

# Spatial patterns of self-recruitment of a coral reef fish in relation to island-scale retention mechanisms

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## Abstract

Oceanographic features influence the transport and delivery of marine larvae, and physical retention mechanisms, such as eddies, can enhance self-recruitment (i.e. the return of larvae to their natal population). Knowledge of exact locations of hatching (origin) and settlement (arrival) of larvae of reef animals provides a means to compare observed patterns of self-recruitment 'connectivity' with those expected from water circulation patterns. Using parentage inference based on multiple sampling years in Moorea, French Polynesia, we describe spatial and temporal variation in self-recruitment of the anemonefish *Amphiprion chrysopterus*, evaluate the consistency of net dispersal distances of self-recruits against the null expectation of passive particle dispersal and test the hypothesis that larvae originating in certain reef habitats (lagoons and passes) would be retained and thus more likely to self-recruit than those originating on the outer (fore) reef. Estimates of known self-recruitment were consistent across the sampling years (~25–27% of sampled recruits). For most (88%) of these self-recruits, the net distance between hatching and settlement locations was within the maximum dispersal distance expected for a neutrally buoyant passive particle based on the longest duration of the larval dispersive phase and the average direction and speed of current flow around Moorea. Furthermore, a parent of a given body size on the outer (fore) reef of Moorea was less likely to produce self-recruits than those in passes. Our findings show that even a simple dispersal model based on net average flow and direction of alongshore currents can provide insight into landscape-scale retention patterns of reef fishes.

**Keywords:** connectivity, coral reef fish, oceanography, parentage analysis, retention, self-recruitment, tropical island

Received 19 May 2016; revision received 11 August 2016; accepted 22 August 2016

## Introduction

Knowledge of animal and plant dispersal is fundamental for understanding both the dynamics of populations and evolution of species (Clobert *et al.* 2001; Ronce 2007). For most marine reef fish, spatially separated

populations are connected primarily via dispersal of larvae. Attributes of dispersal and settlement of marine larvae can be influenced by the oceanographic conditions they experience (Schmitt & Holbrook 2002; Cowen *et al.* 2007; Pineda *et al.* 2007) and their behaviour (Stobutzki & Bellwood 1997; Kingsford *et al.* 2002; Paris & Cowan 2004; Paris *et al.* 2007). Generally, the probability of successful larval dispersal diminishes with distance from the hatching site (Pinsky *et al.* 2010; Buston *et al.*

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2012), and a growing number of studies have shown that net dispersal distances (shortest in-water distance between hatching and settlement sites) of successful fish settlers can be short (~1 km scale). Examples of coral reef fishes that have displayed such short dispersal distances include *Chaetodon vagabundus*, *Amphiprion percula*, *A. polymnus*, *Plectropomus maculatus*, *Stegastes partitus*, and *Elacatinus lori* (Almany *et al.* 2007; Buston *et al.* 2012; Harrison *et al.* 2012; Hogan *et al.* 2012; Saenz-Agudelo *et al.* 2012; D'Aloia *et al.* 2015), while others have been shown to disperse over much larger distances (Planes *et al.* 2009; Berumen *et al.* 2012; Puebla *et al.* 2012; Simpson *et al.* 2014).

A long-standing issue has been the extent to which locally vs. externally produced larvae replenish local populations of reef organisms, with estimates of self-recruitment varying from none to the majority of colonists for reef fishes (D'Aloia *et al.* 2015; Steinberg *et al.* 2016). While high numbers of self-recruits need not imply that a high proportion of the locally produced larvae have been retained (Botsford *et al.* 2009; Berumen *et al.* 2012; Burgess *et al.* 2014; Lett *et al.* 2015), the degree of self-replenishment of populations has vast ecological and management implications. The retention of the dispersive stages of fish near suitable habitats can both occur actively due to larval behaviours and passively through transport promoted by water movement patterns (Paris & Cowan 2004). Coral reef fish larvae have a suite of sensorial and swimming abilities that steer them during the dispersal phase towards their settlement habitats. For example, hearing and smell have been shown to guide reef fish larvae during dispersal (Kingsford *et al.* 2002; Simpson *et al.* 2005; Gerlach *et al.* 2007). Larvae from the same cohort can use behaviour to remain together while dispersing (Paris & Cowan 2004), which can result in them settling concurrently to the same microhabitat (Bernardi *et al.* 2012). While fish larvae can use behaviours to enhance retention (Paris *et al.* 2007), several water circulation features also can act to retain larvae, which may lend insight into spatial patterns of self-recruitment (Swearer *et al.* 1999).

For islands encircled by a barrier reef, breaking waves create more or less a unidirectional flow of water over the reef crest into the lagoon, which later returns to the open ocean through one or more passes (openings in the reef) (Hench *et al.* 2008; Edmunds *et al.* 2010; Leichter *et al.* 2013). At smaller scales, within the lagoon, varying degrees of turbulent mixing are forced by different coral species/morphologies (Monismith 2007; Hench & Rosman 2013); longer water residence time also could contribute to the retention of larvae. Additionally, other meso-scale phenomena operating seaward of the barrier reef, such as eddies or the slower

water flows on the leeward side of tropical islands (Swearer *et al.* 1999), may also favour the retention of larvae and thus influence dispersal. However, there is limited empirical support that spatial patterns of self-recruitment for reef fishes are influenced by physical retention features. Given impracticalities in following individual larvae throughout their entire pelagic dispersal stages (Leis 1991), one approach to this issue has been to use parentage inference to identify larvae that recruit into their population of origin (e.g. Jones *et al.* 2005; Almany *et al.* 2007; Beldade *et al.* 2012) and to map the precise locations of hatching (origin) and of settlement (arrival) of individual self-recruiting larvae.

