



Key Ecological Processes in Kimberley Benthic Communities: Coral Recruitment

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WAMSI Kimberley Marine Research Program

Initiated with the support of the State Government as part of the Kimberley Science and Conservation Strategy, the Kimberley Marine Research Program is co-invested by the WAMSI partners to provide regional understanding and baseline knowledge about the Kimberley marine environment. The program has been created in response to the extraordinary, unspoilt wilderness value of the Kimberley and increasing pressure for development in this region. The purpose is to provide science based information to support decision making in relation to the Kimberley marine park network, other conservation activities and future development proposals.

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Front cover images (L-R)

Image 1: Satellite image of the Kimberley coastline (Image: Landgate)

Image 2: Isopora coral recruit on terracotta settlement plate (Image: AIMS)

Image 3: Humpback whale breaching (Image: Pam Osborn)

Image 4: Coral recruitment tiles on metal frame deployed at Hal's Pool, one of five locations in Cygnet Bay and the Sunday Island group (Image: AIMS)

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Executive Summary

Corals are an essential element of reef ecosystems, providing a structural framework for reef growth, habitat and food source for many other organisms. For benthic organisms like corals, sexual reproduction and the associated pelagic larval stage provides an opportunity for genetic mixing of populations and recovery from disturbances. In the inshore Kimberley, at Cygnet Bay and the Sunday Island group, reproductive and recruitment patterns for corals have not been previously studied. We modified existing, standardised methods of surveying coral larval supply, by attaching coral settlement plates to frames that enabled their deployment and retrieval from the surface, rather than by SCUBA divers. These frames were specifically designed to withstand the strong currents of the macro-tidal Kimberley environment.

A protocol of monthly sampling at 5 locations for a 13 month period was designed to discern temporal patterns in coral spawning and recruitment, identifying likely periods of mass spawning and background brooding. However, extreme water temperatures that persisted through summer and autumn culminated in a coral bleaching event that peaked in March-April, affecting between 30-60% of the community. The bleaching coincided with the predicted mass-spawning period, and reduced rates of recruitment for all corals, particularly for spawning corals. Given the duration and severity of the temperature anomaly, the quantified rates of recruitment are unlikely to reflect those during years without such stress. Nonetheless, the recruitment of *Acropora* peaked in March-April 2016 and to a lesser extent in September-October, at the same time as mass- and multi-specific spawning events documented on oceanic reefs in the Kimberley and in the Pilbara reefs to the south. Recruits from the family Pocilloporidae (comprising both brooders and spawners) and genus *Isopora* were more abundant in the summer months. Additionally, we provide the first definitive evidence of reproductive output and recruitment by corals in family Poritidae, which potentially include both brooding and spawning species, over many months throughout the year, supporting anecdotal evidence from reproductive studies at oceanic reefs in the region.

The number and composition of coral recruits differed considerably among the study locations, reinforcing the spatial heterogeneity evident in most studies of biological communities in the Kimberley. Fine-scale spatial heterogeneity also varied as expected among coral groups, with evidence of recruitment variation in brooding corals over distances of less than a few hundred metres, compared with tens of kilometres for groups of spawning corals. Continuation of sampling in future years would allow a further assessment of spatial and temporal variation in recruitment of corals at inshore Kimberley reefs, and presumably track the recovery of communities to background levels of recruitment following the bleaching disturbance.

Finally, during 2016 water temperatures were extremely high with the hottest sea surface temperature anomalies on record, resulting in widespread coral bleaching in northern Australia (Bureau of Meteorology 2017); this is likely to have impacted fish recruitment and survival (*e.g.* Pankhurst & Munday 2011), potentially leading to underestimates of typical recruit abundance in the Sunday Islands. Furthermore, interannual variability in recruitment is typically very high (Doherty 1991, Sampey et al. 2004, Trip et al. 2014). For these reasons, future monitoring examining recruitment processes in more detail, assess interannual variability and responses to local environmental drivers, is suggested.



1 Introduction

Corals are a critical component of reef ecosystems, providing a structural framework for reef growth, as well as creating habitats and acting as a food source for many species (Knowlton et al. 2010). Reefs of the inshore Kimberley, Western Australia, inhabit a unique environment, but have not been well studied and processes related to the coral life cycle are little known (Wilson 2013).

The movement of pelagic larvae and their subsequent settlement onto the reef (“recruitment”) is an important aspect of the life cycle of corals and other benthic organisms (Harrison & Wallace 1990). For these otherwise sessile organisms, which spend the remainder of their life attached to the reef, larval movement allows the offspring of coral colonies to spread into new habitats, or re-colonize areas where adult corals have been lost or damaged. Larval movement can also allow genetic mixing among populations, although the extent to which this occurs is highly variable (Underwood 2009).

Corals reproduce both sexually, by releasing gametes and/or larvae, and asexually, where fragments of the parent colony that are broken off grow to become new colonies (Harrison & Wallace 1990). In most cases, sexual reproduction is the dominant mode of reproduction among corals, and can be further divided into “spawners” (those which release unfertilized gametes into the water column) and “brooders” (where sperm is released, but eggs are fertilized inside the parent colony, and released as larvae) (Harrison 2011). For spawning corals, larvae routinely travel greater distances (up to 10s of km), than the larvae released by brooding corals, which are competent to settle shortly after being released (less than a few kilometres) (e.g. Berry (2016) and Underwood (2009)). The majority of corals reproduce by spawning, which often occurs during mass- or multi-specific spawning events, with many coral colonies from many species releasing sperm and eggs at the same time (Baird et al. 2009). In other off shore Kimberley reefs (e.g. Scott Reef, Rowley Shoals, Ashmore Reef) the main mass-spawning of the year occurs in autumn, with a smaller multi-specific spawning event in spring (Gilmour et al. 2009, Rosser 2013, Gilmour et al. 2016a, Gilmour et al. 2016b).

For coral communities, a regular influx of larval recruits is a key process for sustaining and renewing populations. Levels of recruitment influence both community structure and recovery times after a disturbance event (e.g. severe bleaching, disease, cyclone, pollution spill); as well as providing an indication of the reproductive health of the overall system (Bak & Meesters 1998). Recent efforts to understand recruitment processes have provided evidence that coral populations are often genetically localized and largely self-seeded at relatively small (<10s km) spatial scales (e.g. Berry et al. (2016), and Underwood (2009)), highlighting the crucial importance of local management. However, spatial patterns of larval supply and recruitment in corals vary considerably, due to the differing reproductive modes and larval duration among coral groups, the variation in large- and small-scale hydrodynamic conditions among sites, and differences in weather conditions throughout the period of larval dispersal. It is therefore important to investigate patterns of larval supply and recruitment at a range of nested scales.

The Kimberley region of Western Australia is diverse, extensive and unique, with coral reefs in the Kimberley facing a range of extreme conditions (Wilson 2013, Richards et al. 2015). In the inshore reefs, large tides drive strong, localized currents, which may act as a barrier to movement of larvae (Wilson 2013, Berry et al. 2016), contributing to the formation of extremely patchy habitat distributions. Large fluctuations in water temperatures, high turbidity and periodic exposure to cyclones are also likely to influence coral communities in this region (Richards et al. 2015, Schoepf et al. 2015). Despite extreme environmental conditions, diverse assemblages of corals have been documented in this region (Richards et al. 2015).

In addition to the typically extreme environmental conditions experienced by corals in the inshore Kimberley, high sea water temperatures in 2016, associated with El Nino conditions, resulted in the occurrence of coral bleaching in the Indian and Pacific Oceans, including extensive bleaching at some reefs in north-western Australia. Bleaching commenced in late March 2016 and continued through April, concurrent with the predicted mass spawning time for corals. Impacts were as expected, based on the NOAA temperature predictions and the history of severe bleaching during extreme El Nino conditions in 1998. In Western Australia, the offshore and

inshore reefs of the Kimberley region were affected. Variation in bleaching among the reefs was similar to that in 1998, but in 2016 the inshore reefs of the Kimberley bleached. At Cygnet Bay and the Sunday Island group, estimates of bleaching ranged from 19-40% (S. Wilson, unpubl. data).

Coral bleaching, as well as causing whole- and partial-colony mortality, can also affect the growth and reproduction of coral colonies at the time of bleaching (Baird & Marshall 2002, Ward et al. 2002, Negri et al. 2007). Post-bleaching, coral mortality may result in large reductions in recruit numbers for extended periods (several years) while surviving colonies regrow. At Scott Reef, an isolated offshore reef in the Kimberley region, extremely low recruitment was documented after the 1998 bleaching, with larval supply reduced by 94% for 6 years post-bleaching (Gilmour et al. 2013).

