reef noise has been shown to vary during day periods, moon phases and seasons (Cato 1992, Montgomery *et al.* 2006, Radford *et al.* 2008). Several studies have thus highlighted that the reef sound attracted fish larvae at settlement (*e.g.*, Tolimieri *et al.* 2004, Simpson *et al.* 2005, Montgomery *et al.* 2006, Radford *et al.* 2007, Holles *et al.* 2013, Parmentier *et al.* 2015a).

In this review we will focus on a few recent studies which examine in detail the response of coral reef fish larvae to sound. Parmentier *et al.* (2015a) explored the attraction of fish larvae to underwater sounds from different reef habitats (barrier reef, fringing reef and mangrove) using the choice chamber experiment at Moorea Island (French Polynesia). Sixteen of the twenty species tested have significantly changed their behavior under at least one of the habitat playback conditions, and a various range of responses was observed: fishes were a) attracted by a single sound but repelled by none (*e.g.*, *Ostorhinchus angustatus*), b) repelled by one or more sounds but attracted by none (*e.g.*, *Pristiapogon fraenatus*), c) attracted by all sounds (*e.g.*, *Ctenochaetus striatus*), d) attracted and repelled by several sounds (*e.g.*, *Dascyllus aruanus*), and e) not influenced by any sound (*e.g.*, *Acanthurus triostegus*). These results confirmed the previous studies that fish larvae are attracted by acoustic cues of coral habitats at settlement. The use of sound to locate habitat has also been recently shown at Lizard Island, Australia, where Pomacentridae larvae were significantly more attracted to patch reefs with lagoon or fringing reef sounds than to patch reefs with no playback sound (Radford *et al.* 2011b). However, the originality of Parmentier study is the highlighting of two settlement strategies: a direct selection of habitats using sound (45 % of the species), or a selection by default with the avoidance of certain sound habitats (35 %). Avoidance of reef noise by pelagic crustacean larvae was previously described by Simpson *et al.* (2011). Thus, sound will not only give information on the attractiveness of a habitat, but also on habitat quality (Kennedy *et al.* 2010) and appropriateness as a site for settlement. Avoidance of inappropriate habitat sounds should thus be included in the future studies. Indeed, acoustic, but also visual and chemical cues of habitat and conspecifics could have an attractive effect, but in some cases, they could repulse fish larvae at settlement. Unfortunately, not

enough studies take into consideration this possible repulsive effect (Simpson *et al.* 2011, Vail & McCormick 2011, Parmentier *et al.* 2015a).

As for chemical cues, the spatial scale over which the signal exceeds background noise and the nature of propagation of sound away from reefs into deeper water remain unknown. The few studies estimating the distances that marine larvae could potentially detect coastal reef noise provide estimates ranging from 500 m to ~100 km (*e.g.*, Mann *et al.* 2007, Wright *et al.* 2010, Radford *et al.* 2011a). Based on fish hearing abilities and ambient sound level, Mann *et al.* (2007) has estimated the maximum detection distance of reef by fish larvae to less than 1 km. Radford *et al.* (2011a), basing the estimation on sound pressure level recorded in the field, estimated this distance could be several kilometers due to a “reef effect” which would increase the propagation distance of reef noise. A recent study conducted by Parmentier *et al.* (2015b) based on field measurement in the ocean around Moorea Island and at various day periods, estimates the distance at which the reef sound gradient overlapped with ocean sound. For all frequencies between 0 and 5000 Hz, which correspond to auditory capacities of most coral reef fishes, field data fit the cylindrical model of sound attenuation up to a distance between 750 m and 1000 m. At longer distances, the sound level recorded along the transect is higher than expected by the model for frequencies below 2000 Hz. Therefore, the reef sound gradient would only be detectable by the fish larvae at distances below one kilometer.

