Session 15

Connectivity, recruitment and isolation among coral reef populations

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Influence of localised currents, benthic community cover and composition on coral recruitment: integrating field-based observations and physical oceanographic modelling

F. Elmer, J. S. Rogers, R. B. Dunbar, S. G. Monismith, J. J. Bell, J. P.A. Gardner

Abstract   Successful recruitment, which encompasses larval dispersal, settlement and post-settlement survival, is vital for the maintenance and recovery of coral populations. However, coral larval dispersal and settlement rates are rarely measured in the field and therefore little is known about these processes that shape coral recruitment despite their importance. This study set out to determine the relative contributions of distant larval supply (as quantified by water flux from other sites within the atoll), local larval supply (as quantified by site-specific multi-taxon coral cover) and the availability of suitable benthic substrata for settlement and post-settlement survival (as quantified by benthic cover on settlement tiles) to coral recruitment success. To measure coral recruitment, settlement tiles were deployed at Palmyra Atoll (central Pacific Ocean), a remote reef complex with high coral cover, which shows variation in coral and benthic composition, flow regimes and wave energy. We tested if pocilloporid and poritid recruitment rates correlated with measures of water flow obtained from a water flux model and measures of coral and benthic cover. Binary logistical and linear regression models were built to investigate the strength of these relationships. Pocilloporid recruitment depended largely on adult pocilloporid cover and decreased as the total deployment time of the tiles increased. This decrease was habitat-specific and associated with an increase in CCA cover at back reef sites and an increase in bryozoan cover at fore reef sites and results from the competitive pressure that these changes exert on the coral recruits. The results from the correlation analysis and binary logistic model for poritid recruitment were contradictory, and we were unable to clearly determine what drives poritid recruitment. Our results suggest that suitable settlement substratum, distant and local larval supply, and current strength and direction all play important roles in coral recruitment.

Keywords: coral recruitment, local larval supply, settlement substratum preference, current direction, ecological modelling,

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Introduction

Coral recruitment is a critical process that helps maintain populations and facilitates recovery after a disturbance (Vermeij and Sandin 2008; Graham et al. 2011; Gilmour et al. 2013), as well as influencing abundance and species composition (Hughes et al. 2010). Corals have a bipartite life cycle consisting of a pelagic dispersive larval phase and a sessile benthic adult stage. During this life cycle they pass through three demographic bottlenecks that influence recruitment: (1) larval supply, (2) settlement, and (3) post-settlement survival (Arnold et al. 2010; Chong-Seng et al. 2014). The number of available larvae for settlement at a site depends on a spatially and temporally complex interplay between local larval production and retention (Swearer et al. 2002) and the number of larvae that arrive from more distant sources (Raimondi and Morse 2000).

Coral larvae disperse at the water surface and descend to the reef substratum where they search for a suitable settlement location (Raimondi and Morse 2000). Settlement refers to coral larvae attaching to the reef substratum and metamorphosing into recruits. Because finding the right nursery habitat is crucial for post-settlement survival, the larvae of many coral species have developed specific habitat preferences for settlement (Arnold et al. 2010). Post-settlement survival from a recruit to a juvenile coral (>5 cm diameter, Penin et al. 2010) is low for hard corals and depends very much on direct and indirect competition with the coral and non-coral benthic community surrounding the coral settler (Birrell et al. 2008). Several processes can reduce the number of successful Scleractinian recruits on a reef. Colony-specific fecundity, local adult coral species diversity and cover, larval mortality and multi-scale hydrodynamic processes all influence larval availability on differing temporal and spatial scales. Subsequent to larval release and dispersal, larval substratum preference combined with availability of suitable benthic substrata will affect immediate settlement success (Arnold and Steneck 2011), whilst competition, predation, facilitation and disturbance can lead to differences in post-settlement survival (Sato 1985; Gilmour 1999; Box and Mumby 2007; Vermeij and Sandin 2008; Penin et al. 2010). However, the relative contributions of these processes to the success of coral recruitment remains unclear (Elmhirst et al. 2009; Arnold et al. 2010). Three main but not mutually incompatible theories have been proposed to explain the patterns of low coral recruitment that are often reported: (1) low recruitment is mainly caused by a reduction of adult corals resulting in a reduced larval pool (Hughes and Tanner 2000; Hughes et al. 2000; Gilmour et al. 2013); (2) low recruitment is mainly caused by a decrease in fecundity of adult corals (Kojis and Quinn 1984; Hughes et al. 2000; Birkeland 2015); and (3) low recruitment occurs because the reef substratum at the site in question is not particularly suitable

for recruitment (Connell et al. 1997; Bellwood et al. 2004; Carpenter and Edmunds 2006; Vermeij 2006; Hughes et al. 2007). Distinguishing amongst these theories is important in both an ecological sense to improve our understanding of coral reef population biology and connectivity, and also in a management sense because if degraded reefs are to be restored then it is critical that we understand which factors contribute most to larval supply and settlement success to maximise conservation efforts (e.g., Rinkevich 2005; Salinas-de-León et al. 2013).

Settling larvae may originate from the natal reef or neighbouring reefs (closed populations, local larval supply) or from more distant reefs (open populations, distant larval supply). For corals, evidence of both open and closed populations exists as several studies have reported positive correlations between adult hard coral cover and recruitment (Harriott and Fisk 1988; Vermeij 2005; Gilmour et al. 2013; Salinas-de-León et al. 2013; Chong-Seng et al. 2014; Kayal et al. 2015), although others have reported no such correlation (Edmunds et al. 2010; Penin et al. 2010; O'Leary and Potts 2011; Penin and Adjeroud 2013). Whether or not coral populations are closed or open depends on several different factors, including the water retention time of a particular reef, the time it takes for a coral larva to reach competency (that is, the potential distance a larva may travel before being ready to settle), and the length of time that a larva takes to make a settlement decision once competency is achieved (this varies between < 2 hours and several days depending on the coral species) (Figueiredo et al. 2013). A commonly used method to study coral recruitment involves a census of coral recruits that are several months old. By this time the recruits have passed through the three stages of recruitment, consequentially little is known about the relative importance of these stages to the success of coral recruitment. It is therefore difficult to determine which factors cause low recruitment and how much they contribute toward this. Additional studies accounting for the three processes of larval supply, settlement and post-settlement survival are needed to determine what ultimately drives coral recruitment.

The reefs surrounding Palmyra Atoll, a remote Central Pacific Atoll, are particularly appropriate for investigating recruitment processes. Outside the lagoon, the back reef and fore reef areas have high coral cover and have experienced low impact from anthropogenic stressors (Knowlton and Jackson 2008; Work et al. 2008; Collen et al. 2009; Williams et al. 2013). Palmyra Atoll exhibits substantial differences in coral composition, flow regimes and wave energy amongst sites in the fore and back reef regions (Williams et al. 2008, 2013; Rogers 2015; Rogers et al. 2016a, 2016b) and is therefore well suited for studying the natural processes that shape coral settlement and recruitment on a variety of

spatial scales.

In this study, a combination of methods was used to evaluate the influence of distant (i.e., another site on the atoll) and local (i.e., the same site) coral larval supply, and the availability of suitable substrata for settlement and post-settlement survival on the recruitment of corals of the families pocilloporidae and poritidae at Palmyra Atoll. In the present study, coral recruitment refers to the three processes explained above, larval supply (production and dispersal), settlement and post-settlement survival. We employed the standard approach of deploying settlement tiles to test for site-specific coral settlement success across different time periods. The non-coral benthic cover that developed on these tiles was used as a proxy for suitable substrata for coral settlement and post-settlement survival. To better understand larval connectivity amongst sites on the atoll we used results from a COAWST (Coupled-Ocean-Atmosphere-Wave- Sediment Transport Modeling System, Warner et al. 2010) wave and hydrodynamic model which modelled particle movement between different areas on the back reef, fore reef and the lagoon. The number of particles arriving at a site served as a proxy for distant larval supply, that is, larvae that are derived from sites other than the site of settlement. Finally, coral cover in large (67- 182 m^2) plots, into which the settlement tiles were deployed, was measured using a novel stereo-photographic method. This served as a proxy for local larval supply (i.e., high local cover = high putative larval supply from within the study site itself). We tested the hypothesis that coral recruitment correlates significantly with larval supply (distant and local as two independent variables) and the availability of suitable settlement substrata. We hypothesised that pocilloporids would dominate the recruit composition and that the larvae of pocilloporids and poritids would originate from different sources, with pocilloporid recruitment correlating with local coral cover and poritid recruitment correlating with the water flow to and from the study sites. Lastly, we hypothesised that total coral recruitment would decline as a function of the deployment duration of the tile (hereafter referred to as successional stage of benthic community) because of coral recruits experiencing enhanced competition with other benthic organisms.

Methods

Study sites

Palmyra Atoll is a U.S. National Wildlife Refuge and part of the Pacific Remote Islands Marine National Monument, situated approximately 1700 km southwest of Hawaii in the Northern Line Islands,