There are no studies of coral recruitment and very few data on coral reproduction for assemblages in the inshore Kimberley region (Gilmour et al. 2016a). Inferences of coral reproduction in the region are largely based on reproductive surveys during one or two years at a small group of islands within the Bonaparte Archipelago. The main season of spawning on inshore Kimberley reefs is probably during autumn (beginning of the dry season), but with a second multi-specific spawning also occurring during spring (beginning of the wet season) at a similar time to the oceanic reefs in the region. Of the species of *Acropora* sampled in spring ($n = 35$) and autumn ($n = 16$), 42% were inferred to spawn in spring and 87% in autumn. Of the 60 common non-*Acropora* species, there was evidence of only 5% spawning in spring and 7% in autumn (Gilmour et al. 2016a). Key knowledge gaps include an understanding of the timing of spawning and planulation for inshore Kimberley reefs, and the proportion of corals that brood or spawn.

Provided they are designed correctly, studies of coral recruitment can provide valuable insights into patterns of reproduction and larval supply. In turn, these data make a valuable contribution to management strategies, by providing a basis for understanding of future demographic trends and the spatial patterns of local and regional adult community structures. In the Kimberley region, pre-bleaching coral recruitment patterns are unknown; however, our monthly surveys throughout the period of bleaching provide a baseline from which to assess increases in post-bleaching recruitment and their relationship to the distribution and abundance of adult colonies. At the same inshore Kimberley reefs studied in several complementary WAMSI projects, at locations around Cygnet Bay and the Sunday Island group, we quantified rates of larval supply and recruitment to determine the main periods of reproductive output for spawning and brooding corals, and to identify any obvious sinks of coral recruitment among the reefs. Our spatially-nested design allowed us to examine the spatial scales over which recruitment processes vary. Quantifying levels of coral recruitment, and their spatial and temporal variation, provides an indication of the current health of coral communities in Cygnet Bay and the Sunday Island group.

2 Materials and Methods

2.1 Coral recruitment

2.1.1 Approach

We used coral settlement plates (“tiles”) to assess coral recruitment in the Cygnet Bay area and Sunday Island group, (e.g. Mundy (2000), Heyward et al. (2010), and Gilmour et al. (2013)). Settlement plates are pre-conditioned terracotta tiles (110 mm x 110 mm x 10 mm), which provide a standard-sized unit of artificial substrate for coral spat to settle on. Settlement plates were deployed for two months. One month is required for the tiles to become covered with a fouling community of natural biofilms and coralline algae that induces settlement in coral larvae (Morse et al. 1988, Heyward & Negri 1999, Harrington et al. 2004, Webster et al. 2004). The second month is required for settling larvae to excrete a calcium carbonate skeleton of sufficient size to be identifiable after tiles are retrieved and bleached. The experimental substrata and the schedule of deployment and retrieval are critical to obtain reasonable estimates of coral recruitment that are also comparable to other studies. By the time the settlement plates were retrieved, the coral spat were of a size that can be counted, and certain taxonomic groups identified, as in numerous previous surveys of coral recruitment in Western Australia.

In this study, we modified existing methods to suit the macro-tidal Kimberley environment, by placing tiles on a frame rather than attaching directly to the reef. Apart from the use of a frame, the methodology was the same so the data were comparable to most other studies of coral recruitment, particularly in Western Australia (e.g. Gilmour et al. (2013)). A previous study has compared recruit density between settlement plates attached directly to the substrate and to metal frames, and found that there was no difference between the two methods (Mundy 2000).

We designed, developed and tested steel frames which could be lowered from the surface, not requiring SCUBA diving, and could withstand the strong currents present at Kimberley reefs (see Figure 1). SCUBA diving was avoided due to the logistical difficulties of working underwater in this region (e.g. large tides and strong currents), the increased exposure to hazards associated with in-water work (exposure to Irukandji jellyfish, crocodiles), and to allow monthly tile changeovers to be conducted by the Bardi Jawi Rangers. The design allowed the frame to be hooked at the apex with a grappling hook, and pulled to the surface for existing settlement plates to be removed and replaced with new plates. The coral settlement plates were fixed to the frames using a threaded bolt and wingnut with a small plastic spacer underneath, to provide cushioning from impacts associated with raising and lowering the frames to and from the seabed, as well as preventing any movement or vibration resulting from the high current flows in the area which can interrupt settlement. Field testing of the frames was completed in March 2015, with the conclusion that the frames were suitable in high-current areas, and could be deployed and retrieved from the work vessel in use.

2.1.1 Study locations and habitats

Coral settlement plates were deployed on frames at five locations across Cygnet Bay and the Sunday Island group in October 2015 (see Figure 1). Locations chosen were subtidal, coral-dominated areas, which varied in coral cover, diversity and exposure to currents (Table 1). Of the 5 locations where frames were deployed, both Jalan and Jorrol experience very strong currents, with a steady flow even during neap tides. Jalan also had the highest overall coral cover and the greatest diversity in coral morphology (morphologies present included massive, tabulate, foliose corals); while Jorrol had the lowest overall coral cover of any location. Hal's Pool experienced moderate currents with little protection, and relatively low coral cover. Catamaran Bay was the most sheltered with minimal current, and coral diversity and abundance were second-highest of the locations (after Jalan). Shenton Bluff was protected from the incoming tide by a rocky outcrop, but experienced strong currents on the outgoing tide. Shenton Bluff also had relatively high coral cover (third highest, after Jalan and Catamaran Bay) but low diversity – corals present were primarily branching (staghorn) *Acropora* (95% of coral present) forming large patches. Catamaran Bay and Shenton Bluff both experienced high levels of sedimentation during the study period.

Habitat comparisons were made for each of the locations using images captured from remote underwater video (RUV) footage. Footage was recorded at five sites in the area around the recruitment tile locations, every eight weeks during the survey period, tide permitting. Habitat images were analyzed using visual estimates of dominant habitat type in a gridded image in Transect Measure (SeaGIS). Habitats were characterized by visually estimating the dominance of broad categories (hard coral, macroalgae) and morphology-based categories within each of the broad categories (for hard corals: branching, erect fine branching, erect coarse branching, columnar, encrusting, foliose/plate, massive, blue corals). Corals were also categorized as live or bleached. Bleached corals included those recently bleached and those with new filamentous algal growth on the bleached structure.

Additionally, surveys of coral bleaching were carried out in late March 2016. Areas of 2 m radius were examined at five locations (Shenton Pool, Shenton Bluff, Jorrol, Catamaran Bay and Jackson Island), three of which coincided with locations where coral recruitment tiles were placed (Shenton Bluff, Jorrol, and Catamaran Bay). Within the survey area, all coral colonies were identified to genus level and recorded as healthy, pale or bleached (Appendix 6, S. Wilson, unpubl. data). At each location, between two and 13 areas (each 2 m radius) were examined, depending on time constraints.

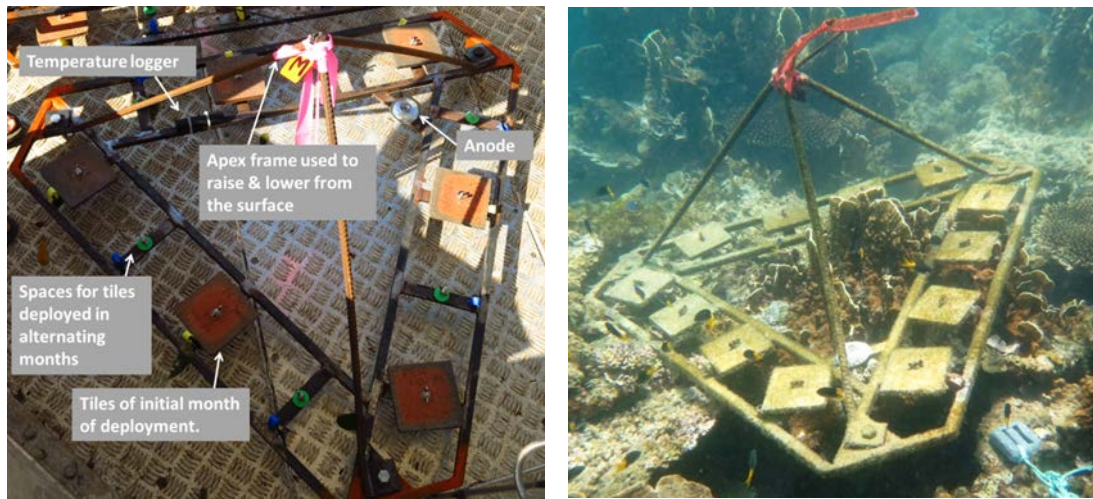


Figure 1. Coral settlement plates on metal frame ready for deployment (left); and deployed at Jalan, one of five locations in Cygnet Bay and the Sunday Island group. Settlement plates on frame have been deployed for one and two months, and are covered with turfing algae and biofilms, making the tiles suitable for coral settlement.