Overall, future studies should continue to explore the propagation distance of sound and hearing capacities of fish larvae at settlement, as discussed in recent papers (*e.g.*, Simpson *et al.* 2011, Parmentier *et al.* 2015a, b). Nevertheless, one fruitful research avenue is to explore “soundscapes and living communities in coral reefs” (Staaterman *et al.* 2012a, Nedelec *et al.* 2015). Soundscape analysis in air has proved very useful for determining how habitat structure may predict soundscapes (Pekin *et al.* 2012) and for assessing species present in habitats where other survey methods may be logistically difficult (Pijanowski *et al.* 2011). Soundscapes are now considered an important part of landscape ecology (Pijanowski *et al.* 2011). Yet, although underwater soundscapes have likely driven the evolution of hearing (Fay 2009), our knowledge of underwater soundscapes is still in its infancy (Staaterman *et al.* 2012b).

New insights on visual cues

Among the sensory cues used by coral reef fish larvae, visual cues are the most discussed and their importance is the least understood (Lecchini *et al.* 2014b). Some works have shown that coral reef fish have a highly developed sensory system during the larval stage (*e.g.*, Kotrschal *et al.* 1990, Fisher *et al.* 2000, Lara 2001). The visual abili-

ties of fish larvae increase during their pelagic life and reach a maximum around metamorphosis (Lara 2001). Fish larvae therefore have the sensory abilities to perceive visual information emitted by conspecifics, heterospecifics and predators. However, only seven studies have explored the importance of visual cues during habitat selection of coral reef fish larvae (Booth 1992, Leis & Carson-Ewart 1999, Lecchini *et al.* 2005a,b, Igulu *et al.* 2011, Huijberg *et al.* 2012, Lecchini *et al.* 2014b).

Igulu *et al.* (2011) showed that fish larvae of *Lutjanus fulviflamma* preferred seagrass and coral above mangrove roots. Fish larvae were more attracted towards visual cues of a combination of conspecifics or heterospecifics and seagrass microhabitats than to seagrass microhabitats alone, but showed a significantly stronger preference for visual cues of conspecifics than of heterospecifics when placed in preferred seagrass or non-preferred mangrove microhabitats. However, vision of fish larvae could be significant over only short ranges in coral reefs (up to 5-10 m) even if water transparency is high (Myrberg & Fuiman 2002). Moreover, coral reef fish larvae usually settle during the night which questions the actual use of visual cues by fish larvae at settlement. Only one study explored the importance of visual cues at night. Lecchini *et al.* (2014b) showed that *Acanthurus triostegus* larvae was attracted to the visual cues of conspecifics and not that of heterospecifics during the day and during bright nights; but did not show such behavior during dark nights. This study highlights the trade-off between “bright night” settlement which favors the visual recognition of conspecifics and predators, and “dark night settlement” which reduces the risk of predation.

Overall, more research is needed in the field of spectral capabilities and differential sensitivities to light intensity of fish species (*e.g.*, Kotrschal *et al.* 1990, Fisher *et al.* 2000, Lara 2001) in order to better understand the temporal patterns of settlement between bright and dark nights. Some species with high spectral and/or light intensity sensitivity could settle during dark night, while others could settle during bright nights and then would be subjected to a stronger predation. Additionally, more work is needed to understand which specific visual factor (shape, color, etc.) is used by larvae to recognize conspecifics, habitats and predators; and how far could fish larvae see under different light intensities.

New insights on the other cues

Some recent studies showed the use of another cue for the fish larvae at settlement: the sun (*e.g.*, Leis & Carson-Ewart 2003, Leis *et al.* 2014). Mouritsen *et al.* (2013) showed that *Ostorhinchus doederleini* larvae oriented using the sun and strikingly, microsatellite markers indicated that fish larvae came from either their natal reef or from a reef 12 km away from it. Similarly, Berenshtein *et al.* (2014) showed that *Premnas biaculeatus* larvae could

orient depending on the sun and polarized light. During sunny conditions larvae oriented in a more directional manner compared with cloudy conditions. However, settlement has been shown to occur mainly during the night, so light might be used at a certain scale but be less useful or even unused during the night. Information about the use of other potential cues for habitat selection such as: rheotactic, magnetic, wave motion and thermal cues is still unknown, except Paris *et al.* (2013b) showing that larval behavior differed in a water mass of different temperature.

Imprinting and/or innate capabilities at settlement?