In this study, we first describe spatial and temporal variation in self-recruitment of a coral reef fish (the orange-fin anemonefish, *Amphiprion chrysopterus*), on Moorea, French Polynesia, over 5 years. Here, we define a self-recruit as a post-settlement juvenile on Moorea that was produced by an adult on the island, and 'self-recruitment connectivity' as the spatial topology between locations of origin and subsequent settlement of self-recruits around Moorea. This enabled us to evaluate the consistency of putative dispersal trajectories of self-recruits to a minimalistic passive particle dispersal model to assess how much of the connectivity in self-recruitment could be accounted for by a simple physical transport model. Moreover, considering water flow patterns, we tested the hypothesis that larvae originating in different reef habitats (lagoon, pass, fore reef), which implies being more or less exposed to certain water circulation regimes, vary in the degree of self-recruitment. Finally, we explore whether self-recruits and exogenous recruits (i.e. not produced by adults on Moorea) differ in the reef habitats to which they settle.

## Methods

### *Study site and model species*

Field work was conducted on Moorea (17°30'S, 149°50'W), French Polynesia. The island is encircled by a barrier reef that forms a system of lagoons that are 0.8–1.3 km wide and 5–7 m deep and are connected to the ocean by several passes. The offshore reef slopes steeply to >500 m depth within about 1 km of the reef crest. Several aspects of Moorea's water circulation that are pertinent to transport and retention of larvae have been described in Leichter *et al.* (2013). An alongshore flow just offshore of the barrier reef follows a net counterclockwise direction (CCW) that may contribute to the retention of larvae near the island (Leichter *et al.* 2013). Several processes such as tides, winds, surface waves and internal waves can cause reversals of the alongshore current in Moorea, and the duration of such

reversals varies from hours to days (Leichter *et al.* 2013). However, over periods of two to three weeks, the net residual flow is counterclockwise at 0.03 per ms, and it is strongest near the surface and appears to turn offshore with depth. Breaking waves create a unidirectional flow of water over the reef crest into the lagoon, which later returns to the ocean through the passes, a process that can take hours to tens of hours (insert in Fig. 1; Lenhardt 1991; Hench *et al.* 2008; Edmunds *et al.* 2010). Some of the surface water exiting the passes might be retained near the reef crest in the CCW flow and later may be forced back over the reef crest by incident waves (Monismith 2007). At a smaller scale (<100 m), spatial flow at the level of coral colonies or patches of coral colonies in the lagoon shows differential degrees of turbulent mixing forced by different coral species/morphologies. Such trapping and recirculating of water in the wakes of corals and other lagoon-bottom structures could provide shelter from peak water velocities and impact larval dispersal (Hench & Rosman 2013).

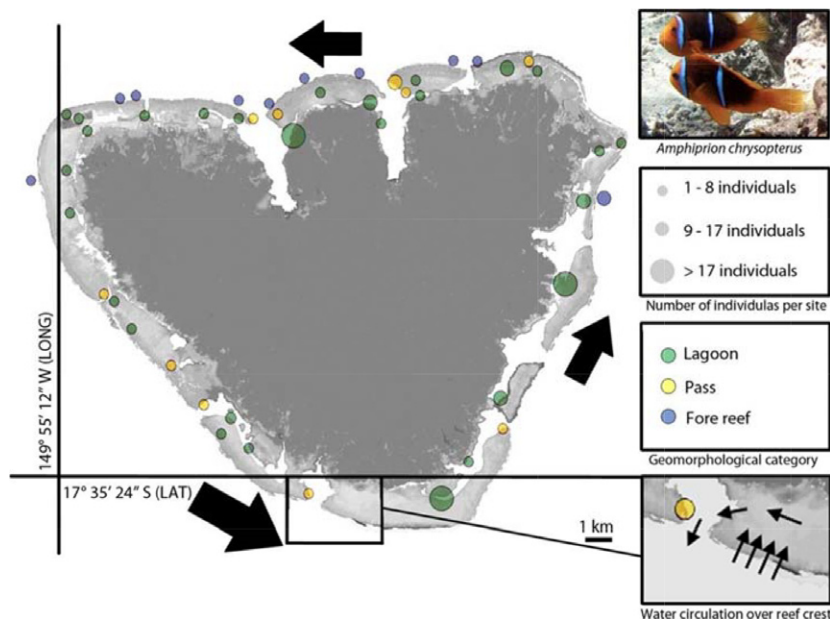
Anemonefish have been used to assess recruitment dynamics to minimize sampling difficulties and statistical constraints of parentage analysis (e.g. Jones & Arden 2003). These difficulties, which include the presence of multiple species and large numbers of potential parents, are largely alleviated in Moorea where a single species of anemonefish is present, the orange-fin anemonefish, *Amphiprion chrysopterus*, and the adult population is relatively small (Fig. 1), in part because populations on Moorea are recruitment limited (Schmitt & Holbrook 2000, 2003). Anemonefish live in small groups consisting of an adult breeding pair and a varying number

of subadults (Fautin & Allen 1997). In Moorea, *A. chrysopterus* enhances the growth and survivorship of its host anemone (Holbrook & Schmitt 2005) and is a superior competitor for anemone space with a co-occurring damselfish (Holbrook & Schmitt 2004). After hatching from an egg mass laid adjacent to host anemone of its parents, larvae of *A. chrysopterus* spend approximately 14–17 days (Pelagic Larvae Duration PLD) (Wellington & Victor 1989) in the pelagic environment before settling onto an anemone.