Table 1. Qualitative ranks of study locations based on site-wide observations coral cover, coral diversity (morphological types; e.g. massive, branching, tabulate), and exposure to current (Philip McCarthy and Camilla Piggott, pers comm).

Ranking	Coral cover	Coral diversity	Exposure to current
1 (highest)	Jalan	Jalan	Jalan
2	Catamaran Bay	Catamaran Bay	Jorrol
3	Shenton Bluff	Hals Pool	Hals Pool
4	Hals Pool	Jorrol	Shenton Bluff
5 (lowest)	Jorrol	Shenton Bluff	Catamaran Bay

2.1.2 Experimental design

The same experimental design was employed as in other coral recruitment studies by AIMS at WA reefs, making recruitment data following mass-spawning events comparable among studies. At each of the five study locations, three frames were deployed 50 m apart, each frame containing 12 tiles. Six tiles were retrieved and replaced each month with a staggered deployment pattern to allow a two month deployment period for each tile set and to ensure that tiles were always available with a suitable fouling community to induce larval settlement. This spatially nested design allowed us to examine differences in recruitment among various spatial scales, to examine the timing of coral settlement throughout the year, to capture predicted mass spawning periods and to record likely recruitment of brooded larvae over several months through the year. Dates of tile deployment and retrieval can be found in Table 2.



Figure 2. The locations of the coral frames in five coral-dominated areas in Cygnet Bay and the Sunday Island group. At each location, there are three frames each containing six tiles per month.

Table 2. Schedule of tile deployment and retrieval over the survey period (October 2015-October 2016). Scheduled deployment dates are 7-9 nights after full moon, to coincide with neap tides (conditions are most workable) and predicted coral spawning times.

Scheduled deployment dates (7-9 nights after full moon)	Deploying tiles labelled	Removing tiles labelled
5-7 Oct 2015	Month 01	-
3-5 Nov 2015	Month 02	-
3-5 Dec 2015	Month 03	Month 01
2-4 Jan 2016	Month 04	Month 02
1-3 Feb 2016	Month 05	Month 03
2-4 Mar 2016	Month 06	Month 04
31 Mar - 2 Apr 2016	Month 07	Month 05
30 Apr - 2 May 2016	Month 08	Month 06
29-31 May 2016	Month 09	Month 07
28-30 Jun 2016	Month 10	Month 08
27-29 Jul 2016	Month 11	Month 09
25-27 Aug 2016	Month 12	Month 10
23-25 Sep 2016	Month 13	Month 11
23-25 Oct 2016	-	Month 12
21-23 Nov 2016	-	Month 13

After being in place for two months, the tiles were removed from the frame and replaced with new tiles. The retrieved tiles were placed onto a metal rod, with foam spacers between each tile to prevent damage to any coral recruits. Rigid plastic squares at the ends of each rod (larger than the settlement plates) further protected the settlement plates from damage during preservation, storage and transport. The settlement plates were placed in seawater until preservation, when they were transferred to a chlorine solution which removed the coral tissue, leaving the coral skeletons behind. The tiles were then air-dried and packed for transport. Monthly tile deployments, collections and tile preservation were conducted by the Bardi Jawi Rangers. Later, the settlement plates were examined under a dissecting microscope and the coral skeletons counted and identified to the highest taxonomic resolution possible.

2.1.3 Sample processing and identification of coral recruits

Recruits on tiles were identified and grouped into those which could be reliably identified at this stage of development: *Acropora*, *Isopora*, Pocilloporidae, Poritidae and Other (AIMS 20??, Babcock et al. (2003)). Example photographs of the coral groups can be found in Figure 3; further examples can be found in Appendix 7. Of these, the genus *Acropora* are spawning corals, and the genus *Isopora* are brooding corals (Baird et al. 2009, Harrison 2011, Gilmour et al. 2016a). The members of the genus *Porites* (within the family Poritidae) that are known to occur in the inshore Kimberley are spawning corals (Veron 2000, Baird et al. 2009, Richards et al. 2014, Richards et al. 2015, Madin et al. 2016). Spawning also occurs in the genus *Pocillopora* of the family Pocilloporidae, but other genera of the same family (*Stylophora*, *Seriatopora*) are brooding corals (Baird et al. 2009, Harrison 2011, Gilmour et al. 2016a). Brooding and spawning species of the families Pocilloporidae or Poritidae could not be distinguished at this stage of growth (AIMS, (Babcock et al. 2003). The 'Other' group includes corals from all other families, which are likely to be mainly spawning corals, given that the majority of corals reproduce by spawning.

2.1.4 Data analyses

Variation in the abundance and composition of recruits among sites, locations and months, was explored through multivariate analyses of transformed (square root) data in the software PRIMER (Clarke & Warwick 2001). Data were averaged to explore the degree of variation in recruitment within and among locations, and among months throughout the year. A Bray-Curtis dissimilarity matrix was produced for each set of transformed and averaged data, and illustrated with a non-metric Multi-Dimensional Scaling (MDS) plot. A 5% metric weighting was applied to the non-metric analyses of variation in recruitment throughout the year to account for the relatively small differences among some months (e.g. winter) compared to others (e.g. April), and the tendency for groups to collapse on top of each other in multi-dimensional space. Vectors were overlaid on each plot to highlight the coral groups that best distinguished the patterns of recruitment in space or time.

To determine importance of various factors, i.e. month of the year and location, data was analysed in R (version 3.2.3, R Core Team (2015)), using a complete-subsets modelling approach where a complete model set was constructed and fitted using the appropriate statistical methods and subsequently compared using Akaike Information Criterion (AICc), AICc weight values (w_i) and R^2 (Burnham & Anderson 2002). Models were fitted using the GAM function in the mgcv package (Wood 2006), with the number of coral recruits modelled as a Tweedie distribution. We used GAMs rather than linear mixed models to allow for potential non-linear relationships between the response variable and the various continuous environmental predictors. Smoothing terms were fit with a cubic spline (Wood 2006), with the "k" argument limited to 5 (to reduce over-fitting and ensure ecologically interpretable monotonic relationships). Assumptions were evaluated using residual plots and found to be adequately met. Following standard convention, the simplest model within 2 AICc values of the model with the lowest AICc was considered the optimal model (Burnham & Anderson 2002). A null model consisting of only an intercept and the random factors was also included in the model set, to test if any of the included factors were indeed useful predictors. The relative importance of each variable (variable importance) was determined by summing the w_i values for all models containing the variable, with higher summed values

representing increased importance of that predictor to the response variable (Burnham & Anderson 2002).