Many studies conducted on fish settlement and their perception of information used naive larvae captured either with light traps or crest nets (*e.g.*, Lecchini *et al.* 2005a, b, 2013, Lecchini & Nakamura 2013). Some studies used also fish larvae reared in aquaria, especially for Amphiprion species (*e.g.*, Dixson *et al.* 2010, 2012). For example, using the crest net, fish larvae were captured just before they entered the lagoon to settle (Lecchini *et al.* 2004, 2006). Obviously, these fish larvae had no prior experience of settlement (*i.e.*, naive larvae). Therefore, how could these naive individuals distinguish between conspecifics (vs. heterospecifics) or predators (vs. non-predatory fish)?

Arvedlund & Nielsen (1996) were the first to highlight the imprinting process in coral reef fish. *Amphiprion ocellaris* eggs were maintained with either the host anemone *Heteractis magnifica* or without anemone. They showed that larvae from treated eggs settled in less than five minutes to the anemone whereas larvae from non-treated eggs remained indifferent to the anemone during 48 hours of experiment. Similarly, Arvedlund (1999) showed that the attraction of *Amphiprion melanopus* larvae was innate recognition for the natural host anemone (*Entacmaea quadricolor*) and it was an imprinting process for the *Heteractis malu* (host of another Amphiprion species). Dixson *et al.* (2012) showed that *A. percula* larvae innately recognize predatory fish based on chemical cues. Lastly, Dixson *et al.* (2014b) showed that Amphiprion larvae imprinted themselves to their host and their environment. *Amphiprion percula* larvae recognized innately their anemone host, but this recognition was stronger when larvae were in contact with the anemone during their development.

Overall, these studies conducted only on clownfish suggest that both processes, imprinted and innate capabilities, could be used at settlement to detect the presence of anemones or predators. Apogonids are mouth brooders (Job & Bellwood 2000) with the male carrying the fertilized eggs and in some apogonid species also the hatched embryos. This close contact during embryogenesis may enable such species to imprint to conspecific cues. However, imprinting can happen only in oviparous

species which lay demersal eggs (40 % of coral reef fish species). For the other species called egg-laying fish or pelagic spawners, the spermatozoids and oocytes are carried away from parental environment by currents. In that case, how can we explain the chemical preference for conspecifics of pelagic spawners without an imprinting process? This is a fruitful research avenue for future studies: do oviparous species with demersal eggs recognize their settlement habitat better than pelagic spawning species? For the latter, it seems that these capacities must be innate (Leis *et al.* 2011). However, a third process could explain these capacities: “pelagic learning”. During the oceanic phase, fish larvae could learn to recognize their conspecifics and to avoid some predators. Indeed, fish larvae swim in the plankton along with many other taxa; but conspecific fish larvae which share similar characteristics and preferences may very well group and form cohorts inside the multi-taxa plankton. Thus, within their group, conspecifics could lead to recognize themselves and some predators via vision, odor and sound. Additionally, mixing conditions could form prevailing patches of eggs or young larvae which “stick together”, resulting in conspecifics-imprinting during the first post-spawning days. Overall, innate behaviors, imprinting process and/or pelagic life experience of fish larvae are still in debate and necessitate more studies.

Orienting in a multiple cues system: sequential and hierarchical use at different spatial scales

Most marine animals dwell in a dynamic environment providing variable chemical, physical and biological factors which could potentially be used as behavioral cues. For example, magnetic fields are used by adult salmon and tuna to perform a homing in combination with a chemical imprinting (Dittman & Quinn 1996). Thus, the animals, in order to move, migrate or find a suitable habitat may take into account a combination of several cues. For coral reef fish larvae at settlement, research has been done mainly on of each sensory cue alone (Leis *et al.* 2011). Yet, fish larvae undergo their settlement in a multifactorial environment, and therefore a few cues are present at any given time (Lecchini *et al.* 2014b).