central Pacific Ocean (**Error! Reference source not found.**). It is amongst the most remote coral reefs on Earth and its reefs are considered exceptionally healthy in a regional and global context (Knowlton and Jackson 2008). From 2012 until 2015, a scientific collaboration called the Reefs Tomorrow Initiative (RTI – www.reefstomorrowinitiative.org) conducted empirical research to determine the effect of biophysical forcing factors on the benthic community of Palmyra Atoll. We worked at four sites on the fore reef at a depth of ~10 m (FR3, FR5, FR7, FR9), and six sites on the back reef at a depth of 3-5 m (RT1, RT4, RT10, RT13, EC1, EC2) (Fig. 1).
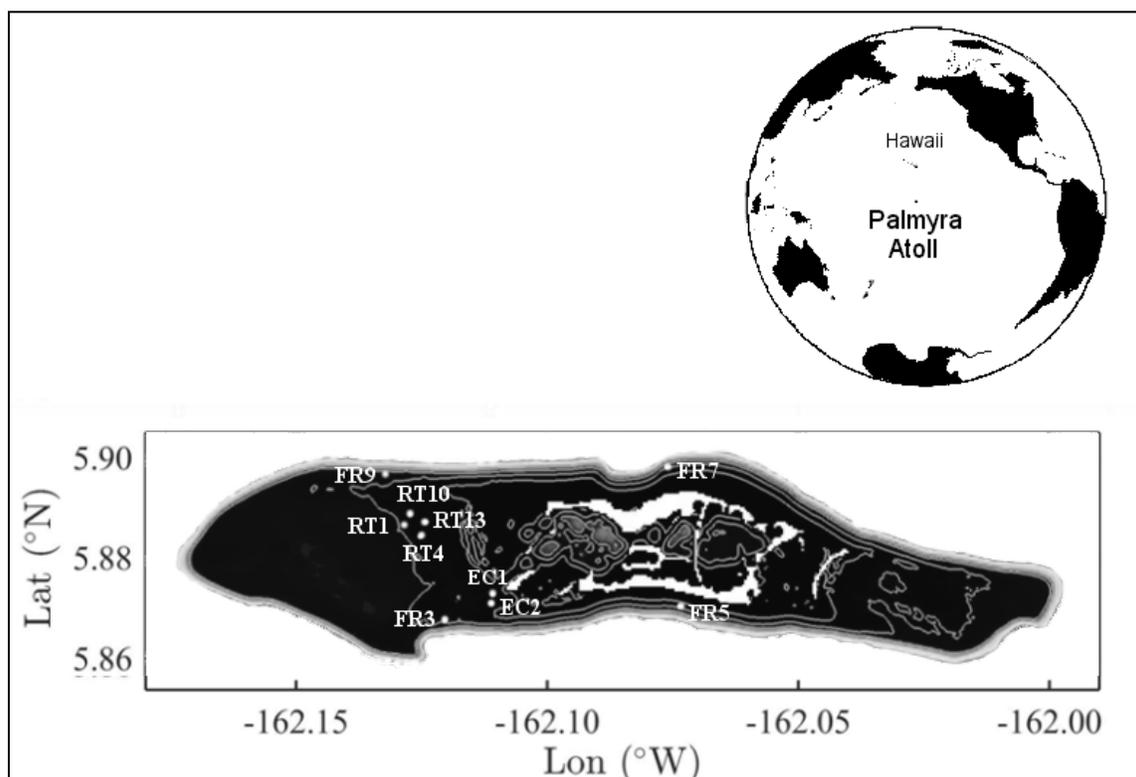
Fig. 1 Location of the study sites. Sites FR3, 5, 7 and 9 are located on the fore reef: tiles were deployed at 10 m depth. RT1, 4, 10, 13 and EC1 and 2 are located on the back reef: tiles were deployed at a depth of 3-5 m. The white areas represent land mass; the water depth is indicated by colour with the darkest areas being the shallowest water depths. The grey isobars are at 5, 10, 50, and 100 m depth.

These sites were chosen based on an earlier study that reported significant differences in benthic cover between the fore reef and the back reef as well as between the Western Reef Terrace (RT) and the Entrance Channel (EC) (Williams et al. 2008). Stuart Sandin and colleagues (unpublished data, Scripps Institute of Oceanography, San Diego, USA) measured percentage coral cover data for RTI using photomosaics of up to 200 m^2. The photomosaics were created by taking continuous photographs with a twin Nikon D7000 SLR set up (F = 18 mm & 55 mm) whilst swimming parallel lines within the plots.

These pictures were stitched together to a single high-resolution picture covering the entire plot (Gracias et al, 2003; Lirman et al. 2007, Lirman et al 2010), within which each adult coral colony was identified to genus.

Waves and tides, currents, near bottom temperatures, and bottom stresses were measured at several of the study sites (Monismith et al. 2015; Rogers 2015; Rogers et al. 2016a, 2016b). As described in Rogers (2015), these data were used to calibrate and validate a 3D circulation model using the COAWST modelling suite (Warner et al. 2010). The combined observational data and model results show that Palmyra Atoll experiences regular tide and wave-driven flushing of the interior lagoons through the main dredged channel (Entrance Channel) located next to sites EC1 and EC2. These water parcels then flow over the reef crest to other sites around the atoll. The two western fore reef sites (FR9 and FR3) receive large volumes of water from the Western Reef Terrace and the Lagoon, respectively (Rogers, 2015). Furthermore, water flow on the fore reef is weakly influenced by the North Equatorial Counter Current (Rogers 2015). The mean wave energy on the southern side of the fore reef (FR3, FR5) is moderate (1-2 m wave height), whilst the northern side of the fore reef (FR7, FR9) experiences higher mean wave energy levels (1-3 m wave height) (Williams et al. 2013; Rogers et al 2015).

Conceptual model

The aim of this study was to determine the influence of distant and local larval supply and the availability of suitable substrata for settlement and post-settlement survival on the recruitment of corals (pocilloporids and poritids) at Palmyra Atoll. Fig. 2 shows a conceptual model, which integrates the main aspects of the three drivers on coral recruitment. For each site, distant larval supply was measured as the number of particles that arrived from different areas within Palmyra Atoll as estimated from the COAWST water circulation model. The retention of larvae at a particular site was estimated through the loss of particles, with retention increasing as loss decreases. Local larval supply was estimated using site-specific adult cover of pocilloporids and poritids. At each of the ten sites, fifteen 10×10 cm terracotta settlement tiles (5 tiles each for groups A, B and C as shown in Fig. 2) were deployed to measure coral recruitment. The multi-species benthic cover on the underside of each tile was assessed to determine the abundance of suitable substrata for settlement and post-settlement survival of the corals (pattern on tiles in Fig. 2). Tiles were deployed for different time periods (length of white arrow in Fig. 2). Some tiles were returned to the reef after analysis (tiles without asterisk in Fig. 2). This made it

possible to determine if coral recruitment Fig. 2) through use of the covariate *Successional stage of the benthic community*. Both rapid settling brooding (*Pocillopora damicornis*, *Stylophora pistillata*) and broadcast spawning pocilloporidae (*Pocillopora eydouxi*, *P. meandrina*, *P. veruucosa*) are found on Palmyra Atoll (Hirose et al. 2000; Harii et al. 2002; Nishikawa et al. 2003; Williams et al. 2008; Baird et al. 2009). Whilst no specific declined as the benthic community developed on the tiles by comparing recruitment onto redeployed is available on the reproductive mode or competency period of the Poritidae at Palmyra Atoll (*Porites superfusa* and massive *Porites* spp.) (Williams et al. 2008), it is likely that they are broadcast spawners because 64% of all Poritidae species are broadcast spawners (Baird et al. 2009).

Measurement of dependent variable and covariates

Coral recruitment and time

To measure coral recruitment rates (dependent variable), fifteen settlement tiles per site were deployed in May/June 2013 at 10 sites on the reefs surrounding Palmyra Atoll (Fig. 1, Fig. 3). Tiles were collected after 3, 9, 12 and 15 months (Fig. 2). Time was measured in terms of (1) collection date, (2) deployment duration and (3) benthic successional stage (total deployment duration of tile) (Fig. 2). This was done to differentiate amongst coral recruitment that was significantly variable due to (1) years or seasons, (2) tiles deployed for different lengths of time and (3) tiles with different benthic successional stages. After deployment, tiles were collected from the reef and the underside (cryptic) surfaces were photographed and examined for coral recruits under a dissecting microscope. Recruits were categorised as pocilloporids, poritids and "others" (Babcock et al. 2003), but because the "others" category was so small we focused only on pocilloporids and poritids.

Suitable substratum for settlement and post-settlement survival

Settlement substratum selection and processes influencing post-settlement survival happen at a spatial scale of millimetres to centimetres (Penin and Adjeroud 2013). Coral recruits on the 100 cm^2 settlement tiles therefore likely settled there based on the benthic community composition on the tile, which later on also influenced their post-settlement survival. The availability of suitable substrata for coral settlement and post-settlement survival was estimated using the cover of the four most abundant benthic functional groups on the underside of the tiles: crustose coralline algae (CCA), bryozoa, bare substratum with biofilm (hereafter referred to as biofilm) and the thalloid red algae, *Peyssonnelia* spp. Together they made up, on average, 85.3% of the area on the undersides of all tiles. CCA and biofilm were

identified as facilitating substrata, bryozoa as an inhibiting substratum and *Peyssonnelia* spp. as a neutral substratum with respect to coral settlement (Elmer, 2016). Percentage cover data for the substratum classes were determined by placing 200 stratified random points in a 10×10 grid on photographs of the underside of the tiles in the coral point count program CPCe 4.0 (Kohler and Gill 2006).

Local larval supply

Previous studies have shown that correlations between coral recruitment and adult cover of the same coral family can be used to determine if larval supply is mainly local (derived from the same study site and therefore equivalent to self-recruitment) (Vermeij 2005; Gilmour et al. 2013). Furthermore, Nozawa et al. (2011) suggested that future studies should measure adult pocilloporid cover when conducting coral recruitment studies because they observed a significant correlation between pocilloporid recruitment and adult pocilloporid cover. In our study, we used site-specific percentage adult coral cover data of pocilloporids and poritids (colonies >5 cm diameter) (Harrison and Wallace 1990) obtained from the photomosaics to test if larvae were supplied locally (*sensu* Nozawa et al. 2011). We also looked at correlations between coral recruitment and the cover of adult hard corals more generally (e.g. Porites adult cover for ocilloporid recruitment, and *vice versa*) to determine if a significant relationship between adult cover and recruitment is likely to be caused by (1) larval supply or (2) larvae preferring to settle close to corals.