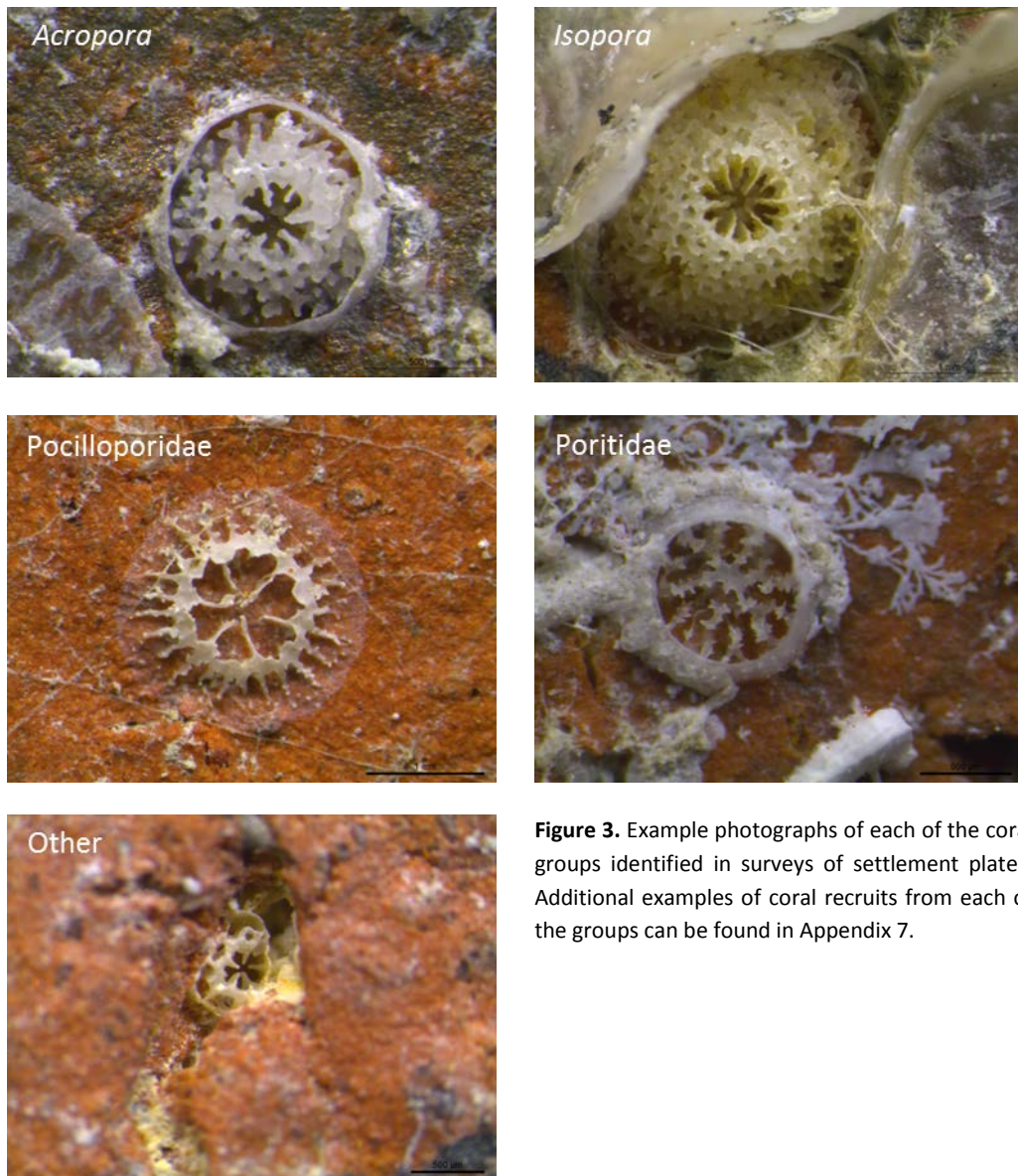


Figure 3. Example photographs of each of the coral groups identified in surveys of settlement plates. Additional examples of coral recruits from each of the groups can be found in Appendix 7.

3 Results

3.1 Coral recruitment

3.1.1 Summary of results

The number and diversity of coral recruits varied in both space and time (Figure 4). There was evidence of *Acropora* spawning at the same time (March-April) as the mass-spawning on most other Western Australian reefs, and at the same time (October-November) as the multi-specific spawning that occurs on the oceanic reefs of the Kimberley and at Pilbara reefs (Figure 4). Poritidae and particularly Pocilloporidae recruits were the most abundant and were present throughout the year, despite *Acropora* and *Isopora* being the most abundant adult

genera (Figure 4, Z. Richards, pers. comm.). However, the *Acropora* and *Isopora* are also among the most susceptible coral genera to bleaching, and their rates of reproductive output and recruitment were likely reduced by the temperature anomalies through summer and autumn (2016), that led to the bleaching of between 30-60% of the coral in the region.

For all five coral groups both month and location (10s km apart) consistently made important contributions to the observed variation in recruitment for all coral groups, but the relative importance of temporal variation (month) and small-scale (site within location; 50-100m) variation reflected their different reproductive modes (Table 3); temporal variation was more important for the spawning corals that recruit during discrete periods than for the brooding corals that recruit over several months, while variation among sites was more important for the brooding corals that have more localized dispersal and recruitment than the spawning corals. The results of this study are consistent with the general patterns of reproduction and recruitment observed at the oceanic reefs of the Kimberley and the Pilbara reefs to the south, while also providing the first definitive evidence of reproduction and recruitment of *Porites* over several months throughout the year.

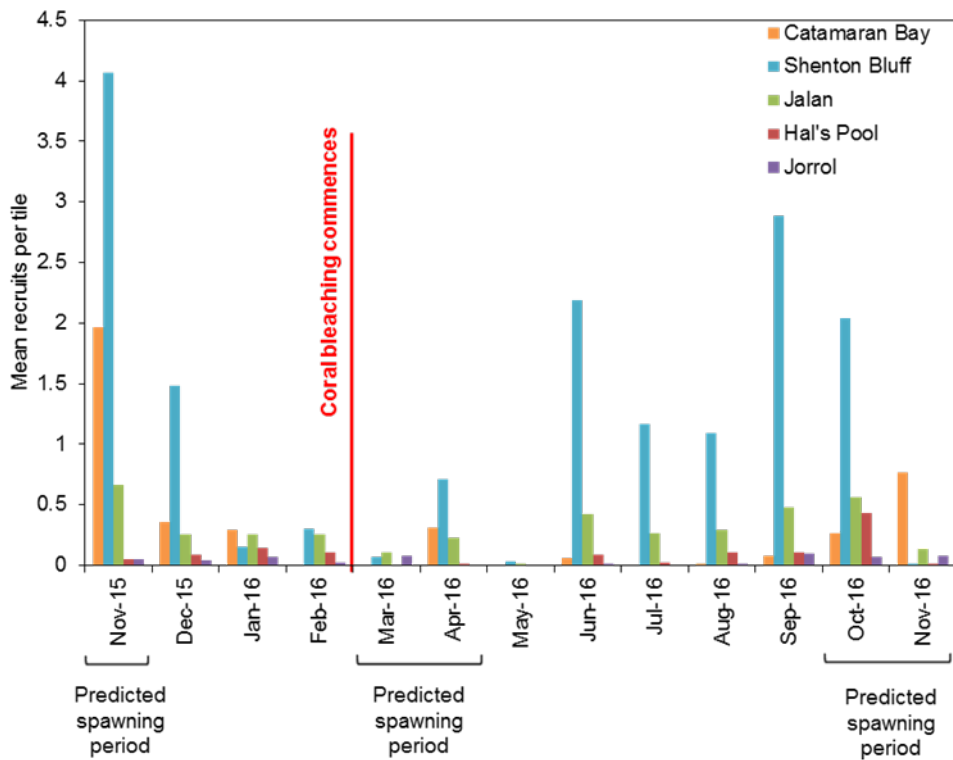


Figure 4. Mean coral recruits at each location over the months surveyed (all coral groups included). Time of coral bleaching event and predicted spawning times are indicated. Note Catamaran Bay tiles were not successfully retrieved in Feb-16 and Mar-16.

3.1.2 Temporal variation in coral recruitment

Recruitment at the inshore western Kimberley reefs displayed similar seasonal variation to that observed at other north-west reefs, but was also affected by severe temperature anomalies through summer and autumn in 2016 (Figure 5). Coral community surveys in late March quantified bleaching at locations surveyed for coral recruitment, ranging from 19% at Jorrol to 40% at Shenton Bluff (Figure 5). Bleaching was reported for all the families identified as recruits: Pocilloporidae (*Pocillopora*, *Seriatopora*, *Stylophora*), Poritidae (*Porites*, *Goniopora*), Acroporidae (*Acropora*, *Montipora*) and Others (Fig 6). The exception was the *Isopora*, which were

not present in the surveys quantifying bleaching, but this genus is typically among the most susceptible to temperature induced bleaching. The bleaching of coral communities was also evident in the broad habitat surveys through March (25%) to May (43%, Figure 5). The temperature stress, coupled with typically low recruitment during winter months, resulted in the lowest rates of recruitment occurring during May, with comparably little variation among the other winter months (Figure 4, 8).

