Coral larval recruitment in north-western Australia predicted by regional and local conditions

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A R T I C L E   I N F O

A B S T R A C T

Understanding ecological processes that shape contemporary and future communities facilitates knowledge-based environmental management. In marine ecosystems, one of the most important processes is the supply of new recruits into a population. Here, we investigated spatiotemporal variability in coral recruitment at 15 reefs throughout the Dampier Archipelago, north-western Australia between 2015 and 2017 and identified the best environmental predictors for coral recruitment patterns over this period. Large differences in recruitment were observed among years with the average density of recruits increasing by 375% from 0.017 recruits cm^{-2} in 2015 to 0.059 recruits cm^{-2} in 2017. Despite differences in recruitment among years, the rank order of coral recruit density among reefs remained similar among years, suggesting that spatial variation in recruitment within the Dampier Archipelago is partly deterministic and predictable. The density of coral recruits was best explained by percent cover of live corals at both local (within 5 m) and meso-scales (within 15 km), water turbidity and an oceanographic model that predicted larval dispersal. The highest density of coral recruits (~0.13 recruits cm^{-2} or 37 recruits per tile) occurred on reefs within sub-regions (15 km) with greater than 35% coral cover, low to moderate turbidity (KD490 < 0.2) and moderate to high modelled predictions of larval dispersal. Our results demonstrate that broad-scale larval dispersal models, when combined with local metrics of percent hard coral cover and water turbidity, can reliably predict the relative abundance of coral recruits over large geographical areas and thus can identify hotspots of recruit abundance and potential recovery following environmental disturbances; information that is essential for effective management of coral reefs.

1. Introduction

Recruitment is a key ecological process in the formation and maintenance of populations. For marine organisms with a dispersive phase, recruitment relies on the supply of planktonic larvae and their ability to settle, metamorphose and survive (Connell 1985). Recruitment, defined here as the successful settlement and survival of coral larvae until eight weeks post settlement (Ritson-Williams et al., 2009), is therefore determined by not just the density of incoming larvae (Cameron and Harrison 2020), but the availability of suitable habitat (Sampayo et al., 2020), active larval behaviour during settlement (Gaines and Roughgarden 1985; Gaines et al., 1985) and environmental conditions that influence the early growth and survivorship of larvae (Babcock and Mundy 1996; Gosselin and Qian 1997; Baird and Hughes 2000). Recruitment is typically variable across a range of spatial and temporal scales and although patterns established at recruitment may be modified by other demographic processes (e.g., post-settlement survival bottlenecks: Doropoulos et al., 2017), recruitment variability remains a major determinant of adult assemblage structure (Done 1982; Connell 1985; Connell et al., 1997) that underpins the recovery of many coral populations (Holbrook et al., 2018). Accordingly, understanding causes of recruitment variation remains a priority in marine systems.

On coral reefs, recruitment variability at the reef or local-scale (i.e. <5 km) is particularly important, because this is often the scale at which coral reefs are managed, marine reserve boundaries are designated (Sobel and Dahlgren 2004) and larval connectivity is investigated (Cowen and Sponaugle 2009; Hock et al., 2014; Feng et al., 2016; Boschetti et al., 2020). Identifying reefs with consistently high rates of recruitment relevant to other locations (i.e. recruitment hotspots), is important for optimising conservation outcomes because populations on these reefs will likely recover quicker following disturbance (Holbrook et al., 2018; Boschetti et al., 2020) and may maintain higher species richness if there is ongoing recruitment of multiple species. From a management perspective, identifying reefs with consistently high and low levels of recruitment is also important because it helps with the prioritisation of reefs for differing conservation outcomes (Sobel and Dahlgren 2004; Game et al., 2008).

Despite considerable effort to understand the role of larval dispersal in driving patterns of coral recruitment among reefs, the relationship is complex, especially in nearshore environments where larval dispersal is difficult to predict due to interactions between environmental variables such as wind, tide and geomorphology (Harrison and Wallace 1990; Banks and Harriott 1996; Connolly and Baird 2010; Feng et al., 2016). The complex nature of these interactions has led to the development of numerical models which aim to predict patterns of larval dispersal and coral settlement over varying spatial scales (Sammarco and Andrews 1989; Crabbe and Smith 2003; Connolly and Baird 2010; Feng et al., 2016). Arguably, one of the most successful attempts to model dispersal of coral larvae was conducted over thirty years ago by Sammarco and Andrews (1989) who accurately predicted high recruitment at sites where eddies were likely to form and persist. However, validation of the model was spatially restricted (5 km) and conducted entirely at off-reef locations (i.e., moorings over sand at depths of 15–18 m), hence applicability to reef-scale coral recruitment remains equivocal. The lack of suitable field validation of larval dispersal models continues to impede our understanding of the role of mesoscale factors (10's to 100's km) in driving variability in coral recruitment (Crabbe and Smith 2003; Radford et al., 2014; Kool and Nichol 2015).