Distant larval supply, wind, waves and environmental factors

Whilst a significant positive correlation between coral recruitment and adult coral cover indicates a high possibility of local larval supply, one cannot automatically conclude that larvae are only supplied from distance sources if such a correlation is absent. For example, a lack of correlation may be caused by differences in fecundity of adult corals rather than absence of local larval supply (Hughes et al. 2000). In the present study, distant larval supply refers to larvae that are derived from sites other than the site at which they settle. Its extent depends on spatial and temporal variations in water mass transport associated with mean currents due to tides, waves and wind, and due to the Stokes drift associated with the surface wave field (see Monismith and Fong 2004). To model the effect of distant larval supply and environmental factors we used hydrographic data (e.g. near-bottom velocities and temperatures) and a connectivity matrix based
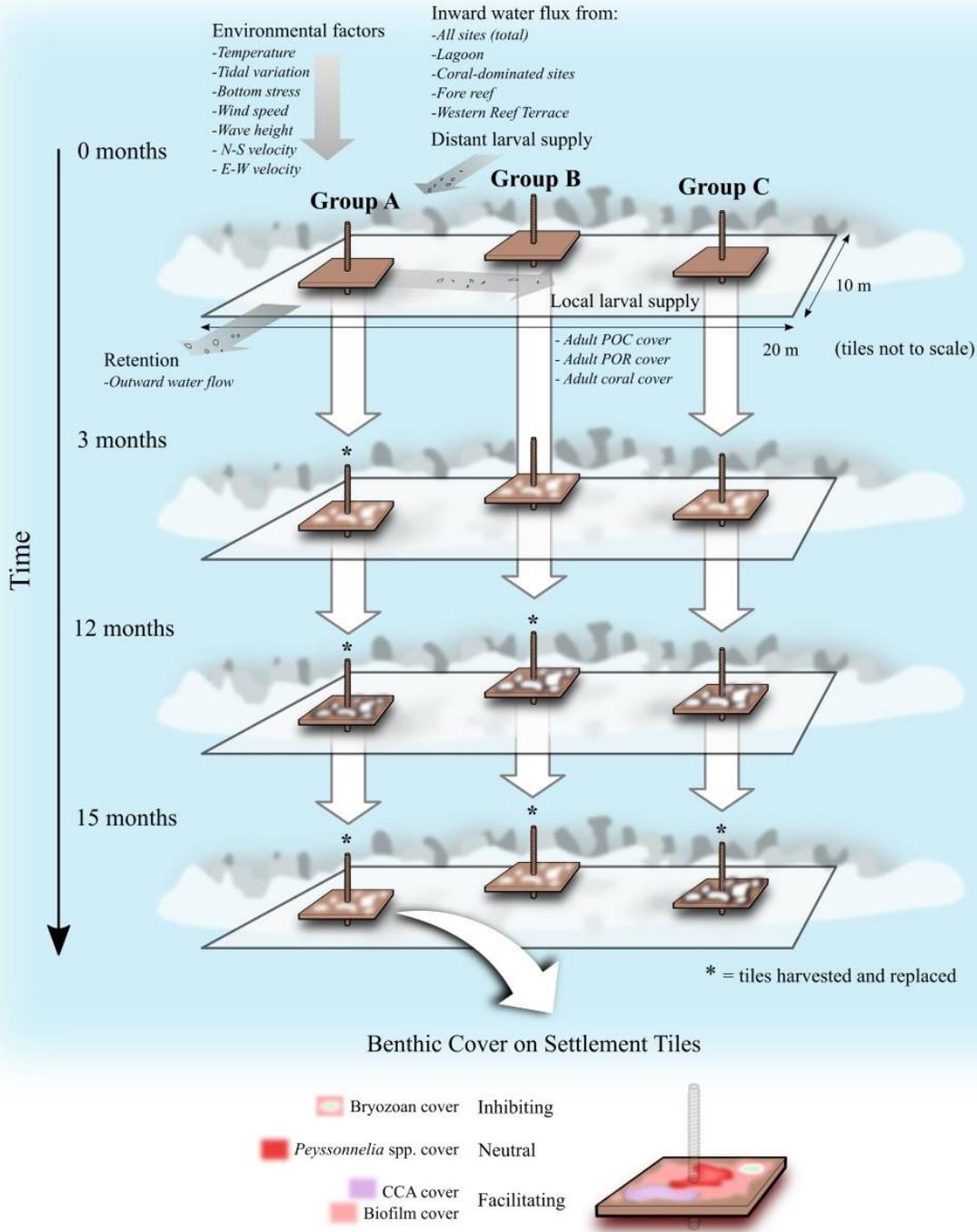
Fig. 2 Conceptual model of factors that influence coral settlement and recruitment. Large font text represents the effects that were modelled (distant larval supply, local larval supply, retention, benthic cover on settlement tiles and environmental factors) and small font text represents the variables that were measured to approximate these effects. At each time point, 15 tiles (5 for each group) were deployed at each of the 10 sites. The white arrows indicate temporal duration of tile deployment. Asterisks indicate that tiles were replaced by new tiles after analysis; tiles

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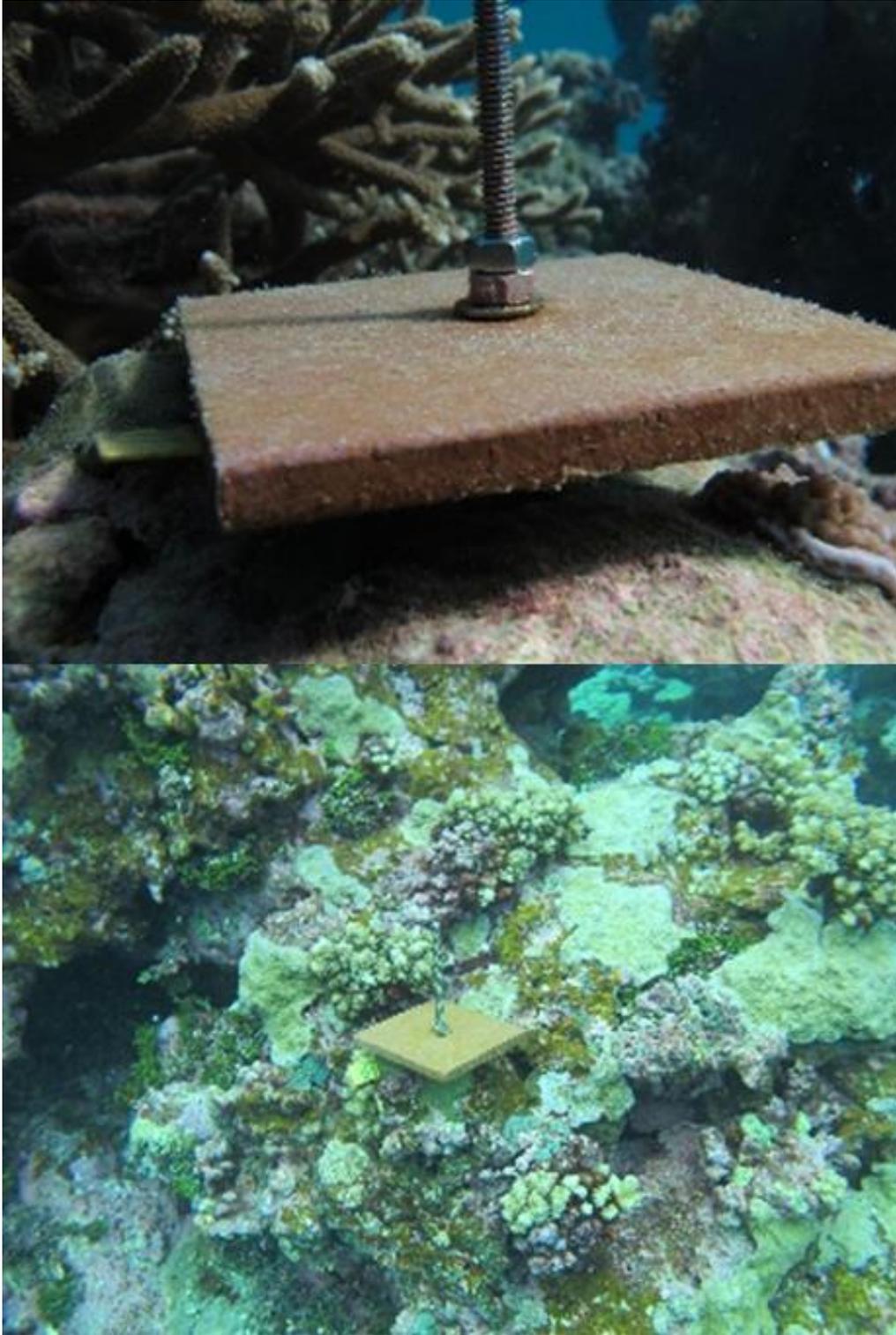
Fig. 3 Close up and overview picture of the experimental set up and placement of tiles on the reef.

on the COAWST model describing water flux rates and pathways within and around Palmyra Atoll. The horizontal grid resolution of the COAWST model was 50 m, which is adequate to resolve the major flow paths on the atoll. The model was run for four separate runs, each of 14 days duration. The four model runs were selected to represent different forcing conditions in wave height, direction, tidal phasing, offshore flow speed and direction: the average connectivity results are presented. The model assumes that larvae can settle immediately after being released, which is adequate for *P. damicornis* and *S. pistillata*, but could lead to an overestimation of retention for the other pocilloporid and poritid species at Palmyra. The COAWST model used to generate the water flux connectivity matrix and the methods used to measure physical oceanographic forcing factors are discussed in detail in Rogers (2015).

Because coral larvae are generally dispersed at the water surface we expect that their transport will be more strongly influenced by winds and waves than they would be by scalars like temperature that are generally uniformly distributed over the water column by mixing. Near-surface transport is caused by wind and Stokes drift (which acts in the direction of wave propagation), and its direction and strength can therefore differ variably from depth-averaged currents. For this reason, wave height and wind speed were also included as covariates along with depth-averaged currents (Fig. 2). For the depth-averaged currents, we included measures of the average strength and direction of the currents during each settlement tile deployment period (N-S and E-W current velocities), as well as the variance of these current velocities over the same time periods (standard deviation of N-S and E-W current velocities). Due to the variability in direction of flow, the variances of the current velocities are better suited as an approximation of the average flow velocity over that time period than the average current velocity itself. Much of the flow variability is the result of oscillating tidal flows (Rogers et al. 2016b), which typically results in low average velocity but high velocity variance. Distant larval supply was measured using the total number of tracer particles arriving at the site (inward water flux) as modelled by the COAWST circulation model (Supplementary Material 1). We divided the 22 points of origin within the COAWST circulation model into four areas that represent potential coral larval dispersal hubs within Palmyra Atoll: (1) coral-dominated, (2) the Western Reef Terrace, (3) the fore reef and (4) the lagoon. Using the matrix (Supplementary Material 1) we calculated the number of water particles that originated from these four areas that arrive at each study site, according to the COAWST circulation model.