#### Field surveys and tissue collection

We searched extensively for anemonefish island-wide by sampling comprehensively in lagoons and using manta tows (divers towed slowly behind a boat) around the island on the more extensive fore reef to locate anemones; deeper locations on the fore reef were targeted by scuba divers (see Beldade *et al.* 2012). While we undoubtedly did not sample the entire population of anemonefish on Moorea, we believe that our surveys provide a good representation of the anemonefish population and we have no evidence of bias in the fraction of anemonefish sampled among lagoon, pass and fore reef locations. It is possible that we under-sampled anemonefish that occurred deep on the fore reef slope, although these tend to be rare compared to shallower reef habitats.

To obtain tissue for genetic analysis, anemones hosting anemonefish were visited by SCUBA divers following previous surveys (Beldade *et al.* 2012). Coordinates (GPS) of each anemonefish individual or group were noted. Anemonefish were captured with a handnet and



**Fig. 1** Location of *Amphiprion chrysopterus* (photograph) at 47 sites in Moorea (French Polynesia). At each site, size (of each circle) is proportional to fish abundance; colour (of each circle) represents a different reef habitat: green for lagoon, yellow for pass, and blue for outer reef. Three large black arrows outside the barrier reef represent the prevailing counterclockwise alongshore current, and arrow size represents speed following Leichter *et al.* (2013). The small insert represents wave-induced water circulation over reef crest and out the nearest pass.

returned to their anemone immediately after obtaining a fin clip for genetic analyses. No mortality due to handling was subsequently detected. Anemonefish were categorized as new recruits if <6 cm total length (TL) (<1 year old), and as adults if >6 cm TL. The anemonefish population in Moorea was sampled three times over a five-year period, in 2006, 2008 and 2010. Patchy spatial distributions and low population densities of host sea anemones result in patchy distributions of *A. chrysopterus* (Fig. 1).

### Genetic analyses

Immediately after collection, fin clips were placed in 95% ethanol. Total genomic DNA was prepared from 20 mg of fin tissue by proteinase K digestion in lysis buffer (10 mM Tris, 400 mM NaCl, 2 mM EDTA, 1% SDS) overnight at 55 °C. This was followed by purification using phenol/chloroform extractions and alcohol precipitation (Sambrook *et al.* 1989). We amplified a total of 11 microsatellites: eight described in Beldade *et al.* (2009) and three (61, 44 and 10TCTA) described for a congener, *Amphiprion polymnus* (Quenouille *et al.* 2004). Scoring of peaks was performed manually using GENEMAPPER version 3.7 (Applied Biosystems). To estimate potential genotyping errors, we randomly selected 20% of all samples and re-amplified, rescored and evaluated concordance between first and second observer scores. Overall in each year, genotyping errors were <1% and missing data <2% for any given locus. Deviations from Hardy–Weinberg (HW) equilibrium due to the presence of null alleles and linkage disequilibrium were tested using ARLEQUIN (Excoffier & Lischer 2010) and MICROCHECKER (Van Oosterhout *et al.* 2004). One locus was dropped because it was not in HWE for any of the years, with 10 loci retained for parentage analysis.

### Parentage analysis and estimates of self-recruitment

We used a maximum-likelihood approach for parentage analysis implemented by FAMOZ (Gerber *et al.* 2003) to identify putative parent–offspring matches and estimate self-recruitment at the scale of the whole island. In FAMOZ, statistical confidence in parentage assignment is based on offspring simulations from genotyped parents and allele frequencies. To account for possible genotyping errors, we set the error level to 0.001 to minimize type I and type II errors (Gerber *et al.* 2000). Type II error (i.e. incorrectly assigning a false parent as a true parent when the true parent was not sampled) was further reduced by rescored all positive parent–offspring to increase confidence in the assignment. Furthermore,

we allowed a maximum of one mismatch between parental and offspring alleles.

### Consistency between putative and passive dispersal distances

Taking into account the minimum and maximum duration of the pelagic larval dispersal (14 and 17 days, respectively) and the long-term mean velocity of the counterclockwise (CCW) alongshore flow (~0.03 m/s) around the island (Leichter *et al.* 2013), we calculated minimum and maximum dispersal distances that anemonefish larvae would be able to travel from their origin if they acted solely as neutrally buoyant passive particles. Net dispersal distance travelled by each self-recruiting larva following the CCW alongshore flow was calculated in Google Earth by tracing the shortest in-water route between hatching and settlement sites that paralleled the reef crest. Finally, we calculated the percentage of net dispersal distances following the CCW alongshore flow that could be explained by the minimum and maximum passive dispersal distances.

### Reef habitat and the origin of self-recruits

We categorized all anemonefish that we sampled as occurring in one of three habitats: lagoon, pass and fore reef. Data from all three years were combined, and any individuals that were resampled were removed from this analysis. We calculated the normalized proportion of self-recruits produced in each habitat by first dividing the number of females that produced self-recruits in a habitat by the total number of females in that habitat. We then divided each of these values by the sum of the proportion of females that produced self-recruits in each habitat to obtain a normalized proportion. Chi-square analysis tested the prediction of equal proportion of self-recruits originating from each habitat category (i.e. 0.33) against the observed normalized proportion (to account for differences in females among habitats); this assumes that we sampled equal fractions of the anemonefish population in each habitat. To determine which categories were different, we further compared lagoon and pass, lagoon and fore reef, and pass and fore reef using chi-square tests, with alpha adjusted following a Bonferroni correction to 0.047.