Orienting in a multifactorial system

One of the first studies using a multiple-cue approach was Lecchini *et al.* (2005b) in Moorea Island. In field experiments, they showed that *Chromis viridis* larvae detected reefs containing conspecifics using visual and/or acoustic cues at distances < 75 cm; detection distances increased to < 375 cm when olfactory information was available (particularly for reefs located up-current). Similarly, Huijbers *et al.* (2012) showed that *Haemulon flavolineatum* larvae only responded to sound from coral reefs and to chemical cues from mangroves/seagrass beds,

while visual cues of conspecifics were prioritized over olfactory cues from mangrove/seagrass water. Igulu *et al.* (2013) showed that fish *Lutjanus fulviflamma* preferred chemical cues from seagrass leaves over those from conspecifics when both were offered at the same time. Visual habitat cues were prioritized over chemical cues only when it concerned preferred cues (i.e. seagrass as opposed to mangrove cues). Overall, these studies (*e.g.*, Lecchini *et al.* 2005b, Huijbers *et al.* 2012, Igulu *et al.* 2013) underline that fish at settlement possess the capacity of using multiple reliable chemical cues to locate suitable habitats, although the ranking of these cues is context-dependent. This flexibility in choice behavior would probably be an adaptive strategy to enhance fitness by increasing successful habitat selection at settlement. Future studies conducted will require simultaneous examination of different cues because, in most cases, several cues are present at settlement.

Different cues for different scales

In the previous section, we reviewed the use of multiple cues by fish larvae; yet there is a need to understand which cue is used at which stage. Successful settlement requires actions at a range of spatial scales: (1) identifying an island or a continental shelf within the seemingly boundless oceanic matrix, (2) locating an appropriate reef patch within this island or this continental shelf, and (3) choosing a suitable microhabitat within this patch. Some studies have highlighted the visual, chemical, and/or acoustic abilities of fish larvae to recognize an island or a continental shelf (*e.g.*, Gerlach *et al.* 2007, Dixson *et al.* 2008), a suitable reef patch (*e.g.*, Huijbers *et al.* 2008, Lecchini *et al.* 2013), a suitable settlement micro-habitat (*e.g.*, Igulu *et al.* 2011, Devine *et al.* 2012), predators (Dixson *et al.* 2012), or conspecifics (*e.g.*, Lecchini *et al.* 2005a, b, Lecchini & Nakamura 2013). However, it is still needed to determine the effective spatial scale of each of these cues. This depends on the location and the physical and biological factors related to each. For example, in turbid waters, visual cues will operate over a smaller scale than in oligotrophic tropical waters.

Paris *et al.* (2013a) suggested that reefs produce plumes of odor all around them which may provide the first hint of the reef's vicinity for larvae. Once in an odor plume, they could navigate directionally towards a preferential reef patch and micro-habitat. However, Lecchini *et al.* (2014a) showed that fish larvae could detect the chemical cues emitted by a live coral reef only up to 1 km away from the reef. Staaterman *et al.* (2012a) modelled larval dispersal of *Stegastes partitus* taking into account orientation behaviors. A threshold of sound detection at 1-5 km gave the highest settlement results. However, Parmentier *et al.* (2015b) suggested that the reef sound gradient would only be detectable by fish larvae at distances below one kilometer. Thus, these different studies showed

some contradictory results about the distance of transmission and of detection of chemical and acoustic cues. A recent synthesis of Staaterman & Paris (2014) suggested a theoretical framework showing the various cues available to fish larvae as they move throughout space. At 100 km away from the reefs, fish larvae would orient by magnetic cues, polarized light, or sun compass, or simply swim towards a particular cardinal direction maintaining an angle relative to the mean direction of surface capillary waves (although no study has demonstrated it yet). At 10 km from the reefs, fish larvae could detect acoustic pressure of a reef/island. Lastly, close to the reef (at less than 5 km), fish larvae could detect odour plumes and may swim upstream along the gradient towards the odor origin. We add to this model the use of visual cues for habitat-selection once fish larvae entered the reef patch, although this would be computationally challenging as it would require an increase of the model's spatial resolution from a few hundreds of meters to a few meters only.

Overall, despite these recent studies presented above, the sensory and behavioral mechanisms by which larvae disperse are still largely unknown (Montgomery *et al.* 2006, Arvedlund & Kavanagh 2009, Leis *et al.* 2011). The detection distance of fish larvae depends on the intensity and frequency components of the soundscape, the concentration of chemicals in the reef, the magnitude of turbulence, the mean current speed and direction near the reef, as well as detection abilities of the larva (Staaterman & Paris 2014). Future studies should be conducted in the field in order to test simultaneously and separately the different cues and at different spatial scales.