Because water parcels from sites with low coral cover will likely contain small numbers of coral larvae we included water flux from four potential coral larval dispersal hubs into the model. As first potential larval dispersal hubs we identified all coral-dominated sites at Palmyra Atoll (yellow, green,

red areas in Fig. 4). However, the fore reef and the back reef vary significantly in their coral community composition (Williams et al. 2008), indicating possible limited larval exchange between the back reef (green and yellow) and the fore reef (red). The fore reef could therefore be mainly self-seeding and was identified as a larval dispersal hub. However, the fore reef site with the highest coral recruitment (FR9) receives a large volume of water from the Western Reef Terrace (green), identifying the latter as a potential larval dispersal hub. The water flux model showed that the retention time of water at Palmyra Atoll is greatest in the lagoon, with water parcels (and therefore larvae) leaving the reef system (coloured areas) within 10 hours of being released from their parent colony unless they pass through the lagoon. For many larvae, failure to spend time passing through the lagoon would mean that they reach offshore waters (white area) before they reach settlement competency (that is, they are lost to the atoll's reef system). The lagoon could therefore act as an important retention mechanism by allowing extra time for larval development before competent coral larvae are moved over the back and fore reef sites where they can settle.
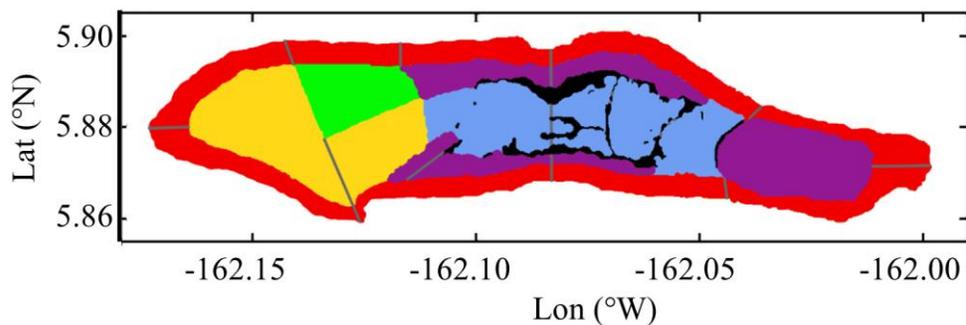
Fig. 4 Visual representation of the different areas from which water flux was measured. The COAWST model measured water flux between 22 points of origin, which are separated in this graph by colour and by grey lines for point of origin that belong to the same larval dispersal hub. The black areas in the centre represent the land mass of Palmyra Atoll. Green, Western Reef Terrace (1 point of origin); red, Fore reef (9 points of origin); blue, lagoon (4 points of origin). Coral-dominated sites are the green, red and yellow areas (12 points of origin). Total water influx and outflux were calculated using all areas (blue, green, yellow, red, purple, 22 points of origin/destination).

Retention time is a measure of the time a larva or parcel of water spends at a certain site and has been found to be positively correlated with coral recruitment (Sammarco and Andrews 1989). Larval retention was estimated using the amount of water that left the site, hereafter referred to as outward water flow (Fig. 2). This is likely to be a good proxy for larval retention because it has been shown that flushing rates can be used to predict coral larvae residence times on coral reef (Black et al. 1990). Near

bottom temperature, tidal variation, N-S and E-W current velocities and their standard deviations and bottom stress were included as environmental covariates in the correlation analysis (Fig. 2). Near bottom temperature was also included as an environmental covariate in the binary logistical and linear regression modelling (see subsequent section).

Statistical analysis

Pocilloporid and poritid recruitment to the underside of the settlement tiles was divided into two subsets: presence/absence of recruits and positive abundance (log transformation of recruit counts) (Fletcher et al. 2005). Positive abundance data included only tiles that received coral recruits; zero values were omitted from the data set. One major advantage of this analytical approach is that presence/absence data and positive abundance data can be modelled separately. This makes it possible to determine if presence/absence and positive abundance are being influenced by the covariates in different ways.

Pearson's correlation coefficient values between pocilloporid recruitment and poritid recruitment and the 21 covariates (listed in Fig. 2) were calculated separately for the presence/absence data and for the log-abundance data. Some covariates had missing data (Supplementary Material 2), which did not pose a problem for the correlation analysis as each covariate was examined separately but did make it difficult to compare models when using all covariates because the number of settlement tiles included in the model building varied depending on which covariates were used because the number of tiles with non-missing covariates values differed. We modelled the fore reef sites and back reef sites separately (note that adult coral cover measurements were missing for the back reef sites) and we excluded the covariates E-W and N-S velocities and their standard deviations, bottom stress, tidal variation, wave height and wind speed because they had missing values. The presence/absence data were modelled using a binary logistic regression, and the log-abundance data were modelled with an ordinary regression. For both types of models, main effects and 1st order effects of the covariates were considered. Factors within the categories distant larval supply, local larval supply and benthic substratum (see Fig. 2) were not combined with each other for 1st order effects because they represented different ways of measuring the same forcing factor. Model adequacy for the ordinary regression was assessed by viewing the residuals plots, which indicated no obvious problems with the model. The Hosmer and Lemeshow goodness of fit test was employed to determine model adequacy for the binary logistic model.

Results

In total, 853 coral recruits were found across all sites on the underside of the tiles (Table 1). pocilloporids made up 77.6%, poritids made up 11.4% and "others" made up 11% of all recruits. Because the "others" category was small and highly variable in composition from site to site, we excluded it from our analyses and have focussed on the pocilloporids and poritids because these constitute the two main groups of recruits.

Correlation analysis

Both the presence and the abundance of pocilloporid recruits was significantly correlated ($p \leq 0.05$) with many of the covariates examined (Table 2). At the back reef sites and for all sites combined, the presence of pocilloporid recruits was correlated with the percentage cover of CCA (-) and biofilm (+) on the settlement tiles. At the fore reef sites, *Peysonnelia* spp. (+) and bryozoan cover (-) were ignificantly correlated with the presence (and abundance for bryozoan cover) of pocilloporid recruits. The successional stage of the benthic community was negatively correlated with pocilloporid recruitment, both at the fore and back reef sites. Presence and abundance of pocilloporid recruits was also correlated with proxies for local and distant larval supply and retention time (summary results in Table 2, full results in Supplementary Material 3).

The presence of poritid recruits was correlated with fewer covariates than the presence of pocilloporid recruits, and mainly with proxies for distant larval supply and retention time (Table 2). The abundance of poritid recruits was only correlated with the standard deviation of the N-S current velocity (summary results in Table 2, full results in Supplementary Material 3).

Binary logistic model

The binary logistic model with the fewest covariates that best predicted the measured presence/absence of pocilloporid recruits at the fore reef sites included the successional stage of the benthic community, the cover of *Peyssonnelia* spp. on the tile, temperature, adult hard coral cover (all hard corals including pocilloporids and poritids) and adult poritid cover ($\chi^2 = 83.924$, df = 5, $p < 0.001$; Table 3).

This model correctly predicted the presence of pocilloporid recruits in 90.2% of cases. The binary logistic model that best predicted the presence/absence of pocilloporid recruits at the back reef sites included the volume of water received from the fore reef and the interaction term CCA $\times$ the

Table 1 Mean number of recruits found on the cryptic underside of the tiles (100 cm^2) after each deployment time. Values are recorded as mean±SE. POC = pocilloporid, POR = poritid.

Site	3 mo 2013		9 mo		12 mo		15 mo		3 mo 2014	
	POC	POR	POC	POR	POC	POR	POC	POR	POC	POR
EC1	9.6±4.1	0	5.2±2.4	0	1.5±0.7	0	1.2±1.0	0	5.8±4.4	0
EC2	3.3±1.5	0	2.4±1.6	0	1.2±0.7	0	0.6±0.6	0	4.9±2.8	0
RT1	0.2±0.2	0	0	0.2±0.2	0.3±0.2	0	0	0.6±0.4	0	0
RT4	1.1±0.7	0	0	0	0.2±0.1	0	0.8±0.8	0	0	0
RT10	0.5±0.3	0	0	0	0.7±0.4	0	0.2±0.2	0	0	0
RT13	0.8±0.4	0	1.4±0.8	0	0.6±0.2	0	0.8±0.5	0	0	0
FR3	3.0±0.7	0.3±0.2	0.6±0.4	0	0	0	0.2±0.2	0	0.4±0.2	0.1±0.1
FR5	0	1.2±1.2	0	0.2±0.2	0.1±0.1	0	0	0.6±0.4	0.1±0.1	0.3±0.2
FR7	0	0	0	2.7±1.8	0	0	0	0.5±0.3	0	0.3±0.2
FR9	10.5±2.9	0.1±0.1	6.8±4.2	4.2±0.4	7.0±2.2	0	0.2±0.2	1.0±1.2	6.1±2.4	0.7±0.4

Refer to Figure 1 for location of the study sites

successional stage of the benthic community. This model correctly predicted the presence of pocilloporid recruits in 74.4% of cases ($\chi^2 = 32.085$, df = 1, p = 0.001; Table 4). The best binary logistic model for presence/absence of Poritid recruits at the fore reef sites correctly predicted the presence of Poritid recruits in 86.0% of cases ($\chi^2 = 27.278$, df = 13, p = 0.011; (Supplementary Material 4). No ordinary regression model was found that predicted pocilloporid recruit abundance at the back reef sites or poritid recruit abundance at the fore reef or back reef sites at a level of statistical significance (p < 0.05).

Correlation between covariates

The covariates used to model pocilloporid recruitment were strongly correlated ($R^2 > 0.85$) with other covariates not present in the model and could therefore easily be substituted by them (Supplementary Material 4). For example, adult hard coral cover was negatively correlated with water received from the

Table 2 Pearson's correlation analysis test results for the influence of multiple individual variables on two types of coral abundance data. Non-significant correlations are in grey, positive significant correlations (p < 0.05) in green and negative significant correlations (p < 0.05) in red. P/A = presence/absence data, Log = log abundance data, POC = Pocilloporid, POR = Poritid. For detailed statistics see Supplementary material 3.