### Reef habitat and settlement of recruits

We compared the numbers of self- and exogenous recruits (offspring from parents that were not in the

sampled population) that settled into each reef habitat and tested whether there were differences in settlement between these two groups using chi-square analysis.

## Results

### *Temporal variation in self-recruitment*

We collected a total of 540 adult samples and 155 recruit samples, over three two-month-long sampling periods across five years. The number of adults sampled varied slightly over the years: 172 in 2006, 197 in 2008 and 171 in 2010. Numbers of recruits sampled were similar across years (50, 52 and 53, respectively). Parentage analysis based on ten variable microsatellite loci (Table S1, Supporting information) was performed separately for each year. A total of 40 self-recruits (recruits whose identified parents were present in Moorea) were identified across the three years. The number and proportion of self-recruits was similar among the three sampling periods. In 2006, there were 13 self-recruits (~26% of all recruits); in 2008, there were 14 (~27%); and in 2010, there were 13 (~25%). Details of parentage inference results are given in Table S2 (Supporting information) (LOD thresholds; average and standard deviation LOD scores for singles and couples; allele mismatches between parents and offspring; and estimates of type I and type II errors).

### *Consistency between putative and passive dispersal distances*

During the dispersal stage (14–17 days), *Amphiprion chrysopterus* larvae acting as passive particles in the CCW shelf current could cover a minimum distance of 36 km (14 day larval duration) to a maximum of 44 km (17-day larval duration). Overall, the net dispersal distances covered by *A. chrysopterus* larvae during dispersal (assuming a CCW trajectory) ranged from 60 m to over 48 km with an average of 17.5 km over all years (Fig. 2a–d). Net dispersal distances were shorter than the 44 km threshold in 88% of the cases (30 of 34 self-recruits) and under the 36 km threshold in 76% of the cases (26 of 34 self-recruits) (Fig. 2d). These calculations excluded six larvae that originated and settled into the same lagoon sector (north, east or west when their putative trajectories did not cross a pass) as they might not have left the lagoon and been subjected to the alongshore flow. For comparison, we also calculated net dispersal distances with no directional forcing and minimal in-water distance between hatching and settlement sites (Fig. S1, Supporting information) and the respective yearly averages (Table S2, Supporting information).

### *Reef habitat and the origin of self-recruits*

The likelihood of producing a self-recruit among reef habitats (lagoon, pass, fore reef) was found to be significantly different from random (chi-square = 9.43;  $P = 0.008$ ) (Table 1). Self-recruitment differed significantly between the fore reef and pass (chi-square = 8.51,  $P = 0.003$ ) and between the lagoon and pass (chi-square = 4.60,  $P = 0.04$ ), but not between the lagoon and the fore reef (chi-square = 0.65,  $P = 0.42$ ) (Table 1). Overall, there were fewer self-recruits produced by adults on the fore reef than expected. Our earlier study revealed that larger females contribute more to the production of self-recruits than their smaller counterparts (Beldade *et al.* 2012). However, in this study, the size of females did not differ significantly among the habitats [mean  $\pm$  SD TL (mm) in lagoon:  $128.2 \pm 17.7$ , fore reef  $131.8 \pm 21.6$  and pass  $133.4 \pm 17.8$ ; ANOVA  $F_{2,244} = 1.128$ ,  $P = 0.33$ ]. Thus, the observed among-habitat difference in the production of self-recruits was not driven by differences in female size.

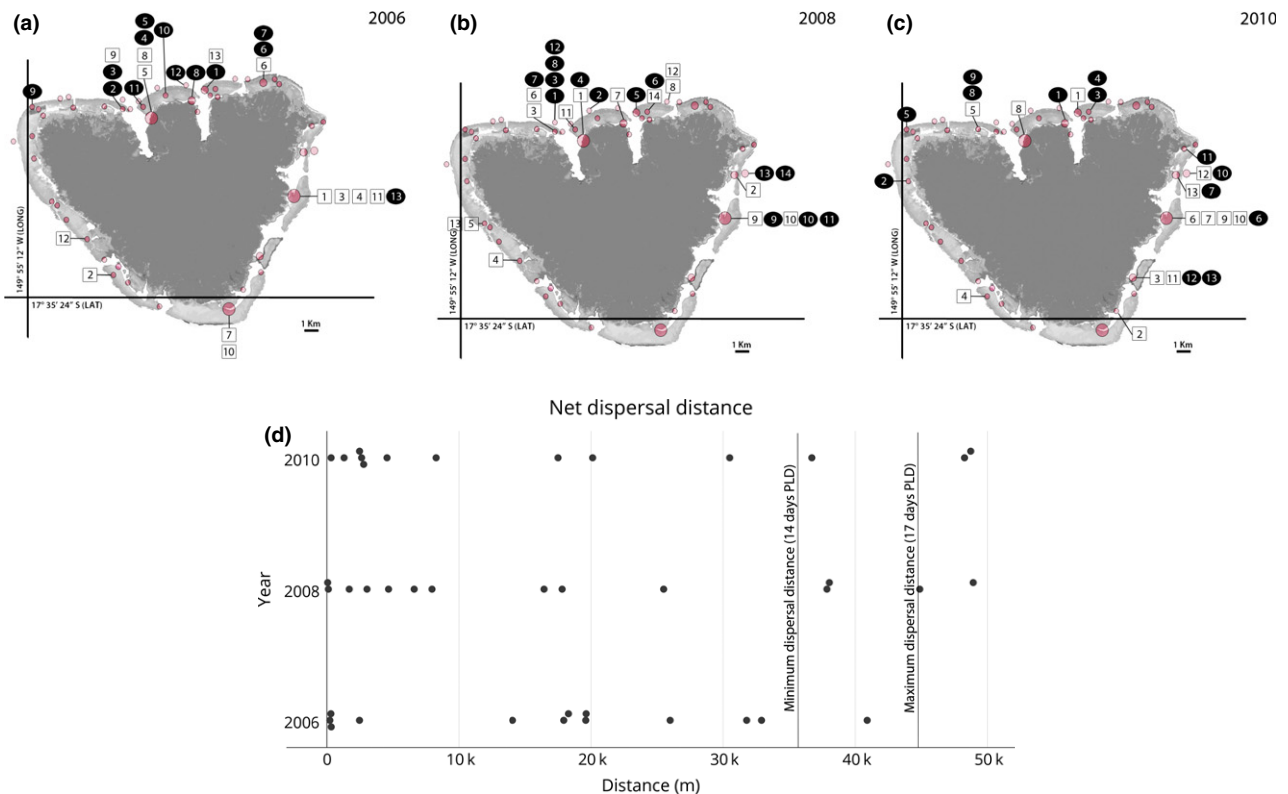
### *Reef habitat and settlement of recruits*