The use of bio-physical models

Studying the cues used by fish larvae during settlement is highly important by itself. However if we wish to synthesize all this accumulated information and realistically examine the consequences of the larvae behavior, we must use bio-physical models. Individual Based Lagrangian stochastic bio-physical models have been already used for a few decades to simulate larval dispersal. These models usually transport thousands of virtual larvae according to currents data (advection) normally extracted from General Circulation Models, turbulent diffusion, and the behavioral traits (*e.g.*, swimming speeds, diel vertical migration and mortality rates) of the simulated organism (*e.g.*, Paris *et al.* 2013b). Only recently, larvae's orientation capacities were incorporated in such models providing an essential assessment of the ecological consequences of these capacities, namely their effect on dispersal and connectivity (Staaterman *et al.* 2012a). Wolanski *et al.* 2014 showed that the degree of self seeding in swimming virtual larvae (fish) is significantly higher (> 20 %) than that of passive (coral planulae) virtual larvae (< 2 %), and that the dispersal outcome, specifically self-seeding, are highly affected by the larvae response to auditory and olfactory cues.

Perceiving the information in a changing world

Coral reef ecosystems are among the most biologically diverse and complex marine ecosystems worldwide. Coral reefs harbour 25 % of the biodiversity in the seas while only constituting 0.02 % of the ocean, thus they are critical for conservation biology and resources management. In the early 90's, questions were raised concerning the resilience of coral reefs to global changes (Grigg & Dollar 1990). Over the past three decades climate change and increasing anthropogenic pressure lead to the destruction of 20 % of the coral reefs, another 25 % are in great immediate threat and another 25% will be threatened by 2050 (Hughes *et al.* 2007, Chin *et al.* 2011). Jones *et al.* (2004) showed that the decline in adult populations of coral reef fish in degraded habitats had more to do with settlement failure than adult mortality. They suggested that the rescue effect of settlement might be completely ineffective in a degraded habitat. Despite the strong impact of natural and human stressors on coral reef biodiversity, the mechanisms that determine how marine larvae respond to different stages of coral stress and the extent of coral loss during larval settlement remain poorly understood (for exception see: Gleason *et al.* 2009, Munday *et al.* 2009, Lecchini *et al.* 2013, Dixon *et al.* 2014b, Siebeck *et al.* 2015).

Lecchini *et al.* (2013) explored how chemical cues emitted from coral vs. algal reefs attract fish larvae at Rangiroa Atoll (French Polynesia). They showed with 2-channel choice chambers that at settlement, seven 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*, *Sargocentron spiniferum*). The authors suggested that fish larvae could respond to: (1) many different types of chemical cues associated with coral or algae directly, (2) chemical cues of conspecifics whose presence changes in response to coral vs. algal cover, or (3) the concentration of settlement cues emitted from the environment. In addition to the natural stressors, several anthropogenic stressors could also modify the level of taxis towards suitable habitat or away from predators. For example, Holles *et al.* (2013), using choice chambers, showed that boat noise induced a lower settlement rate in coral reef fish. Thus, if boat noise disrupts the settlement process (Tolimieri *et al.* 2004, Radford *et al.* 2011b, 2014), nearby reefs will suffer from depletion in larval supply, whereas fish larvae may remain in the open ocean after metamorphosis, thus increasing their risk of predation. Another anthropogenic stressor widely studied is the ocean acidification. Munday *et al.* (2009) showed that acidification in the ocean could disrupt the olfactory mechanism by which clownfish larvae discriminate between cues which may be used in locating suitable adult habitat. Dixon *et al.* (2010) showed that when eggs and larvae of *Amphiprion percula* were exposed to seawater with lowered pH (simulat-

ing ocean acidification), settlement-stage larvae became strongly attracted to the smell of predators, and the ability to discriminate between predators and non-predators was lost. Similarly, Munday *et al.* (2013) reared *Plectropomus leopardus* at settlement in different CO₂ concentrations during four weeks (490, 570, 700 and 900 μ atm). They showed that *P. leopardus* reared in acidified water were attracted to olfactory cues from potential predators, rather than seeking shelter, whereas fish reared under natural conditions exhibited the predicted sheltering response.