	All sites				Fore reef				Back reef			
	P/A POC	P/A POR	Log POC	Log POR	P/A POC	P/A POR	Log POC	Log POR	P/A POC	P/A POR	Log POC	Log POR
Time												
Deployment duration	grey	grey	grey	grey	grey	grey	grey	grey	grey	grey	grey	grey
Collection date	grey	grey	grey	grey	grey	grey	grey	grey	grey	grey	grey	grey
Successional stage of benthic community	red	grey	red	grey	red	grey	grey	grey	red	grey	red	grey
Suitable settlement substrata												
CCA cover	red	grey	grey	grey	grey	grey	grey	grey	red	grey	grey	grey
Peyssonnelia spp. cover	grey	grey	grey	grey	green	grey	grey	grey	grey	grey	grey	grey
Bryozoans cover	red	grey	grey	grey	red	grey	red	grey	NA	NA	NA	NA
Biofilm cover	green	grey	grey	grey	grey	grey	grey	grey	green	grey	grey	grey
Local larval supply												
Adult hard coral cover	green	grey	green	grey	green	grey	green	grey	NA	NA	NA	NA
Adult Pocilloporid cover	green	grey	green	grey	green	grey	green	grey	NA	NA	NA	NA
Adult Poritid Cover	grey	grey	grey	grey	grey	grey	grey	grey	NA	NA	NA	NA
Distant larval supply												
Inward water flux	green	grey	grey	grey	green	grey	red	grey	green	grey	green	grey
Water received from lagoon	green	red	grey	grey	green	grey	red	grey	green	grey	green	grey
Water received from fore reef	grey	grey	grey	grey	red	grey	red	grey	grey	grey	grey	grey
Water received from Western Reef Terrace	green	green	green	grey	green	grey	green	grey	NA	NA	NA	NA
Water received from coral-dominated sites	green	grey	green	grey	green	grey	grey	grey	green	grey	green	grey
Retention												
Outward water flow	green	red	grey	grey	grey	red	red	grey	green	grey	green	grey
Environmental factors												
Tidal variation	grey	grey	grey	grey	grey	grey	grey	grey	grey	grey	grey	NA
Temperature	red	grey	grey	grey	grey	grey	grey	grey	red	grey	grey	grey
Wave height	grey	green	grey	grey	green	grey	grey	grey	red	green	grey	grey
EW Velocity	red	grey	grey	grey	red	grey	grey	grey	red	grey	grey	NA
NS Velocity	red	grey	grey	grey	red	grey	grey	grey	red	grey	grey	NA
EW Velocity STDEV	green	green	green	grey	green	grey	green	grey	green	grey	grey	NA
NS Velocity STDEV	grey	red	grey	red	red	grey	grey	red	green	grey	grey	NA
Wind speed	grey	grey	grey	grey	green	grey	grey	grey	grey	grey	grey	grey
Bottom Stress	grey	green	grey	grey	green	grey	grey	grey	red	green	grey	grey

fore reef ($R^2 = 0.915$) and adult pocilloporid cover had a strong positive correlation with the volume of water received from the Western Reef Terrace ($R^2 = 0.954$).

Discussion

Coral recruitment is dependent on (1) larval supply, (2) substratum availability and settlement choice, and (3) post-settlement survival. At Palmyra Atoll, pocilloporid recruitment was correlated with proxies for larval supply (both local and distant) and the availability of suitable substratum. According to the binary logistic and linear regression models, pocilloporid recruitment was largely influenced by adult coral cover at the study site. Minor decreases in pocilloporid recruitment rates were also predicted as the age of the benthic community on the settlement tiles increased. poritid recruitment was more difficult to predict using the chosen proxies. The only correlations found were with proxies of distant larval supply whilst the binary logistical model used exclusively proxies of benthic community composition (corals and substrata).

Table 3 Estimates of coefficients for best fit binary logistic model of presence/absence of pocilloporid recruits on tiles deployed at four sites on the fore reef (FR3, FR5, FR7, FR9).

Variables in the Equation

	B	S.E.	Wald	df	Sig.	Exp(B)
Adult poritid cover	-0.325	0.160	4.138	1	0.042	0.723
Temperature	-3.629	1.831	3.928	1	0.048	0.027
Adult hard coral cover	0.338	0.058	34.187	1	<0.001	1.402
Successional stage of benthic community	-0.257	0.069	13.971	1	<0.001	0.774
Peyssonnelia spp.	0.049	0.023	4.313	1	0.038	1.050
Constant	98.014	52.111	3.538	1	0.060	3.691E+42

Local larval supply

The extent to which coral reefs are self-seeding is a hotly debated topic (see Harrison and Wallace 1990; Harrison 2006; Graham et al. 2008). The current consensus is that the importance of local and distant larval supply differs across locations, with coral populations varying from being completely closed (100% self-recruitment) to completely open (0% self-recruitment) (Jones et al. 2009). In this study, we used two different indices of local (based on site-specific coral cover) and distant (based on particle supply in the water flow model) larval supply. These measures are independently derived based on field observations (Nozawa et al. 2011) and well established modelling procedures (Rogers 2015),

Table 4 Estimates of coefficients for best fit binary logistic model of presence/absence of pocilloporid recruits on tiles deployed at six sites on the back reef (EC1, EC2, RT1, RT4, RT10, RT13).

Variables in the Equation

	B	S.E.	Wald	df	Sig.	Exp(B)
Water received from fore reef	0.001	0.000	19.608	1	0.000	1.001
CCA x succession stage of benthic community	-0.002	0.001	9.440	1	0.002	0.998
Constant	-1.214	0.358	11.519	1	0.001	0.297

respectively. In terms of local larval supply, the presence and abundance of pocilloporid recruits at Palmyra Atoll was positively correlated with adult pocilloporid cover, whilst no such correlation was observed for poritids. Our results are consistent with previous reports of positive correlations between adult cover and recruitment rates for pocilloporids but not for poritids (Harriott and Fisk 1988; Penin et al. 2010; Penin and Adjeroud 2013; Chong-Seng et al. 2014; Kayal et al. 2015). More than 50% of the larvae of the two brooding pocilloporid species found on Palmyra Atoll (*P. damicornis* and *S. pistillata*) are expected to settle within a day of being released (Harii et al. 2002; Nishikawa et al. 2003). They are therefore likely to settle close to their parent colony (Figueiredo et al. 2013) as demonstrated by the relatively weak connection of *S. pistillata* populations on the Great Barrier reef (Ayre and Hughes 2000). The correlation between adult pocilloporid cover and pocilloporid recruitment in this study is therefore likely to be caused by the rapid settlement rates of *P. damicornis* and *S. pistillata*. The other pocilloporids species found on Palmyra Atoll are broadcast spawners (Baird et al. 2009), whose larvae are expected to be located away from their natal reef when they reach settlement competency (Hughes et al. 2000). The results from the correlation analysis suggest that poritid species on Palmyra are broadcast

Table 5.Estimates of coefficients for best fit binary logistic model of presence/absence of Poritid recruits on tiles deployed at four sites on the fore reef.

Variables in the Equation

	B	S.E.	Wald	df	Sig.	Exp(B)
CCA	2.765	1.647	2.818	1	0.093	15.876
Bryozoa	3.595	2.170	2.744	1	0.098	36.402
Adult hard coral cover	0.561	0.189	8.799	1	0.003	1.753
CCA × Temperature	-0.090	0.058	2.447	1	0.118	0.914
Adult hard coral cover × CCA	-0.009	0.004	5.303	1	0.021	0.991
Adult hard coral cover × Bryozoa	0.275	0.163	2.836	1	0.092	1.316
Adult Pocilloporid cover × Bryozoa	-1.110	0.672	2.731	1	0.098	0.329
Adult Porites cover × Bryozoa	-0.817	0.486	2.828	1	0.093	0.442
Biofilm × Temperature	0.006	0.002	7.287	1	0.007	1.006
Adult hard coral cover × biofilm	-0.007	0.003	6.366	1	0.012	0.993
Adult hard coral cover × succession stage of benthic community	-0.101	0.046	4.879	1	0.027	0.904
Adult Pocilloporid cover × succession stage of benthic community	0.197	0.078	6.328	1	0.012	1.218
Adult Poritid cover × succession stage of benthic community	0.201	0.098	4.249	1	0.039	1.223
Constant	-13.423	4.063	10.915	1	0.001	0.000

Table 6 Estimates of coefficients for best fit log positive abundance model of pocilloporid recruits on tiles deployed at four sites on the fore reef.

Model	Unstandardised Coefficients		Standardised Coefficients		
	B	Std. Error	Beta	t	Sig.
1 (Constant)	0.187	0.429		0.437	0.664
Adult hard coral cover	0.062	0.013	0.674	4.808	0.000
Water received from coral-dominated sites	-0.135	0.060	-0.317	-2.264	0.028

spawners with a longer competency period than *P. damicornis* and *S. pistillata*. The presence of poritid recruits on the settlement tiles was positively correlated with wave height and negatively with outward water flow, a proxy for retention time. However, the results from the binary logistical model suggest that larval retention does not play a role in poritid recruitment and that it is mainly influenced by adult coral cover and benthic cover. Due to these contradictary results it is hard to draw any clear conclusions on what influences poritid recruitment.

Distant larval supply – current direction matters as much as strength

Both pocilloporid and poritid recruitment correlated with the standard deviation of current velocities, a measure of how much the current velocity varied during the study period. Tidal flow, and to a lesser extent winds and waves, are responsible for much of this variation (Rogers et al. 2016b). Sites with higher standard deviations of current velocity therefore likely have greater flow variability (within the E-W or N-S directions). We found that pocilloporid recruitment (presence and abundance) and poritid recruitment (presence) correlated positively with the standard deviation of the E-W current velocity. The presence and abundance of poritid recruits correlated negatively with the standard deviation of the N-S current velocity. Because of the east-west elongated geometry of Palmyra Atoll, the E-W tidal currents generally transport coral larvae from one reef to another and therefore supply sites with larvae. The N-S tidal currents generally either transport larvae offshore (from the north shore) or toward the interior of the atoll (from the south shore), both areas where larvae are unlikely to find a suitable settlement substratum. These offshore or lagoon areas do not contain hard corals, and therefore N-S currents generally do not supply reefs with additional coral larvae. The exception to this is the reef system located on the Western Reef Terrace and the adjacent fore reef sites, which are connected via N-S currents. It is therefore not surprising that both pocilloporid and poritid recruitment on the fore reef correlated positively with the volume of water received from the Western Reef Terrace, and pocilloporid and poritid recruitment on the back reef correlated positively with the volume of water received from the fore reef. Unfortunately, we were not able to include the standard deviations of the E-W and N-S current velocities in the modelling as data for these covariates were only available for approximately half of our study sites for each deployment time (Table S2.1). It would however, be interesting to see how strong their influence is on pocilloporid and poritid recruitment compared to the other covariables. Other studies (Sammarco and Andrews 1989; Adjeroud et al. 2007) have reported that recruitment increased as flushing rates decreased, as was found for the N-S currents on Palmyra, or that recruitment increased with swell exposure (Adjeroud et al. 2007; Penin and Adjeroud 2013), as was found for the E-W

currents on Palmyra. Our results show that it is important to determine not only the magnitude, but also the direction and source of currents, as these are likely to influence the supply or removal of larvae from a site.