The frequency of settlement into lagoon, pass or outer reef habitats did not differ between self-recruits and exogenous recruits (chi-square = 0.56;  $P = 0.76$ ). Recruits were distributed similarly among the three habitats regardless of their origin (Table 2).

## Discussion

At the scale of the island of Moorea, self-recruitment for *Amphiprion chrysopterus* was remarkably consistent among three estimates made over five years, ranging from 25% to 27% of the total recruitment. While these likely are underestimates (due to incomplete sampling and possibly overly stringent parent–offspring classification criteria), the levels of self-recruitment we found are similar to estimates for anemonefish species in other geographic locations [~15% to 31% for *A. polymnus* in Papua New Guinea (Jones *et al.* 2005); ~42% for *A. percula* in Papua New Guinea (Almany *et al.* 2007; Planes *et al.* 2009; Saenz-Agudelo *et al.* 2011)]. Furthermore, the temporal consistency in our self-recruitment estimates is similar to two other self-recruitment studies that were carried out over multiple years (Berumen *et al.* 2012; Saenz-Agudelo *et al.* 2012). By contrast, our results differ from estimates of interannual variability in self-recruitment reported for another tropical damselfish (*Dascyllus aruanus*), which ranged from 0% to 21% (Cuif *et al.* 2015).

Our results revealed that anemonefish larvae originating in the passes were more likely to self-recruit than



**Fig. 2** Location of *Amphiprion chrysopterus* at 47 sites in Moorea (French Polynesia) for each of the sampling years (a: 2006, b: 2008, c: 2010). The location of parents that produced self-recruits is given by a number in a white square (corresponding to the origin or hatching site) and the location of its corresponding self-recruiting offspring by the same number in a black oval (corresponding to the arrival or settlement site) in each sampling year. Figure 2d shows the net dispersal distances following the alongshore average net flow around Moorea in each year (see Methods section), and solid vertical lines indicate the minimum and maximum dispersal distances.

**Table 1** Total number of females (All females) and females that produced self-recruits (SR females), indicating the putative and actual origin of self-recruits, in each reef habitat (lagoon, pass and fore reef)

Origin	Lagoon	Pass	Fore reef
All females	198	19	27
SR females	31	6	3
Normalized proportion	0.27	0.54	0.19
Expected proportion	0.33	0.33	0.33

larvae originating from the fore reef or the lagoon. One explanation is that larvae born in passes may be exposed to several retention mechanisms, operating both within the lagoon and on the fore reef. Larvae originating on the fore reef may be less likely to be entrained in lagoon processes that favour retention, especially if their parents are on deeper sections of the outer reef where they are also less likely to become entrained in the shelf current that has a net counter-clockwise flow. The differences in proportion of self-

**Table 2** Number of self-recruits and exogenous recruits collected in each reef habitat (lagoon, pass and fore reef) over three sampling events. Self- and exogenous recruits were similarly distributed among the three habitats (chi-square = 0.56;  $P = 0.76$ )

Recruitment	Lagoon	Pass	Fore reef
Self-recruits	28	3	9
Exogenous recruits	72	9	32

recruits found between lagoon and pass may be related to the fact that there is a much larger number of females in the lagoon thus diluting the proportion of those that produced self-recruits. Simultaneously, perhaps the alongshore currents are more relevant to self-recruitment than the currents at a smaller scale (experienced within the lagoon). Furthermore, our calculations based solely on the number of females producing or not self-recruits in each habitat implicitly assume that all females produce the same approximate number of offspring. Differences in fish fecundity are

correlated to the body size of an individual. Although larger females have been found to contribute more to the production of self-recruits than their smaller counterparts (Beldade *et al.* 2012; Saenz-Agudelo *et al.* 2015), in the current study, the size of females did not differ significantly among the reef habitats. Thus, our findings are not driven by differences in female size. However, our analysis assumes that we sampled the same fraction of anemonefish populations in the three habitats, and although we have no evidence of biased sampling, it is possible we may have missed proportionately more anemonefish on the outer reef than elsewhere. Occasionally and elsewhere in the French Polynesia, *A. chrysopterus* has been observed beyond the 40 m depth, at those depths searching becomes logistically difficult.