Overall, all the studies above demonstrate negative effects of natural and anthropogenic stressors on the larval sensory abilities. Although fish larvae do not die in presence of algal reef water, acidified water or noisy environment, the indirect consequences are behavioral responses which reduce the larval fitness (Leis *et al.* 2011, Siebeck *et al.* 2015). Thus, if polluted seawater disrupts the settlement process, fish larvae may spend more time in the planktonic environment, resulting in increased energetic costs and predation risk, and consequently a lower larval settlement. As the stability of fish communities is dependent, in part, on the stability of social interactions, the disruption of "larvae-habitat relationships" can have major consequences for larval settlement into adult population with further repercussions for the ecosystem as a whole. Indeed, if the settlement potential of coral reefs declines due to these natural and anthropogenic stressors, the populations of reef organisms (fish, cephalopods, and crustaceans) may also decline due to a reduction in larval supply. Understanding the relationship between reef status and settlement potential will allow management planning for the maintenance of coral reefs that are increasingly degraded.

CONCLUSION AND PERSPECTIVES

We have reviewed some of the latest researches on orientation, early sensory development, and the role of specific environmental cues in the settlement process of coral reef fish. We highlighted that fish larvae use a variety of cues and senses at different distances from the reef, in order to find a suitable reef habitat that will facilitate post-settlement survival and growth. At present, we will use some papers already published to point out particular gaps and to stimulate further research.

- **Using naive fish larvae** – For example, Igulu *et al.* (2013) used recently settled fish to study the importance of sensory cues at settlement. The authors suggested that it is unlikely that fish lose their attraction to preferred chemical cues directly after settlement. Some studies showed that recently settled fish had the same cue preference even if they had been collected from different settlement habitats (Grol *et al.* 2011, Huijbers *et al.* 2012). However, Danilowicz (1996) showed that preferences for coral species may differ depending on whether fish

are tested at or after settlement. Similarly, Lecchini *et al.* (2005a) showed that four of the five species tested used the same sensory modalities at larval and juvenile stages to detect their reef habitat. But, *Chrysiptera leucopoma* used different senses at different developmental stages, with larvae recognizing conspecifics by visual cues and juveniles by chemical cues. Overall, these studies showed different results depending on the sensory abilities of fish at and after settlement; therefore, it is necessary to further investigate these abilities throughout ontogeny.

• **Using several heterospecifics as control cues** – For example, Lecchini *et al.* (2005a) showed that *Abudefduf sordidus* larvae were more attracted by the visual cues of conspecifics than the ones of heterospecifics. However, the authors used *Lutjanus fulvus* juveniles as heterospecifics. Would the authors get the same result if they use *A. sexfasciatus*, species having a color pattern relatively similar to *A. sordidus*? The future studies on sensory abilities of fish larvae should use more than one species as heterospecifics with heterospecific species belonging to same and different families in order to know until which taxonomic level fish larvae could distinguish cues between conspecifics and heterospecifics.

• **Conduct the experiments on several fish species** – For example, Holles *et al.* (2013) showed that boat noise induced a lower settlement rate in coral reef fish at Moorea. The study was only conducted on one species, *Apogon doryssa*. Yet, Parmentier *et al.* (2015a) tested the larval attraction to sound cues of different Moorea reefs. They showed that among the 21 species tested, there was a great variation in the larval attraction inside and among fish families. It is impossible to conclude that one family is attracted, for example, by the sound of barrier reef. Therefore, future studies should ideally be conducted on several fish species belonging to the same and to different families in order to generalize the results.

• **Conduct mainly some field experiments** – Leis & McCormick (2002) indicated the importance of finding ‘innovative means’ to study the behavior of larvae at night. Today, this issue is still relevant because of the difficulty to work directly in the field (see for exception, Lecchini *et al.* 2005b, Paris *et al.* 2013a). Paris *et al.* (2013a) tried to tackle the problem of *in situ* observations using a “Drifting In Situ Chamber”. Therefore, the main priority in future studies should be focused on innovative *in situ* methods testing, at night, the sensory abilities of naïve larvae to cues of fish conspecifics vs. fish heterospecifics, of different coral species, or of different predator species.

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