Availability of suitable substratum for settlement and post-settlement survival

According to the binary logistical models, both pocilloporid and poritid recruitment are affected by the successional stage (age) of the benthic community. Presence of pocilloporid recruits on settlement tiles decreased as the benthic community on the settlement tiles aged, whilst poritid recruitment may benefit from an older benthic community with higher CCA and bryozoan cover. Even though pocilloporid recruitment decreased at both the fore reef and the back reef sites as the age of the benthic community on the settlement tiles increased, it is likely that this is due to different processes. The results of the correlation analysis and the binary logistical model indicate that pocilloporid recruitment at back reef sites is likely to be diminished due to CCA recruiting onto bare space covered in biofilm. Whilst CCA is a major post-settlement competitor of coral recruits at Palmyra Atoll (Elmer 2016) it also facilitates coral settlement at Palmyra Atoll and at other reef locations (Carlon 2001; Vermeij 2005; Vermeij and Sandin 2008; Elmer 2016). At Palmyra Atoll, pocilloporid recruits that settled within the 2 weeks before tile analysis were found more frequently on CCA and bare substrate covered in biofilm than expected due to chance alone, indicating that at Palmyra Atoll these substrata are well suited for settlement and early post-settlement survival (Elmer 2016). Settlement onto CCA has a major disadvantage over settlement onto biofilm because it places the coral recruit immediately into a situation where it has to compete for space and access to other resources with an established benthic organism. Our results indicate that at the back reef sites the negative effect of post-settlement competition overshadows the positive effect that CCA has on coral recruitment. The availability of bare space covered in biofilm does not seem to affect pocilloporid recruitment at the fore reef sites, despite them being early recruiters with high settlement rates onto biofilm (Harrigan 1972; Baird and Morse 2004). At the fore reef sites, the increase in bryozoan cover over time likely leads to lower pocilloporid recruitment. Bryozoan cover on the settlement tiles increased substantially between tiles deployed for 3 and 9 months and decreased slowly between 9 to 15 months of deployment. We found a negative correlation between bryozoan cover and pocilloporid recruit presence on the settlement tiles and research conducted in the Red Sea and on the Great Barrier Reef also reported that bryozoan cover negatively affected coral recruitment (Dunstan and Johnson 1998; Glassom et al. 2004).

Limiting and regulating factors

Recruitment is influenced by factors that limit settlement and modify post-settlement survival and factors that regulate them (Caley et al. 1996). It is important to distinguish between limiting and regulating factors when predicting population size fluctuations. Limiting factors determine whether or not recruitment is present, whilst regulating factors increase or decrease the number of recruits. The results reported in this study indicate that the availability of suitable substrata for coral settlement and post-settlement survival acts mainly as a limiting factor on pocilloporid recruitment, whilst larval supply acts as both a limiting factor and a regulating factor on pocilloporid recruitment at Palmyra Atoll. The only regulatory factor for poritid recruitment was N-S flow variability, which likely decreased larval retention and larval supply. Vermeij (2005) and Carlon (2001) came to a similar conclusion for reefs in the Florida Keys and the British Virgin Islands, respectively, identifying habitat availability as a limiting factor and the presence of adult coral colonies as a regulatory factor. Recruitment to the reefs of Palmyra Atoll is therefore limited and regulated in a similar way to reefs that are more impacted by anthropogenic activities. These findings may suggest some inherent properties of coral recruitment processes, regardless of coral reef health, and therefore require further examination so that management and conservation of coral reefs can be better achieved.

Limitations of this study

We detected spatial autocorrelation in recruit presence/absence amongst tiles that were deployed onto the same stake (e.g. tiles put onto the same stake often had the same outcome: coral recruits present or absent). Some of this autocorrelation is likely to be accounted for by the correlations found between recruitment and benthic cover on the settlement tiles. However, coral recruitment is also likely to be affected by factors acting on the spatial scale of 10 cm - 10 m (e.g. topographic properties of stake location, proximity to coral colonies), which we were not able to account for in this study. Further examination of such factors is required to provide an enhanced understanding of coral settlement and recruitment success.

Overall conclusion

The results of this study indicate that pocilloporid recruitment is likely to be strongly dependent on the local production of pocilloporid larvae, which suggest that recovery rates may be slow after high local pocilloporid cover loss. The results of this study did not provide a clear answer to what factors affect poritid recruitment, but they do emphasise the difference in recruitment patterns between poritids and

pocillioporids, something that needs to be taken into account in restoration efforts. Within the Palmyra Atoll reef system we found no single area that acts as a larval dispersal hub but we did identify that tidal flow plays an important role in coral recruitment. Tidal flow connections (strength and direction of flow) should therefore be considered when areas are selected for Marine Protected Areas as our results imply that reefs that are connected to neighbouring reefs through tidal flow have higher pocilloporid and poritid recruitment.

Acknowledgements

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Supplementary Material 1
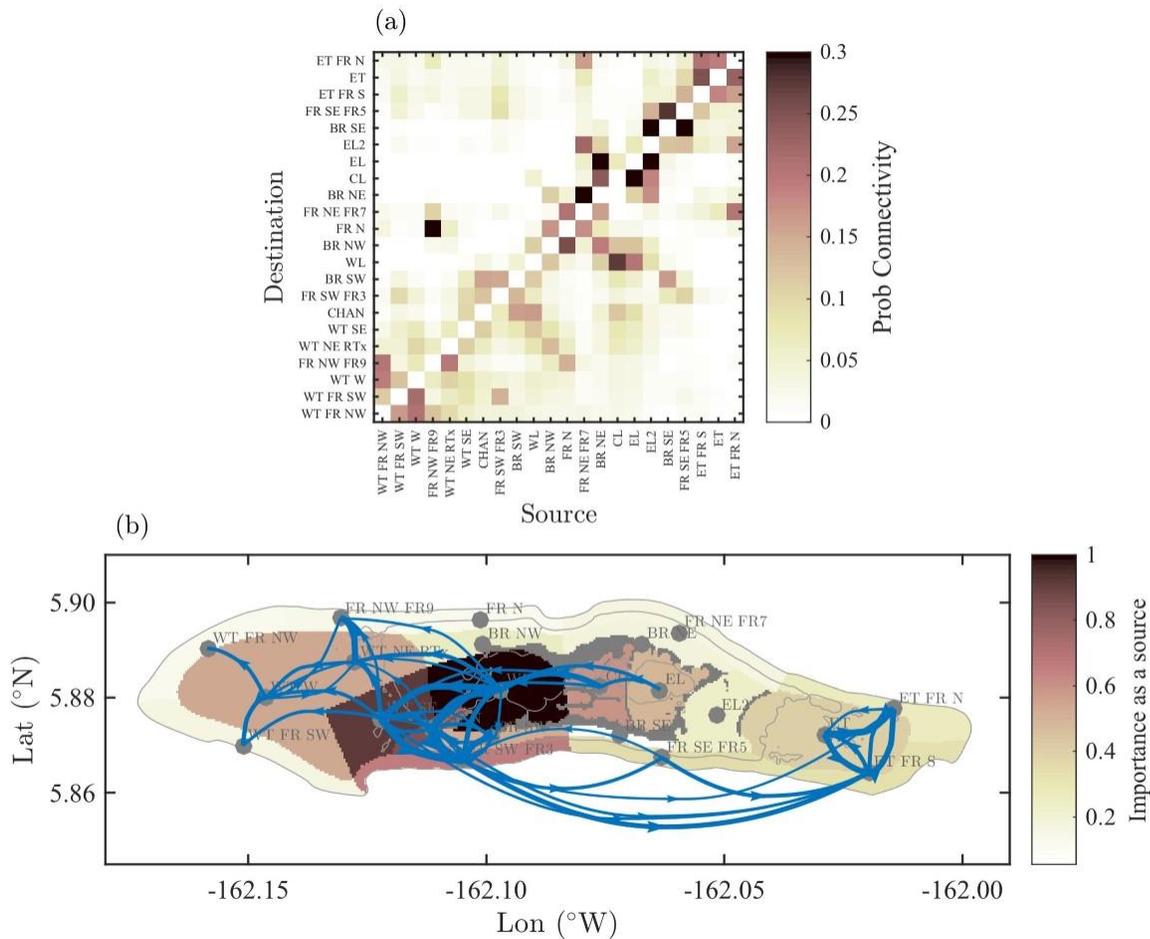
Fig S1.1 Connectivity between hydrodynamic zones. (a) connectivity matrix showing the probability a water parcel passing through a destination zone came from a given source zone, and (b) geographic connectivity of top 10% of pathways, where shading is relative importance as an overall source, and width of line is relative strength of connection. Results based on average of all COAWST model runs; grey shading is land mass, grey lines are 5 and 60 m depth contours. The first letters in the site code refer to the area the site is located in: BR = Back Reef, EL = Eastern Lagoon, ET = Eastern Terrace, CHAN= Channel, CL = Central Lagoon, FR = Fore Reef, WL = Western Terrace. WL = Western Lagoon. For some sites it is also noted in which corner of the above mentioned area they are located: E = East, N = North, NE = North East, NW = North West, S = South, SE = South East, SW = South West. FR3, 5, 7, 9 and the RT sites (RTx) are also marked in the site code, EC1 and EC2 are located inside CHAN.