Mechanisms of larval retention, which can promote self-recruitment, operate across several spatial scales. At a very localized scale, larvae may benefit from increased turbulent flows to remain near corals. We report several examples of larvae that hatched from and arrived to anemonefish groups in the same lagoon (Fig. 2a–c), within the same lagoon sector, and some that were very close to each other (e.g. couples 9 and 10 and their offspring, Fig. 2b). No such cases of recruitment close to the point of origin were found for anemonefish on the outer reef. On a somewhat larger scale, larvae originating in the lagoon and passes may be retained in eddies created by the waves breaking over the crest. In our study, two sites located in the lagoon near the major pass on the northwest shore produced larvae that settled to a site (downstream) just outside the pass (e.g. Couple 1 in Fig. 2b). At the whole-island scale, our results show that retention occurs even when recruits travel substantial distances outside the barrier reef. Many of the self-recruits in our study likely travelled as larvae offshore of the barrier reef to settle within the lagoons or passes. For example, in 2006 (Fig. 2a), couples 1, 3, 4 and 11 located on the eastern side of the island all produced larvae that later settled onto the north shore. Dispersal across the north-eastern tip of the island, where the lagoon is absent, implies an open ocean journey, demonstrating that retention may have operated at a meso-scale.

Much of the spatial pattern of self-recruitment we observed conformed to expectations from the most simple passive dispersal model for Moorea, at least at the whole-island scale. For example, the average net velocity and direction of the alongshore current flow (Leichter *et al.* 2013) could transport a passive particle around the 55 km perimeter of the island in ~21 days; thus, a passive larva with a 14- to 17-day PLD that was entrained in the alongshore current of Moorea could, on average, be transported as a passive particle 65–80%

of the distance around the island. The large majority of the self-recruitment net dispersal distances were smaller than the distance estimated considering even the shortest pelagic larval duration (Fig. 2d). Similarly, Nanninga *et al.* (2015) used a sophisticated passive particle dispersal model with real-time forcing to predict a low probability of reef-scale self-recruitment of an anemonefish (*Amphiprion bicinctus*) in the central Red Sea, which also mapped well onto observed levels of self-recruitment based on parentage analyses. Of course, this does not imply that larval behaviour was unimportant or absent. Fish larvae are capable of sustained swimming and have well developed behaviours prompted by sensory capabilities (e.g. Leis *et al.* 2009), and fish larvae have been shown to use bio-physical mechanisms that enhance retention (Paris & Cowan 2004; Paris *et al.* 2007). There were several cases in which net dispersal distances were smaller than 500 m. Given the 2+-week pelagic larval duration of our focal species, it seems unlikely that the highly localized retention can be achieved without active larval behaviour being coupled with small-scale physical retention features.

There is, of course, a difference between self-recruitment (in our case, the fraction of recruits produced by adults on Moorea) and local retention (the fraction of larvae produced on Moorea that recruited to Moorea) (Burgess *et al.* 2014). While it appears there is a substantial level of exogenous recruitment of *A. chrysopterus* on Moorea (i.e. larvae produced elsewhere), we found no difference between locally produced and exogenous larvae in their relative pattern of recruitment among the three major types of reef habitats (lagoons, passes, fore reef). We believe the alongshore flow around Moorea serves as both a delivery and retention feature, and that larvae may then be entrained by another smaller scale retention feature such as lagoon – fore reef circulation cells that could result in advection across all three habitat types. Despite the fact that fish larvae are unlikely to behave as passive particles, our findings suggest that knowledge of key oceanographic transport and retention mechanisms can provide insight into landscape-scale patterns of larval connectivity in general and self-recruitment in particular. While incorporating behaviour into models of larval connectivity is a necessary and useful endeavour, knowledge of multiple-scale transport and retention features can provide insight into patterns of population replenishment useful for conservation and management.

### Acknowledgements

We thank all the people involved in field work including Marina Ramon, Todd Skelton, Jeremie Vidal-Dupiol, Marianne Guillame, Katie McConnell, Gary Longo and many other

members of CRIOBE and the UC Berkeley Gump Research Station. Dan Malone and Pete Raimondi helped with data analysis, and Glenn Almany, Cassidy d'Aloia, Libe Washburn and Suzanne Mills gave valuable comments. This research was supported by the National Science Foundation (OCE 12-36905, OCE 16-37396 and earlier Moorea Coral Reef LTER awards), the Gordon and Betty Moore Foundation, ANR Stay or Go and LabEx 'CORAIL' ('Where do we go now?'). R. Beldade was funded by Fundação para a Ciência e Tecnologia (SFRH/BPD/26901/2006) and LabEx 'CORAIL' ('Where do we go now?').