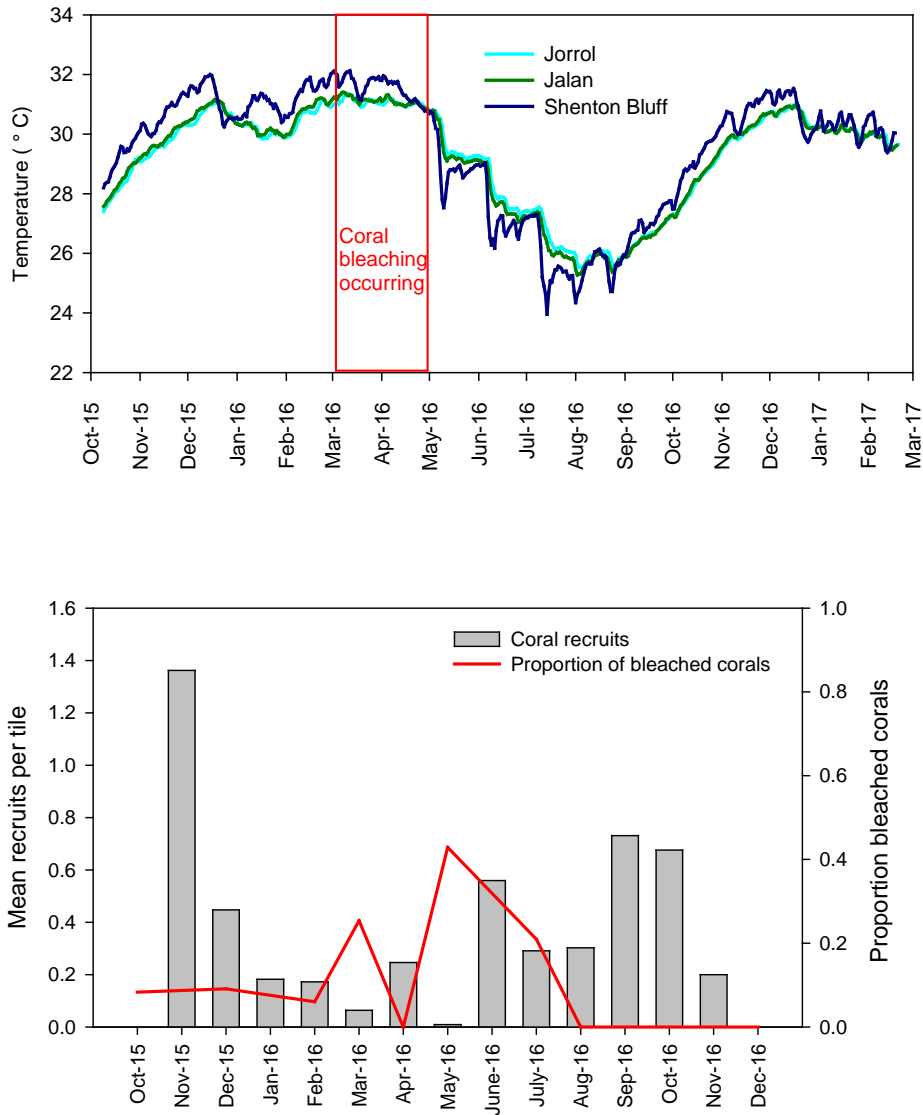


Figure 5. Average daily temperature data from loggers deployed alongside coral settlement tiles at Jalan, Jorrol and Shenton Bluff (top panel); and (bottom panel) variation in mean recruits over the survey period (for all locations and family groups), overlaid with observations of bleaching (proportion of bleached corals) from the habitat comparison. Note: In April 2016, bleaching observations were from 1 location only (Jalan).



Figure 6. Example images of bleached corals from bleaching surveys conducted in late March 2016, at 5 locations around Cygnet Bay and the Sunday Island group. Several different coral genera and families can be seen, bleached, in the images.

The low abundance of *Acropora* recruits overall ($n = 57$) may reflect the effects of temperature stress, given the bulk of their reproductive output probably coincided with the timing of the mass-bleaching in March and April (Figure 4, 5). However, the relative peaks in recruitment for the spawning *Acropora* occurred during March, April, and October, during the predicted period of mass- and multi-specific spawning, respectively (Figure 7, 9). At one location (Jalan), *Acropora* recruits were seen in February, in addition to March, April and October (Figure 7, 9). The peak in recruitment of spawning *Acropora* in autumn clearly differentiated the March-April period from other months through the year (Figure 9). The absence of *Acropora* recruits in November 2015 (Figure 7, 9), coupled with the high number of other recruits during that month, and the signal of spring spawning even after the bleaching on 2016, suggest that the *Acropora* may have participated in a multi-specific spawning in October,

prior to the commencement of this study (Figure 7). Full-subsets modelling of factors influencing recruitment revealed the best fitting model for this group included an additive effect of month of the year and location, with this model having a higher model weight and lower AICc than other models (Table 3, Figure 9). The impact of location did appear limited as the model with only month had an AICc within 2 (Table 3). Month appears to be highly important to *Acropora* colonies.

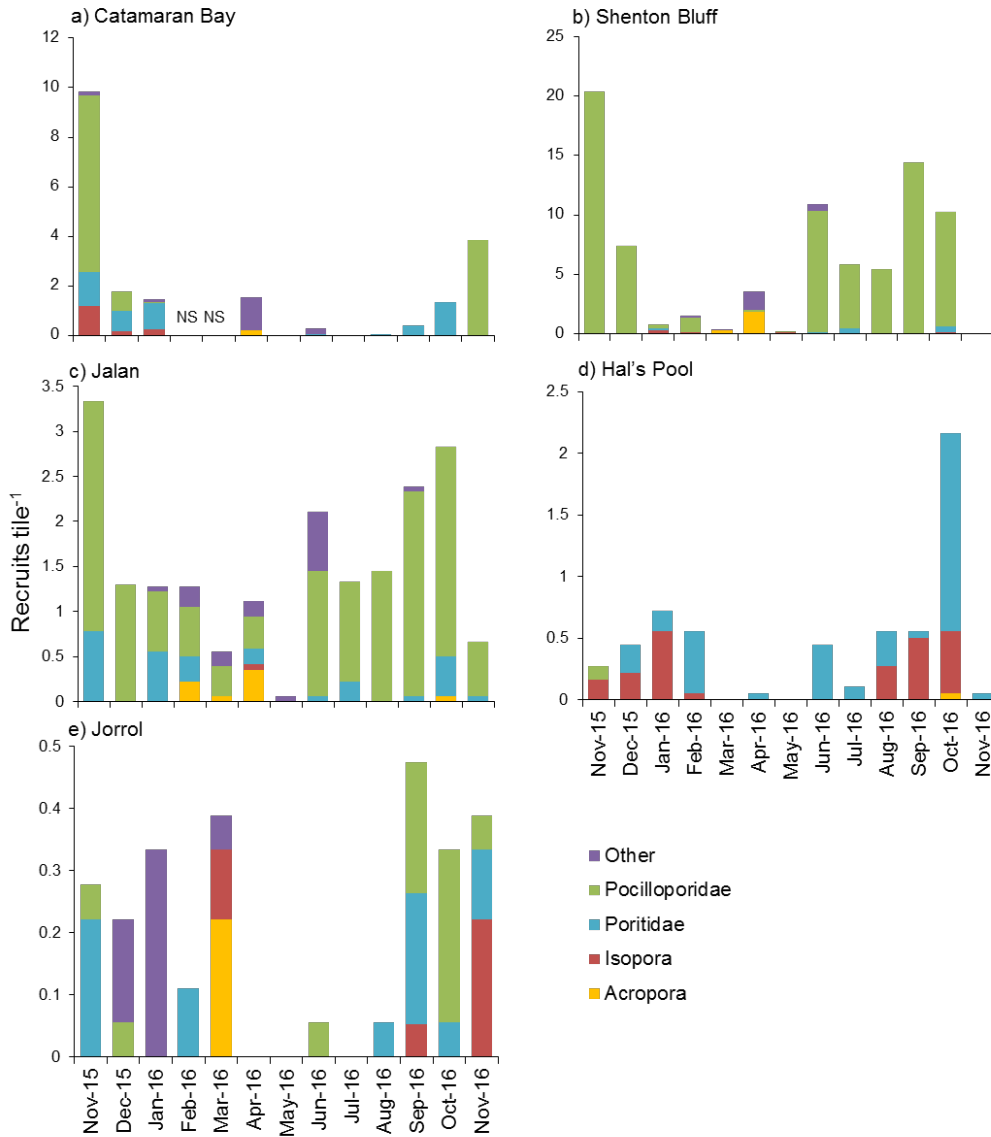


Figure 7. Mean coral recruits of the groups *Acropora*, *Isopora*, Pocilloporidae and Poritidae at each location. Note differing scales on the vertical axes. NS = Not surveyed; Catamaran Bay tiles were not successfully retrieved in 2 months (March and April 2016).

Apart from the *Acropora*, the Poritidae were the other family containing spawning corals, but their recruitment occurred consistently over many months of the year, rather than peaking during autumn and/or spring (Figure 7, 9). The Poritidae were the second most abundant ($n = 240$) group of recruits, after the Pocilloporidae, which also recruited over most months throughout the year and were by far the most abundant ($n = 1833$). The Pocilloporidae, which probably include both spawning (*Pocillopora*), and brooding (*Seriatopora*, *Stylophora*) species, had distinct peaks in recruitment during the summer months, as did the *Isopora*, which are exclusively

brooding corals and recruited in relatively low abundance ($n = 91$). Recruitment of *Isopora* was generally low and variable, and appeared to vary across all locations. The highest number of *Isopora* recruits were observed at Hal’s Pool (Fig 7, 9).