Table S2.1 All the predictors that were tested in the correlation analysis and the model building. The dark grey boxes represent sites and time periods for which data are available for the predictors. White boxes represent missing data. The last column shows the unit in which the predictor was measured. FR= Fore reef regression models, BR = Back reef regression models

Predictor	Included in models	EC		RT				FR				Unit
		1	2	1	4	10	13	3	5	7	9	
Time												
Collection date	FR, BR											Month field trip was conducted in
Deployment duration	FR, BR											Number of months deployed after last analysis
Successional stage of benthic community	FR, BR											Total number of months deployed
Suitable settlement substrata												
CCA cover	FR, BR											Percentage cover
Biofilm cover	FR, BR											Percentage cover
Peyssonnelia spp. cover	FR, BR											Percentage cover
Bryozoan cover	FR, BR											Percentage cover
Local larval supply												
Adult hard coral cover	FR											Percentage cover
Adult Pocilloporid cover	FR											Percentage cover
Adult Poritid cover	FR											Percentage cover
Distant larval supply												
Inward water flux	FR, BR	14	14	6	6	6	6	25	10	5	11	Nr of particles (1000)
Water received from coral-dominated sites	FR, BR	6	6	3	3	3	3	9	6	4	8	Nr of particles (1000)

Table S2.1 continued

Predictor	Included in models	EC		RT				FR				Unit
		1	2	1	4	10	13	3	5	7	9	
Water received from lagoon	FR, BR	5	5	1	1	1	1	5	2	0.3	1	Nr of particles (1000)
Water received from Western Reef Terrace	FR	0.4	0.4					0.6	0.2	0.2	3	Nr of particles (1000)
Water received from fore reef	FR, BR	5	5	2	2	2	2	7	5	3	4	Nr of particles
Retention												
Outward water flow	FR, BR	17	17	7	7	7	7	17	10	2	2	Nr of particles (1000)

Table S2.1 continued

Predictor		Included in models	EC		RT				FR				Unit
			1	2	1	4	10	13	3	5	7	9	
Environmental Factors													
Temperature	May 2013-Sept 2013	FR	28.4	28.4	28.5	28.5	28.5	28.5	28.5	28.5	28.5	28.5	°C
	Sept 2013-May 2014		28.4	28.4	28.5	28.5	28.9	28.5	28.5	28.5	28.4	28.5	
	May 2014-Sept 2014		28.6	28.6	28.8	28.8		28.8	28.8	28.8	28.8	28.8	
E-W velocity, N-S velocity & Standard deviation of the above	May 2013-Sept 2013	None				0.00 0.01 0.05 0.04	0.00 0.02 0.05 0.05		-0.03 -0.01 0.10 0.03		0.05 0.00 0.11 0.06	0.01 0.01 0.19 0.05	m s⁻¹
	Sept 2013-May 2014		-0.07 -0.03 0.13 0.07	-0.06 -0.03 0.13 0.07		-0.01 0.01 0.05 0.03	-0.01 0.01 0.03 0.04			0 -0.01 0.08 0.04	0.04 0.02 0.09 0.07	-0.01 0.15 0.00 0.04	
	May		-	-							0.01	-	

		None											units
	2014-Sept 2014		0.03 - 0.01 0.13 0.07	0.03 - 0.01 0.13 0.07							0.01 0.07 0.06	0.05 0.13 - 0.02 0.04	
Bottom stress	May 2013-Sept 2013	None	0.00	0.00	0.03	0.01	0.01	0.00	0.14	0.13	0.06	0.10	$m^2 s^{-2}$
	Sept 2013-May 2014		0.02	0.02	0.03	0.01	0.02	0.00	0.07	0.07	0.16	0.19	
	May 2014-Sept 2014		0.02	0.02							0.01	0.02	
Tidal variation	May 2013-Sept 2013	None				0.25	0.26	0.24	0.24	0.24	0.24	0.25	m
	Sept 2013-May 2014		0.25	0.25		0.25	0.24		0.25	0.25	0.25	0.25	
	May 2014-Sept 2014		0.24	0.24						0.24	0.24		

Table S2.1 continued

Predictor		EC		RT				FR				Unit
		1	2	1	4	10	13	3	5	7	9	
Wave height	May 2013-Sept 2013	0.12	0.12	0.35	0.25	0.28	0.11	1.14	1.51	0.79	0.88	m
	Sept 2013-May 2014	0.10	0.10	0.35	0.22	0.27	0.17	0.96	0.91	1.32	1.40	
	May 2014-Sept 2014							1.01	1.03			
Wind speed	May 2013-Sept 2013	4.86	4.89	4.82	4.80	4.89	4.8	4.74	4.78	4.66	4.66	m s^{-1}
	Sept 2013-May 2014	3.62	3.64	3.62	3.65	3.62	3.65	3.63	3.64	3.64	3.621.01	
	May 2014-Sept 2014	4.79		5.08		4.92					4.94	

Table S3.1 Pearson's correlation and its test statistic for correlations between the presence data (P/A) and the log abundance data of Pocilloporid and Poritid recruits and the covariates described in Supplementary Material 2. * = p-value between 0.01 and 0.05, ** = p-value < 0.01.

		P/A POC	P/A POR	Log abundance POC	Log abundance POR
Time					
Deployment duration	Pearson's Correlation	-0.054	0.059	-0.068	-0.114
	Sig. (2-tailed)	0.295	0.254	0.441	0.534
	N	379	379	131	32
Collection date	Pearson's Correlation	-0.077	-0.082	-0.029	-0.192
	Sig. (2-tailed)	0.133	0.112	0.741	0.294
	N	379	379	131	32
Successional stage of benthic community	Pearson's Correlation	**-0.200****	0.025	**-0.216***	-0.254
	Sig. (2-tailed)	**<0.001**	0.627	**0.013**	0.160
	N	**379**	379	**131**	32
Suitable settlement substrata					
CCA cover	Pearson's Correlation	**-0.129***	-0.042	-0.004	-0.065
	Sig. (2-tailed)	**0.013**	0.421	0.967	0.725
	N	**366**	366	128	32
Peyssonnelia spp. cover	Pearson's Correlation	0.067	-0.050	-0.072	0.167
	Sig. (2-tailed)	0.199	0.342	0.419	0.361
	N	366	366	128	32
Bryozoan cover	Pearson's Correlation	**-0.178****	0.092	-0.131	-0.239
	Sig. (2-tailed)	**0.001**	0.078	0.140	0.188
	N	**366**	366	128	32
Biofilm cover	Pearson's Correlation	**0.162****	0.071	0.082	0.149
	Sig. (2-tailed)	**0.002**	0.174	0.356	0.415
	N	**366**	366	128	32
Local larval supply					
Adult hard coral cover	Pearson's Correlation	**0.548****	0.062	**0.505****	-0.034
	Sig. (2-tailed)	**<0.001**	0.454	**<0.001**	0.871
	N	**150**	150	**50**	25
Adult Pocilloporid cover	Pearson's Correlation	**0.538****	0.150	**0.529****	0.017
	Sig. (2-tailed)	**<0.001**	0.066	**<0.001**	0.937
	N	**150**	150	**50**	25
Adult Poritid cover	Pearson's Correlation	-0.049	-0.091	-0.272	-0.029
	Sig. (2-tailed)	0.553	0.269	0.056	0.889
	N	150	150	50	25
Distant larval supply					
Inward water flux	Pearson's Correlation	**0.276****	0.000	0.047	-0.171
	Sig. (2-tailed)	**<0.001**	0.997	0.592	0.349
	N	**379**	379	131	32

Table S3.1 continued

		P/A POC	P/A POR	Log abundance POC	Log abundance POR
Water received from lagoon	Pearson's Correlation	**0.302****	**-0.129***	0.007	-0.176
	Sig. (2-tailed)	**<0.001**	**0.012**	0.941	0.334
	N	**379**	**379**	131	32
Water received from fore reef	Pearson's Correlation	0.004	0.087	0.118	0.016
	Sig. (2-tailed)	0.931	0.089	0.178	0.929
	N	379	379	131	32
Water received from Western Reef Terrace	Pearson's Correlation	**0.346****	**0.203****	**0.324****	0.017
	Sig. (2-tailed)	**<0.001**	**0.002**	**0.001**	0.936
	N	**227**	**227**	**95**	25
Water received from coral-dominated sites	Pearson's Correlation	**0.263****	0.090	**0.235****	-0.100
	Sig. (2-tailed)	**<0.001**	0.080	**0.007**	0.586
	N	**379**	379	**131**	32
Retention					
Outward water flow	Pearson's Correlation	**0.195****	**-0.167****	-0.122	-0.151
	Sig. (2-tailed)	**<0.001**	**0.001**	0.165	0.410
	N	**379**	**379**	131	32
Environmental factors					
Tidal variation	Pearson's Correlation	0.018	-0.040	0.086	-0.284
	Sig. (2-tailed)	0.787	0.538	0.459	0.225
	N	237	237	76	20
Temperature	Pearson's Correlation	**-0.130***	-0.050	-0.024	-0.129
	Sig. (2-tailed)	**0.013**	0.338	0.790	0.481
	N	**364**	364	126	32
Wave height	Pearson's Correlation	-0.034	**0.239****	0.065	-0.145
	Sig. (2-tailed)	0.579	**<0.001**	0.554	0.479
	N	261	**261**	85	26
E-W Velocity	Pearson's Correlation	**-0.374****	0.106	0.030	0.142
	Sig. (2-tailed)	**<0.001**	0.139	0.795	0.550
	N	**198**	198	76	20
N-S Velocity	Pearson's Correlation	**-0.322****	0.034	0.000	-0.076
	Sig. (2-tailed)	**<0.001**	0.636	0.998	0.749
	N	**198**	198	76	20
E-W Velocity Standard deviation	Pearson's Correlation	**.458****	**.176***	**.328****	.087
	Sig. (2-tailed)	**<0.001**	**.013**	**.004**	.715
	N	**198**	**198**	**76**	20
N-S Velocity Standard deviation	Pearson's Correlation	-0.029	**-0.164***	-0.054	**-0.490***
	Sig. (2-tailed)	0.690	**0.021**	0.641	**0.028**
	N	198	**198**	76	**20**

Table S3.1 continued

		P/A POC	P/A POR	Log abundance POC	Log abundance POR
Wind speed	Pearson's Correlation	0.105	-0.011	0.127	0.065
	Sig. (2-tailed)	0.074	0.850	0.194	0.732
	N	290	290	107	30
Bottom Stress	Pearson's Correlation	0.035	**0.248**[**]	0.052	-0.097
	Sig. (2-tailed)	0.546	**<0.001**	0.594	0.610
	N	292	**292**	107	30

Table S3.2 Pearson's correlation table for presence data (P/A) and the log abundance data of Pocilloporid (POC) and Poritid (POR) and the covariates described in Table 1 at the four fore reef sites. * = p-value between 0.01 and 0.05, ** = p-value < 0.01.