## References

- Almany GR, Berumen ML, Thorrold SR *et al.* (2007) Local replenishment of coral reef fish populations in a marine reserve. *Science*, **316**, 742–744.
- Beldade R, Holbrook SJ, Schmitt RJ *et al.* (2009) Isolation and characterization of eight polymorphic microsatellite markers from the orange-fin anemone fish, *Amphiprion chrysopterus*. *Conservation Genetics Resources*, **1**, 333–335.
- Beldade R, Holbrook SJ, Schmitt RJ *et al.* (2012) Larger female fish contribute disproportionately more to self-replenishment. *Proceedings of the Royal Society: Biological Sciences*, **279**, 2116–2121.
- Bernardi G, Beldade R, Holbrook SJ *et al.* (2012) Full-sibs in cohorts of newly settled coral reef fishes. *PLoS ONE*, **7**, e44953.
- Berumen ML, Almany GR, Planes S *et al.* (2012) Persistence of self-recruitment and patterns of larval connectivity in a marine protected area network. *Ecology and Evolution*, **2**, 444–452.
- Botsford LW, White JW, Coffroth MA *et al.* (2009) Connectivity and resilience of coral reef metapopulations in marine protected areas: matching empirical efforts to predictive needs. *Coral Reefs*, **28**, 327–337.
- Burgess SC, Nickols KJ, Griesemer CD *et al.* (2014) Beyond connectivity: how empirical methods can quantify population persistence to improve marine protected area design. *Ecological Applications*, **24**, 257–270.
- Buston PM, Jones GP, Planes S *et al.* (2012) Probability of successful larval dispersal declines fivefold over 1 km in a coral reef fish. *Proceedings of the Royal Society: Biological Sciences*, **279**, 1883–1888.
- Clobert J, Danchin E, Dhondt AA, Nichols JD (eds) (2001) *Dispersal*. Oxford University Press, New York.
- Cowen RK, Gawarkiewicz GG, Pineda J *et al.* (2007) Population connectivity in marine systems. *Oceanography*, **20**, 14–21.
- Cuif M, Kaplan DM, Fauvelot C *et al.* (2015) Monthly variability of self-recruitment for a coral reef damselfish. *Coral Reefs*, **34**, 759–770.
- D'Aloia CCD, Bogdanowicz SM, Francis RK *et al.* (2015) Patterns, causes, and consequences of marine larval dispersal. *Proceedings of the National Academy of Sciences of the United States of America*, **112**, 13940–13945.
- Edmunds PJ, Leichter JJ, Adjeroud M (2010) Landscape-scale variation in coral recruitment in Moorea, French Polynesia. *Marine Ecology Progress Series*, **414**, 75–89.
- Excoffier L, Lischer HEL (2010) ARLEQUIN suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. *Molecular Ecology Resources*, **10**, 564–567.
- Fautin D, Allen GR (1997) *Anemonefishes and their Host Sea Anemones*. Western Australian Museum, Perth.
- Gerber S, Mariette S, Streiff R *et al.* (2000) Comparison of microsatellites and amplified fragment length polymorphism markers for parentage analysis. *Molecular Ecology*, **9**, 1037–1048.
- Gerber S, Chabrier P, Kremer A (2003) FAMOZ: a software for parentage analysis using dominant, codominant and uniparentally inherited markers. *Molecular Ecology Notes*, **3**, 479–481.
- Gerlach G, Atema J, Kingsford MJ *et al.* (2007) Smelling home can prevent dispersal of reef fish larvae. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 858–863.
- Harrison HB, Williamson DH, Evans RD *et al.* (2012) Larval export from marine reserves and the recruitment benefit for fish and fisheries. *Current Biology*, **22**, 1023–1028.
- Hench JL, Rosman JH (2013) Observations of spatial flow patterns at the coral colony scale on a shallow reef flat. *Journal of Geophysical Research: Oceans*, **118**, 1142–1156.
- Hench JL, Leichter JJ, Monismith SG (2008) Episodic circulation and exchange in a wave-driven coral reef and lagoon system. *Limnology and Oceanography*, **53**, 2681–2694.
- Hogan JD, Thiessen RJ, Sale PF *et al.* (2012) Local retention, dispersal and fluctuating connectivity among populations of a coral reef fish. *Oecologia*, **168**, 61–71.
- Holbrook SJ, Schmitt RJ (2004) Population dynamics of a damselfish: effects of a competitor that also is an indirect mutualist. *Ecology*, **85**, 979–985.
- Holbrook SJ, Schmitt RJ (2005) Growth, reproduction and survival of a tropical sea anemone (Actiniaria): benefits of host anemonefish. *Coral Reefs*, **24**, 67–73.
- Jones AG, Arden WR (2003) Methods of parentage analysis in natural populations. *Molecular Ecology*, **12**, 2511–2523.
- Jones GP, Planes S, Thorrold SR (2005) Coral reef fish larvae settle close to home. *Current Biology*, **15**, 1314–1318.
- Kingsford MJ, Leis JM, Shanks A *et al.* (2002) Sensory environments, larval abilities and local self-recruitment. *Bulletin of Marine Science*, **70**, 309–340.
- Leichter JJ, Alldredge AL, Bernardi G *et al.* (2013) Biological and physical interactions on a tropical island coral reef: transport and retention processes on Moorea, French Polynesia. *Oceanography*, **26**, 52–63.
- Leis JM (1991) The pelagic stage of reef fishes: the larval biology of coral reef fishes. In: *The Ecology of Fishes on Coral Reefs* (ed. Sale PF), pp. 183–230. Academic Press, San Diego, California.
- Leis JM, Hay AC, Howarth GJ (2009) Ontogeny of in situ behaviours relevant to dispersal and population connectivity in larvae of coral-reef fishes. *Marine Ecology Progress Series*, **379**, 163–179.
- Lenhardt X (1991) Hydrodynamisme des lagons d'atolls et d'îles hautes en Polynésie française. Collection Etudes et Thèses (ORSTOM: Paris).
- Lett C, Nguyen-Huu T, Cuif M *et al.* (2015) Linking local retention, self-recruitment and persistence in marine metapopulations. *Ecology*, **96**, 2236–2244.
- Monismith SG (2007) Hydrodynamics of Coral Reefs. *Annual Review of Fluid Mechanics*, **39**, 37–55.
- Nanninga GB, Saenz-Agudelo P, Zhan P *et al.* (2015) Not finding Nemo: limited reef-scale retention in a coral reef fish. *Coral Reefs*, **34**, 383–392.