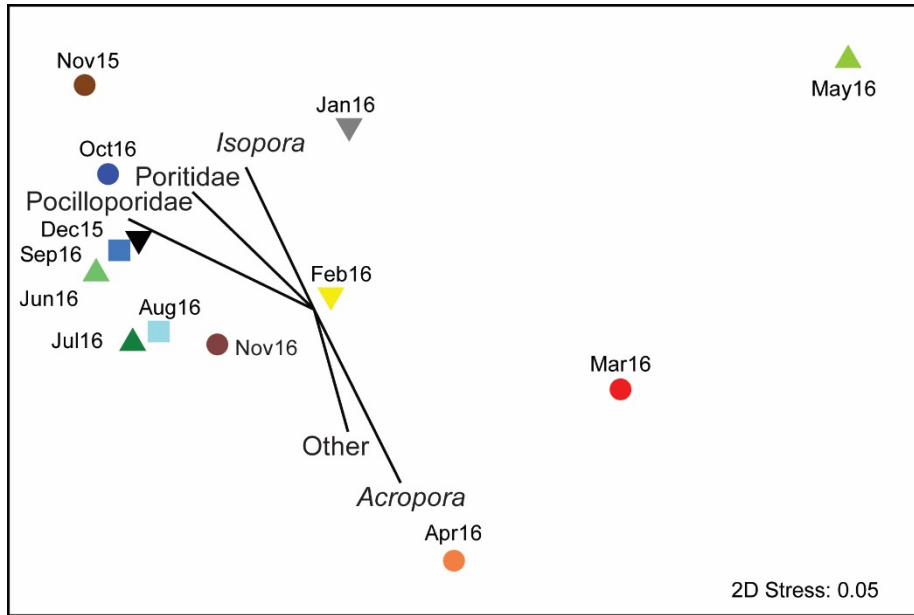


Figure 8. Multivariate plot of variation in the abundance and diversity of coral recruits among months throughout the year. Vectors highlight coral groups that distinguish the variation among months.

When conducting full-subsets analysis of factors influencing recruitment for Poritidae, it was apparent that recruitment was best described by an additive effect of month and location (Figure 9, Table 3). The model best describing recruitment of Pocilloporidae was a complex interaction between month of the year and location, along with additive impacts of location and site (Table 3, Figure 9). Recruitment of *Isopora* colonies was best described by an interaction between month and location, while site is included in the next best model (Figure 9, Table 3).

Based on relative explanatory values of the fixed predictors, month appeared to be the most important factor across all family groups (Figure 10). The number of Pocilloporidae recruits was most well explained by the model fits, and from this location had the largest impact on recruitment, followed by site and then month (Figure 10). For Poritidae, site had the largest impact on recruitment, followed by month and location (Figure 10). Corals grouped as “Other” were most impacted by month, followed by site and then location (Figure 10). *Acropora* recruitment was most impacted by month, followed by location and there was very limited impact of site. Lastly, *Isopora* recruitment was equally impacted by month, location and site, which all had limited impact (Figure 10).

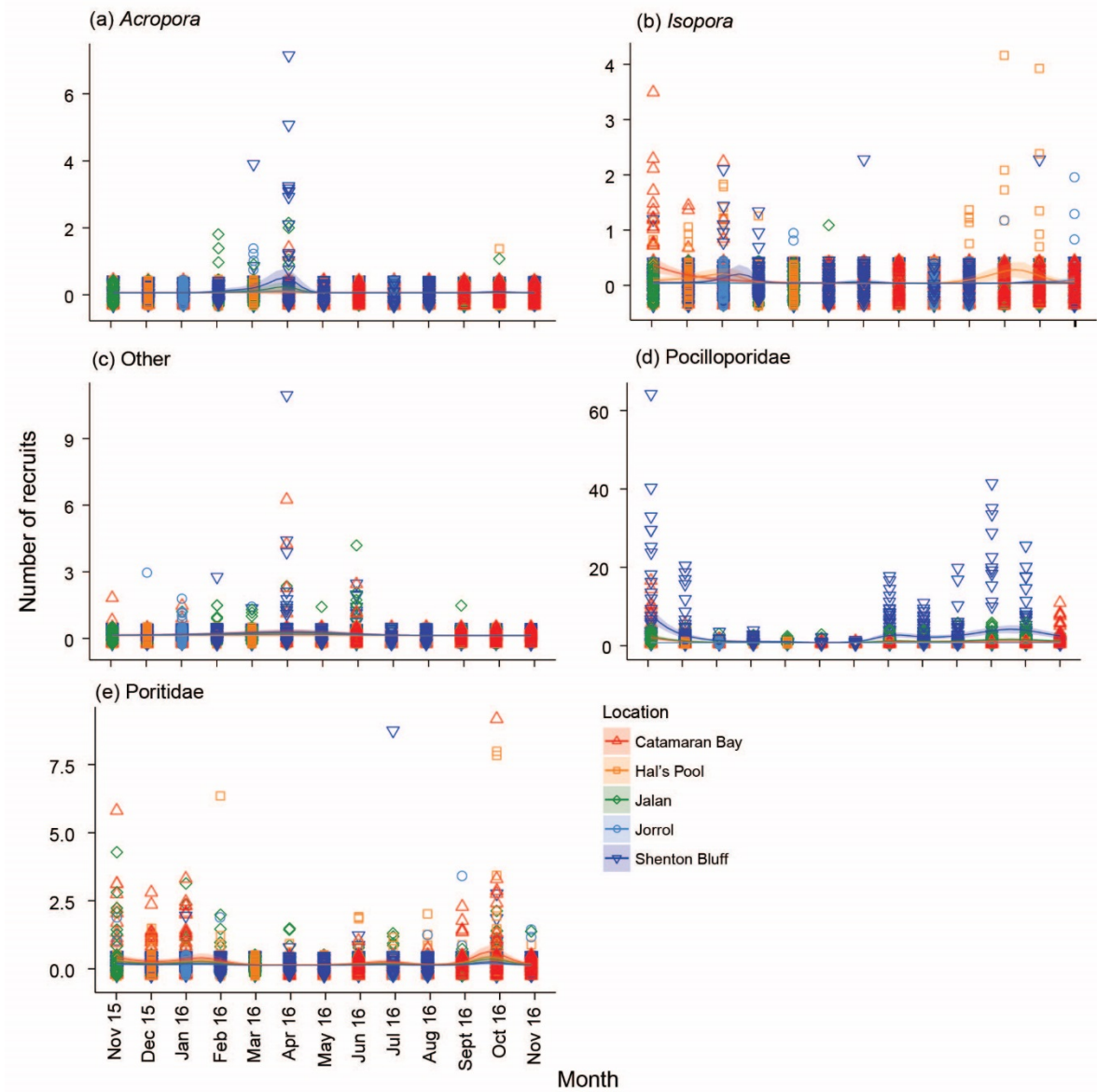


Figure 9. Number of settled recruits of (a) *Acropora*, (b) *Isopora*, (c) Other, (d) Pocilloporidae and, (e) Poritidae during each month at the 5 locations. Raw data (triangles) is presented with modelled relationships (lines) and 95% confidence intervals (ribbons).

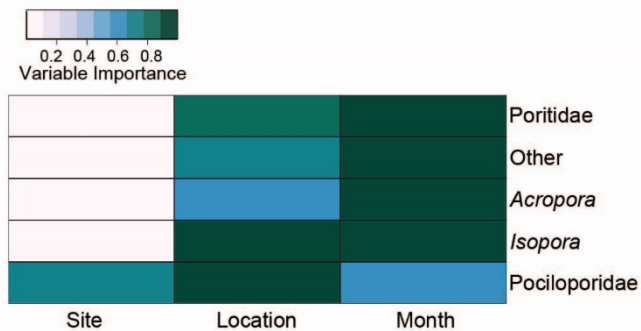


Figure 10. Variable importance of each of the fixed factors included in the models, including Month, Location and Site, with darker colours indicating increased importance of that variable.

Table 3. Top model fits (generalised additive model) for the number of settled recruits for each of the fixed factors, location and month of settlement. Shown are the fitted model, number of parameters (n), Akaike information criterion (AICc), δ AICc, model weights, and R^2 values. The model with the fewest parameters within 2 AICc is considered the most parsimonious, and therefore the best model.