		P/A POC	P/A POR	Log abundance POC	Log abundance POR
Time					
Deployment duration	Pearson's Correlation	-0.049	0.051	-0.044	-0.149
	Sig. (2-tailed)	0.563	0.542	0.764	0.478
	N	143	143	49	25
Collection date	Pearson's Correlation	-0.087	-0.126	0.151	-0.201
	Sig. (2-tailed)	0.299	0.134	0.300	0.335
	N	143	143	49	25
Successional stage of benthic community	Pearson's Correlation	**-0.253****	0.003	-0.062	-0.248
	Sig. (2-tailed)	**0.002**	0.969	0.672	0.233
	N	**143**	143	49	25
Suitable settlement substrata					
CCA cover	Pearson's Correlation	0.109	0.077	0.254	-0.096
	Sig. (2-tailed)	0.194	0.361	0.078	0.647
	N	143	143	49	25
Peyssonnelia spp. cover	Pearson's Correlation	**0.190***	0.103	-0.009	0.072
	Sig. (2-tailed)	**0.023**	0.223	0.950	0.734
	N	**143**	143	49	25
Bryozoan cover	Pearson's Correlation	**-0.326****	-0.030	**-0.320***	-0.307
	Sig. (2-tailed)	**<.001**	0.721	**0.025**	0.136
	N	**143**	143	**49**	25
Biofilm cover	Pearson's Correlation	0.159	0.004	-0.099	0.228
	Sig. (2-tailed)	0.057	0.966	0.497	0.273
	N	143	143	49	25
Local larval supply					
Adult hard coral cover	Pearson's Correlation	**0.560****	0.072	**0.511****	-0.034
	Sig. (2-tailed)	**<0.001**	0.395	**<0.001**	0.871
	N	**143**	143	**49**	25
Adult Pocilloporid cover	Pearson's Correlation	**0.538****	0.150	**0.529****	0.017
	Sig. (2-tailed)	**<0.001**	.066	**<0.001**	0.937
	N	**150**	150	**50**	25
Adult Poritid cover	Pearson's Correlation	-0.032	-0.087	-0.277	-0.029
	Sig. (2-tailed)	0.702	0.301	0.054	0.889
	N	143	143	49	25
Distant larval supply					
Inward water flux	Pearson's Correlation	**0.269****	-0.119	**-0.380****	-0.223
	Sig. (2-tailed)	**0.001**	0.157	**0.007**	0.283
	N	**143**	143	**49**	25

Table S3.2 continued

		P/A POC	P/A POR	Log abundance POC	Log abundance POR
Water received from lagoon	Pearson's Correlation	**0.229**[**]	-0.129	**-0.403**[**]	-0.224
	Sig. (2-tailed)	**0.006**	0.125	**0.004**	0.282
	N	**143**	143	**49**	25
Water received from fore reef	Pearson's Correlation	**-0.454**[**]	-0.030	**-0.359**[*]	0.043
	Sig. (2-tailed)	**<0.001**	0.725	**0.011**	0.840
	N	**143**	143	**49**	25
Water received from Western Reef Terrace	Pearson's Correlation	**0.573**[**]	0.164	**0.550**[**]	0.017
	Sig. (2-tailed)	**<0.001**	0.051	**<0.001**	0.936
	N	**143**	143	**49**	25
Water received from coral-dominated sites	Pearson's Correlation	**0.518**[**]	-0.014	0.029	-0.157
	Sig. (2-tailed)	**<0.001**	0.868	0.846	0.453
	N	**143**	143	49	25
Retention					
Outward water flow	Pearson's Correlation	0.014	**-0.166**[*]	**-0.487**[**]	-0.197
	Sig. (2-tailed)	0.866	**0.047**	**<0.001**	0.344
	N	143	**143**	**49**	25
Environmental factors					
Tidal variation	Pearson's Correlation	0.131	0.080	0.315	-0.284
	Sig. (2-tailed)	0.166	0.398	0.090	0.225
	N	114	114	30	20
Temperature	Pearson's Correlation	-0.018	-0.113	0.163	-0.104
	Sig. (2-tailed)	0.829	0.179	0.264	0.621
	N	143	143	49	25
Wave height	Pearson's Correlation	**0.213**[*]	0.125	0.180	-0.196
	Sig. (2-tailed)	**0.023**	0.188	0.293	0.408
	N	**113**	113	36	20
E-W Velocity	Pearson's Correlation	**-0.570**[**]	-0.035	-0.032	0.142
	Sig. (2-tailed)	**<0.001**	0.745	0.846	0.550
	N	**90**	90	38	20
N-S Velocity	Pearson's Correlation	**-0.343**[**]	-0.016	-0.062	-0.076
	Sig. (2-tailed)	**0.001**	0.883	0.710	0.749
	N	**90**	90	38	20
E-W Velocity Standard deviation	Pearson's Correlation	**0.558**[**]	0.138	**0.317**[*]	0.087
	Sig. (2-tailed)	**<0.001**	0.176	**0.049**	0.715
	N	**97**	97	**39**	20
N-S Velocity Standard deviation	Pearson's Correlation	**-0.265**[**]	-0.083	0.223	**-0.490**[*]
	Sig. (2-tailed)	**0.009**	0.421	0.173	**0.028**
	N	**97**	97	39	**20**

Table S3.2 continued

		P/A POC	P/A POR	Log abundance POC	Log abundance POR
Wind speed	Pearson's Correlation	**0.245***	0.088	0.166	0.165
	Sig. (2-tailed)	**0.014**	0.384	0.299	0.451
	N	**99**	99	41	23
Bottom Stress	Pearson's Correlation	**0.210***	0.110	-0.166	-0.093
	Sig. (2-tailed)	**0.024**	0.243	0.300	0.666
	N	**115**	115	41	24

Table S3.3 Pearson's correlation table for the presence data (P/A) and the log abundance data of Pocilloporid (POC) and Poritid (POR) and the covariates described in Table 1at the six back reef sites. * = p-value between 0.01 and 0.05, ** = p-value < 0.01.

		P/A POC	P/A POR	Log abundance POC	Log abundance POR
Time					
Deployment duration	Pearson's Correlation	-0.046	0.100	-0.075	-0.055
	Sig. (2-tailed)	0.485	0.131	0.504	0.907
	N	229	229	81	7
Collection date	Pearson's Correlation	-0.086	-0.002	-0.164	-0.079
	Sig. (2-tailed)	0.197	0.971	0.143	0.867
	N	229	229	81	7
Successional stage of benthic community	Pearson's Correlation	**-0.158**[*]	0.085	**-0.275**[*]	-0.340
	Sig. (2-tailed)	**0.017**	0.200	**0.013**	0.455
	N	**229**	229	**81**	7
Suitable settlement substrata					
CCA cover	Pearson's Correlation	**-0.292**[**]	0.101	-0.195	-0.100
	Sig. (2-tailed)	**0.000**	0.132	0.085	0.831
	N	**223**	223	79	7
Peyssonnelia spp. cover	Pearson's Correlation	0.025	-0.014	-0.019	0.513
	Sig. (2-tailed)	0.709	0.839	0.865	0.239
	N	223	223	79	7
Bryozoan cover	Pearson's Correlation	NA	NA	NA	NA
	Sig. (2-tailed)				
	N				
Biofilm cover	Pearson's Correlation	**0.197**[**]	-0.096	0.111	-0.040
	Sig. (2-tailed)	**0.003**	0.151	0.330	0.932
	N	**223**	223	79	7
Local larval supply					
Adult hard coral cover	Pearson's Correlation	NA	NA	NA	NA
	Sig. (2-tailed)				
	N				
Adult Pocilloporid cover	Pearson's Correlation	NA	NA	NA	NA
	Sig. (2-tailed)				
	N				
Adult Poritid cover	Pearson's Correlation	NA	NA	NA	NA
	Sig. (2-tailed)				
	N				
Distant larval supply					
Inward water flux	Pearson's Correlation	**0.350**[**]	-0.085	**0.309**[**]	
	Sig. (2-tailed)	**0.000**	0.200	**0.005**	0.000
	N	**229**	229	**81**	7

Table S3.3 continued

		P/A POC	P/A POR	Log abundance POC	Log abundance POR
Water received from lagoon	Pearson's Correlation Sig. (2-tailed) N	**0.350**** **0.000** **229**	-0.085 0.200 229	**0.309**** **0.005** **81**	.c 0.000 7
Water received from fore reef	Pearson's Correlation Sig. (2-tailed) N	**0.350**** **0.000** **229**	-0.085 0.200 229	**0.309**** **0.005** **81**	.c 0.000 7
Water received from Western Reef Terrace	Pearson's Correlation Sig. (2-tailed) N	NA	NA	NA	NA
Water received from coral-dominated sites	Pearson's Correlation Sig. (2-tailed) N	**0.350**** **0.000** **229**	-0.085 0.200 229	**0.309**** **0.005** **81**	.c 0.000 7
Retention					
Outward water flow	Pearson's Correlation Sig. (2-tailed) N	**0.350**** **0.000** **229**	-0.085 0.200 229	**0.309**** **0.005** **81**	.c 0.000 7
Environmental factors					
Tidal variation	Pearson's Correlation Sig. (2-tailed) N	-0.131 0.161 116	0.032 0.737 116	-0.067 0.660 45	.c 0
Temperature	Pearson's Correlation Sig. (2-tailed) N	**-0.206**** **0.002** **214**	-0.056 0.417 214	-0.225 0.050 76	-0.243 0.599 7
Wave height	Pearson's Correlation Sig. (2-tailed) N	**-0.429**** 0.000 142	**0.273**** **0.001** **142**	-0.221 0.131 48	0.017 0.974 6
E-W Velocity	Pearson's Correlation Sig. (2-tailed) N	**-0.330**** **0.001** **101**	-0.159 0.112 101	-0.082 0.631 37	.c 0
N-S Velocity	Pearson's Correlation Sig. (2-tailed) N	**-0.360**** **0.000** **101**	-0.125 0.211 101	-0.151 0.373 37	.c 0
E-W Velocity Standard deviation	Pearson's Correlation Sig. (2-tailed) N	**0.386**** **0.000** **101**	0.088 0.379 101	0.216 0.200 37	.c 0
N-S Velocity Standard deviation	Pearson's Correlation Sig. (2-tailed) N	**0.341**** **0.000** **101**	0.080 0.428 101	0.253 0.130 37	.c 0

Table S3.3 continued

		P/A POC	P/A POR	Log abundance POC	Log abundance POR
Wind speed	Pearson's Correlation	0.029	-0.067	0.088	-0.126
	Sig. (2-tailed)	0.698	0.361	0.487	0.788
	N	185	185	65	7
Bottom Stress	Pearson's Correlation	-0.237**	0.264**	-0.092	-0.017
	Sig. (2-tailed)	0.002	0.001	0.466	0.974
	N	170	170	65	6

Table S4.1 List of ordinary regression models for pocilloporid recruitment that had a p value < 0.001. Models that differed from these models by adding an additional covariate were only included if including them increased the adjusted R^2 value (e.g. adding water received from coral-dominated sites to adult hard coral cover).

Adjusted R^2	ANOVA p-value	Covariates included in model
0.306	< 0.001	Adult hard coral cover, Water received from coral-dominated sites
0.287	< 0.001	Water received from Western Reef Terrace
0.264	< 0.001	Adult Pocilloporid cover
0.245	< 0.001	Adult hard coral cover