- Paris CB, Cowan RK (2004) Direct evidence of a biophysical retention mechanism for coral reef fish larvae. *Limnology and Oceanography*, **49**, 1964–1979.
- Paris CB, Chérubin LM, Cowan RK (2007) Surfing, spinning, or diving from reef to reef: effects on population connectivity. *Marine Ecology Progress Series*, **347**, 285–300.
- Pineda J, Hare JA, Sponaugle S (2007) Larval transport and dispersal in the coastal ocean and consequences for population connectivity. *Oceanography*, **20**, 22–39.
- Pinsky ML, Montes HR, Palumbi SR (2010) Using isolation by distance and effective density to estimate dispersal scales in anemonefish. *Evolution*, **64**, 2688–2700.
- Planes S, Jones GP, Thorrold SR (2009) Larval dispersal connects fish populations in a network of marine protected areas. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 5693–5697.
- Puebla O, Bermingham E, McMillan WO (2012) On the spatial scale of dispersal in coral reef fishes. *Molecular Ecology*, **21**, 5675–5688.
- Quenouille B, Bouchenak-Khelladi Y, Hervet C *et al.* (2004) Eleven microsatellite loci for the saddleback clownfish *Amphiprion polymnus*. *Molecular Ecology Notes*, **4**, 291–293.
- Ronce O (2007) How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annual Review of Ecology, Evolution, and Systematics*, **38**, 231–253.
- Saenz-Agudelo P, Jones GP, Thorrold SR *et al.* (2011) Connectivity dominates larval replenishment in a coastal reef fish metapopulation. *Proceedings of the Royal Society: Biological Sciences*, **278**, 2954–2961.
- Saenz-Agudelo P, Jones GP, Thorrold SR *et al.* (2012) Patterns and persistence of larval retention and connectivity in a marine fish metapopulation. *Molecular Ecology*, **21**, 4695–4705.
- Saenz-Agudelo P, Jones GP, Thorrold SR *et al.* (2015) Mothers matter: contribution to local replenishment is linked to female size, mate replacement and fecundity in a fish metapopulation. *Marine Biology*, **162**, 3–14.
- Sambrook J, Fritsch EF, Maniatis T (1989) *Molecular Cloning: A Laboratory Manual*, 2nd edn. Cold Spring Harbor Laboratory, Cold Spring Harbor.
- Schmitt RJ, Holbrook SJ (2000) Habitat-limited recruitment of a coral reef damselfish. *Ecology*, **81**, 3479–3494.
- Schmitt RJ, Holbrook SJ (2002) Spatial variation in concurrent settlement of three damselfishes: relationships with near-field current flow. *Oecologia*, **131**, 391–401.
- Schmitt RJ, Holbrook SJ (2003) Mutualism can mediate competition and promote coexistence. *Ecology Letters*, **6**, 898–902.
- Simpson SD, Meekan M, Montgomery J *et al.* (2005) Homeward sound. *Science*, **308**, 221.
- Simpson SD, Harrison HB, Claereboudt MR *et al.* (2014) Long-distance dispersal via ocean currents connects Omani clownfish populations throughout entire species range. *PLoS ONE*, **9**, e107610.
- Steinberg R, van der Meer M, Walker E *et al.* (2016) Genetic connectivity and self-replenishment of inshore and offshore populations of the endemic anemonefish, *Amphiprion latezonatus*. *Coral Reefs*, **35**, 959–970.
- Stobutzki IC, Bellwood DR (1997) Sustained swimming abilities of the late pelagic stage of coral reef fishes. *Marine Ecology Progress Series*, **149**, 35–41.
- Swearer SE, Caselle JE, Lea DW *et al.* (1999) Larval retention and recruitment in an island population of a coral reef fish. *Nature*, **402**, 799–802.
- Van Oosterhout C, Hutchinson WF, Wills DPM *et al.* (2004) MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. *Molecular Ecology Notes*, **4**, 535–538.
- Wellington GM, Victor BC (1989) Planktonic larval duration of one hundred species of Pacific and Atlantic damselfishes (Pomacentridae). *Marine Biology*, **101**, 557–567.

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R.B., S.J.H., R.S., S.P. and G.B. designed the experiment; R.B., S.J.H., R.S., S.P. and G.B. collected the data; R.B. and G.B. performed the laboratory work; R.B., S.J.H., R.S. and G.B. performed the data analysis; and R.B., S.J.H., R.S., S.P. and G.B. wrote the manuscript.

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#### Data accessibility

Sampling locations, sex and microsatellite genotypes for the three sampled years were deposited in: Dryad doi: 10.5061/dryad.q4p07.

#### Supporting information

Additional supporting information may be found in the online version of this article.

**Fig. S1** Net dispersal distances, i.e., minimal in-water distance between hatching and settlement sites in the three sampling years.

**Table S1** For each year's adult population, Observed Heterozygosity (Ho), Expected Heterozygosity (He), significant deviations to Hardy-Weinberg Equilibrium are marked with an asterisk, potential presence of null alleles (na), and  $F_{IS}$  marked with an asterisk in the cases it is significant, for the 10 loci used.

**Table S2** Parentage inference details: threshold LOD scores for single fathers (tLOD SP) and parents (tLOD P); Estimated average ( $\pm$  standard deviation) of estimated LOD scores for single fathers (eLOD SP) and parents (eLOD P); type I and type II error for each estimate (given as proportions); Number of assignments to single parents (SP), parents (P) and total; number of cases with one mismatch in single parents (SP) and parents (P) and net dispersal distance (m) with no forcing (see Fig. S1, Supporting information) between hatching and settlement sites per year.