Coral group	Model	n	AICc	δ AICc	AICc weight	R^2
<i>Acropora</i>	Month + Location	13	3409.31	0	0.64	0.01
	Month	9	3410.70	1.4	0.32	0.01
	Month x Location	19	3415.97	6.7	0.02	0.00
<i>Isopora</i>	Month x Location	23	3382.47	0	0.91	0.02
	Month + Site	27	3400.15	17.7	0.00	0.02
	Month + Location	13	3433.24	50.8	0.00	0.01
Other	Month + Location	11	3464.54	0	0.39	0.01
	Month	7	3467.14	2.6	0.10	0.01
	Month x Location	15	3467.55	3.0	0.08	0.01
Pocilloporidae	Month x Location + Location + Site	44	4972.63	0	0.35	0.23
	Month x Location + Site	44	4972.96	0.3	0.29	0.22
	Month x Location + Location	29	4973.21	0.6	0.26	0.21
Poritidae	Month + Location	15	3644.47	0	0.87	0.01
	Month x Location	21	3648.50	4.0	0.11	0.02
	Month x Location + Location	27	3653.48	9.0	0.01	0.02

3.1.3 Spatial variation in coral recruitment

Coral recruitment varied considerably among the five locations surveyed, and among the coral groups identified. Differences were apparent in both the numbers and families of recruits present on the tiles (Figure 7, 11). Variation among locations (10s km apart) was considerable, while there was comparatively little variation among sites (50-100 m apart, Figure 12). Variation among sites reflected variations in the local conditions (exposure, current speed) at each location, and the reproductive modes of the dominant recruits.

The five study locations differed considerably in the abundance and composition of recruits. Of all the locations, Jorrol had the lowest coral cover, the lowest proportion of hard corals (44%) and second lowest diversity of coral forms (Table 1). Coral recruitment was most unique at Jorrol (Figure 11, 12), having a very low abundance ($n = 48$), but relatively high diversity and proportional representation of coral groups: Pocilloporidae (27%), Poritidae (29%), Other (21%), *Isopora* (15%) and *Acropora* (8%). Hal's Pool was also distinguished by a low total abundance ($n = 107$) of coral recruits, but the sites had moderate cover (ranked 4th) and diversity (ranked 3rd) of corals, which composed 65% of the community. Recruitment at Hal's Pool was distinguished by a relatively high proportion of Poritidae (59%) and particularly *Isopora* (38%), and a very low proportion of *Acropora* (1%) and Pocilloporidae (2%).

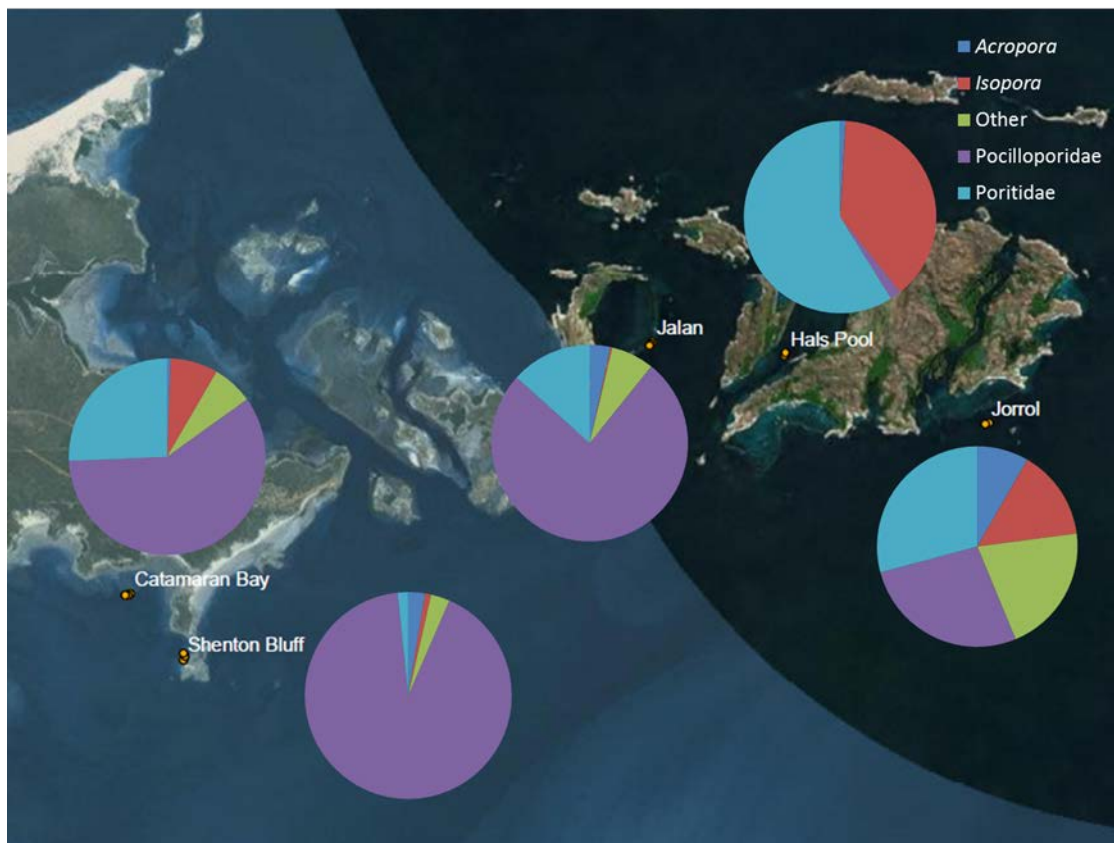


Figure 11. Overall composition of recruits at each location, from November 2015 - November 2016.

The remaining locations had large differences in the total number of recruits, but a similar composition of recruits that was dominated by the Pocilloporidae and with a mix of other coral groups (Figure 10). Shenton Bluff recorded the highest total number of recruits ($n = 1458$) of all locations, of which the majority were Pocilloporidae (92%). Shenton Bluff also had high coral cover, with a community that was dominated by hard corals (98%). However, the community had relatively low diversity because most of the corals were branching *Acropora*. Despite their dominance, only 2% of the recruits at Shenton Bluff were *Acropora*, and the remaining coral groups (*Isopora*, Poritidae, Other) were also in low abundance (<3%).

Catamaran Bay had a high total number of recruits ($n = 358$), and the sites had a high cover and diversity of hard corals that dominated (93%) the community. The Pocilloporidae were the most common (58%) group of coral recruits, with the Poritidae (26%) and particularly the *Isopora*, Other and *Acropora* recruits in low or very low abundance (<8%). Jalan also had a high total number of recruits ($n = 352$), and a high cover and diversity of corals (Table 1); although the abundance of macroalgae at the location in December 2015 and August 2016 resulted in corals composing only 55% the community throughout the year. The Pocilloporidae were again the most common (76%) group of coral recruits, with the Poritidae (13%) and other groups (<7%) in low abundance

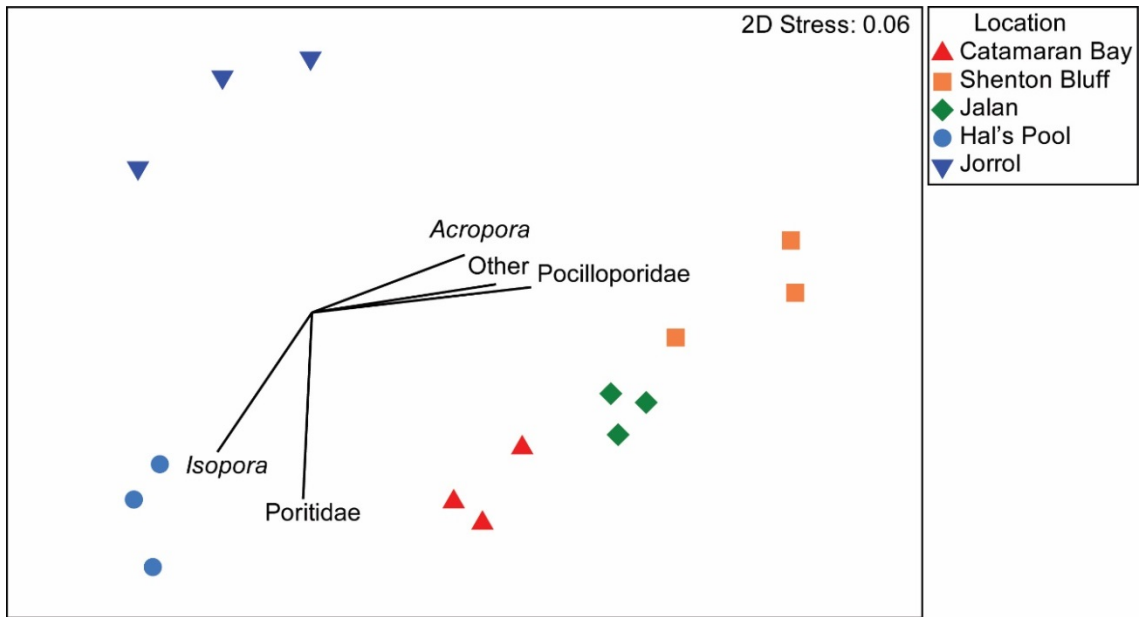


Figure 12. Multivariate plot of variation in the abundance and diversity of coral recruits among locations, and sites (within locations). Vectors highlight coral groups that distinguish the variation among locations and sites.

4 Discussion and Conclusions

Unusually high temperatures in early 2016 resulted in an unprecedented coral bleaching event in the Cygnet Bay area and Sunday Islands group (Fig 5, 6). At our study locations, estimates of bleaching ranged from 19-40% in late March, with higher overall proportions of bleaching recorded later in May (43%, Fig 6). The months March and May were associated with very low total recruit numbers, which coincided with the highest proportion of bleached corals. Recruit numbers in the months following the bleaching were not obviously reduced in comparison to pre-bleaching, possibly because temperature stress through summer had already stressed corals and reduced their reproductive output prior to the mass bleaching. Around half the corals had not bleached and continued to produce recruits over the following months. Whether recruitment rates in the months before and after the mass-bleaching were lower than in the absence of temperature stress remains unknown. Temperature stress and coral bleaching has been shown to reduce reproductive output in corals for up to two years (Michalek-Wagner & Willis 2001) and above (Baird & Marshall 2002). Therefore, it is important to interpret these results in the context of this study occurring during an exceptional year. To establish an understanding of the typical recruitment patterns of the region, sampling during multiple additional years would be necessary, as inter-annual variation in coral recruitment is common (Harriott & Banks 1995, Dunstan & Johnson 1998).

Recruits settling on tiles were most commonly from the family Pocilloporidae, followed by Poritidae. Adults from these families were recorded at all locations surveyed (S. Wilson, unpubl. data), however they were not the most common adult genera (*Acropora* and *Isopora* were observed to be the most common adult genera, Z. Richards, pers. comm.). However, the *Acropora* and *Isopora* are also among the most susceptible to temperature stress and coral bleaching. The extreme temperatures that persisted through summer and autumn most likely caused prolonged stress, injury and mortality to the *Acropora* and *Isopora*, reducing their reproductive output and recruitment for much of the study period.

Acropora recruits (produced by spawning) were present at the times of predicted spawning, in March-April and October-November, although we did not detect a large pulse of *Acropora* recruits, as would be expected from a mass, multi-specific spawning event. As the time of predicted spawning occurred after coral bleaching conditions began, the reproductive output of *Acropora* (and other corals) during this year may have been abnormally low due to temperature stress. However, *Acropora* recruits were present only in these months, plus in February at one location (Fig 7), providing evidence that spawning events do occur at the same times of year as other Western Australian reefs. The absence of *Acropora* recruits in November 2015 suggests that the *Acropora* may have spawned in the previous month, before the beginning of the surveys. Repeating the surveys in additional years would assist with determining whether our observed results were within the normal range, or reduced due to temperature stress.

March and April were clearly differentiated from other months, with *Acropora* numbers driving the difference (Fig 8). Modelling also showed that Month was the most important factor affecting numbers of *Acropora* recruits (Table 3, Fig 9), reflecting the prevalence of synchronous spawning within this coral genus. This suggests that in other years (when coral bleaching does not occur), spawning would likely occur primarily in March-April, and secondarily in October-November. Corals in the 'Other' group were also most abundant in April (Fig 9), and were likely predominantly spawning corals, given that the majority of corals do reproduce by spawning. This aligns with the mass spawning events documented in other Kimberley reefs (Gilmour et al. 2009, Heyward et al. 2010). Further reproductive sampling would be necessary to determine the species and proportion of colonies which participate in either spawning event; we are unable to determine this from our results given that recruits cannot be identified to species level.

The month of May was the most different from other months (Fig 8), with virtually no recruits of any type recorded during this month (Fig 4, 9). This coincided with an increased proportion of bleached corals (quantified by habitat comparison, Fig 5). It is likely that the decreased numbers of recruits in May were a result of temperature stress associated with coral bleaching. Additionally, winter months (June, July, August) were grouped together (Fig 8). There was a trend towards lower recruit numbers during winter in some of the coral

groups (Pocilloporidae, *Isopora*), although other groups reproduced during winter. On other WA reefs, there is little evidence of reproductive output and spawning through winter months (Gilmour et al. 2016a).

Pocilloporidae reproduced mainly during the summer months (Fig 7, 9), over several months. The model best describing recruitment of Pocilloporidae was a complex interaction between month of the year and location, along with additive impacts of location and site (Table 3, Fig 9). This pattern of reproduction is similar to that expected for brooding corals, with recruitment affected by local population structure at smaller scales than for brooders, although the family Pocilloporidae contains both brooding (genera *Seriatopora* and *Stylophora*) and spawning corals (genus *Pocillopora*), which could not be separated reliably at this stage of development. All three of these genera were recorded in at least one of the study locations (S. Wilson, unpubl. data), so further reproductive sampling would be required to determine whether the recruitment patterns represent brooding corals releasing larvae monthly, spawning occurring in multiple months, or a combination of brooders and spawners reproducing at different times throughout the year.

Recruits from the family Poritidae were present throughout the year, including during winter (Fig 7, 9). This was reflected by the increased importance of location, compared to *Acropora*, in the best model (Fig 9, 10). Previously, spawning in the *Porites* has only been documented over the summer months in Australia (Kojis & Quinn 1981, Harriott 1983, Stoddart et al. 2012). *Porites* corals are known to spawn in early December in Dampier (Stoddart et al. 2012). However, additional spawning at another time was possible, as colonies were not sampled throughout the year (September-December only), although nearly all *Porites* colonies (92%) sampled did have mature oocytes prior to the December spawning (Stoddart et al. 2012). Studies on the Great Barrier Reef have also recorded *Porites* spawning in December (Harriott 1983), and in another case spawning occurred over several months during summer (November-April, Kojis and Quinn (1981)). Conversely, our data suggests corals from the family Poritidae reproduce throughout the year in the Cygnet Bay and the Sunday Island group. However, we are not able to differentiate between recruits produced by spawning over multiple months, and those produced from brooded larvae, as recruits could only be identified to the family level.

Most corals in the family Poritidae reproduce by spawning, but there are exceptions which brood larvae (Madin et al. 2016). Of the Poritidae, two species known to be brooding corals, *Porites murrayensis* and *P. stephensoni* (Madin et al. 2016) have recently been identified in the inshore Kimberley (Z. Richards, pers. comm.). This suggests that brooding corals within the family Poritidae may exist around Cygnet Bay and the Sunday Island group, and some of the recruits documented in this study may be a result of brooded larvae. Our results, where recruits from the family Poritidae were found during months when spawning has not been documented, suggest that brooding larvae could be an important means of reproduction in this coral family. Further reproductive sampling would be required to confirm the relative importance of each reproductive mode (brooding larvae vs spawning gametes) within the Poritidae in the inshore Kimberley region.

Isopora recruit numbers were low and variable (Fig 7, 9). Recruits were mainly present in the summer months, and were most common at Hal's Pool (Fig 7, 9). Recruitment of *Isopora* colonies was best described by an interaction between month and location, while site is included in the next best model (Fig 9, Table 3). This is consistent with the classification of *Isopora* as a brooding coral (Fig 9). The factors location, month and site explained only low, but equal, amounts of variance in the model (Fig 10). As a brooding coral, *Isopora* recruits generally travel a relatively short distance (<500m) from the parent colony, which has been recently confirmed in the inshore Kimberley (Berry et al. 2016). For brooding corals like the *Isopora*, variation at smaller spatial scales is often expected to be more important than for spawning corals, as seen in our results, although the amounts of variance explained by the model were low.

In conclusion, these results demonstrate the variation in larval supply among months, coral groups and at various spatial scales (from 10s of kilometres to 50-100 metres). Assessing coral recruitment with extended monthly sampling over more than a year-long period confirmed predicted patterns of recruitment for spawning corals (March-April and, to a lesser extent, October-November spawning periods, as for other Western Australian reefs), and revealed that coral recruits from some groups were settling during more months than expected (Poritidae during the winter months). Temperature stress associated with a coral bleaching event during the year

likely affected the numbers of recruits occurring in some months, particularly during the predicted spawning period in March-April, and also in May, so sampling in additional years would likely yield different results.

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