Our ability to predict reef-scale patterns in coral recruitment is further limited by uncertainty around the relative importance of meso-scale (i.e., hydrodynamics, regional brood stock, temperature) versus local scale factors (i.e., local broodstock, reef complexity, surface orientation, depth) on observed patterns of coral recruitment. Variation in coral recruitment at multiple spatial scales is well documented (Sammarco and Andrews 1989; Fisk and Harriott 1990; Hughes et al., 2000; Turner et al., 2018) and is attributed to complex interactions between factors pre- and post-settlement. Pre-settlement processes typically act at mesoscales and include the abundance and fecundity of broodstock and large-scale hydrodynamics (Sammarco 1994; Eagle et al., 2012). Post settlement processes typically act at local scales and include light availability, substrate type and orientation (Carleton and Sammarco 1987), turbidity (Fabricius 2005; Evans et al., 2020), competition for space (Bak and Engel, 1979; Mundy and Babcock, 2000), predation (Trapon et al., 2013), and the presence of adult conspecifics (Vermeij 2006). Patterns in recruitment are also likely to vary among corals with different modes of reproduction and/or dispersal. In particular, larvae of brooding corals often have shorter dispersal distances than those of broadcast spawning corals. Accordingly, the scale at which environmental parameters influence supply of recruits is expected to differ among corals with different reproductive strategies. For example, the abundance of adult broadcast spawning corals is often a poor predictor of recruitment over larger scales (>10 km) (Davidson et al., 2019; Eagle et al., 2012; Hughes et al., 1999), whereas the presence of adult conspecifics can promote aggregated recruitment at small scales (<1 m) (Carleton and Sammarco 1987; Mundy and Babcock 2000; Vermeij 2005). Disentangling the relative importance of meso-versus local-scale interactions on patterns of coral recruitment therefore remains a priority to inform predictive modelling (Boschetti et al., 2020;

Feng et al., 2016; Kool et al., 2015).

Here, we investigate the relative importance of a range of meso- and local-scale predictors on coral recruitment throughout a coastal archipelago over a three-year period. Specifically, we describe spatio-temporal patterns in coral recruitment throughout the Dampier Archipelago north-western Australia. The Archipelago represents one of the most diverse regions for hard corals in Western Australia and has been identified as an area of high conservation value and possible World Heritage Area site (CALM 1994). The region is subject to strong cross-shelf gradients in turbidity, wave exposure and ocean temperatures (Moustaka at al. 2019) and as such presents a unique opportunity to investigate the importance of meso-versus local-scale interactions on patterns of coral recruitment. Moreover, an oceanographic dispersal model has been developed for the region (Feng et al., 2016), though it is unclear how well this model relates to field estimates of coral recruitment. Our aims were to 1) identify reefs with consistently high or low levels of coral recruitment 2) identify the best spatial predictors of coral recruitment 3) assess the importance of mesoscale (i.e., larval dispersal model, regional turbidity and coral cover) versus local scale (reef structural complexity, depth and local coral cover) influences on recruitment and 4) validate larval dispersal model predictions for the region.

2. Methods

2.1. Site description

The study region consists of a group of inshore islands (<20 km from the mainland coast) that extends from Cape Preston to Legendre Island off the north-western coast of Western Australia, henceforth referred to as the Dampier Archipelago (Fig. 1). The Dampier Archipelago is characterised by 12 large islands and 30 small islands or shoals, most with fringing reefs (Semeniuk 1982). The region experiences low annual rainfall (mean = 306 mm.yr^{-1}) and associated terrigenous sediment and nutrient input is minimal, due to the absence of significant riverine or freshwater inputs (Wilson et al., 2019). However, large tidal ranges (max 5.1 m, mean 1.9 m), combined with a wide shallow continental shelf and numerous narrow island passages, can produce tidal currents in excess of 0.5 ms^{-1} (Pearce et al., 2003). Suspended sediment loads are accordingly variable and are strongly influenced by the prevailing conditions of wind and tide. Suspended sediment loads on reefs within the region typically vary from 0.7 mg.L^{-1} (offshore locations) to 2.6 mg. L^{-1} (nearshore locations during large tides) (Pearce et al., 2003). Cyclones are common between November and March (mean = 0.6 cyclones per year) and typically result in dramatic but relatively short-lived (days) increases in freshwater input, turbidity and wave generated currents (Griffith 2004). The region has significant commercial development, including the world's second largest bulk export port facility, regular dredging programs, and ongoing commercial vessel traffic for the export of iron ore, salt, natural gas, and cargo (Wilson et al., 2019).

The region is influenced by large-scale oceanographic currents, including the southwesterly-flowing Holloway current, which transports warm, clear, oligotrophic waters to the northernmost reefs between March and September (Semeniuk 1982). These reefs include those adjacent to Kendrew Island, Rosemary Island, Hammersley Shoal and Legendre Island, where the influx of clear oceanic waters results in generally low turbidity (Fig. 1). In contrast, the nearshore waters surrounding East Lewis, Goodwyn and Regnard islands are characterised by high levels of turbidity and reduced water clarity (Moustaka et al., 2019).

Well-developed coral assemblages occur throughout the Dampier Archipelago with 229 scleractinian coral species from 57 genera and approximately 18,300 ha of suitable reef habitat (Griffith 2004). Coral cover and composition vary markedly throughout the region with the highest coral cover and diversity on mid-shelf reefs, and cover of broadcast spawning *Acropora* corals highest on reefs closer to shore
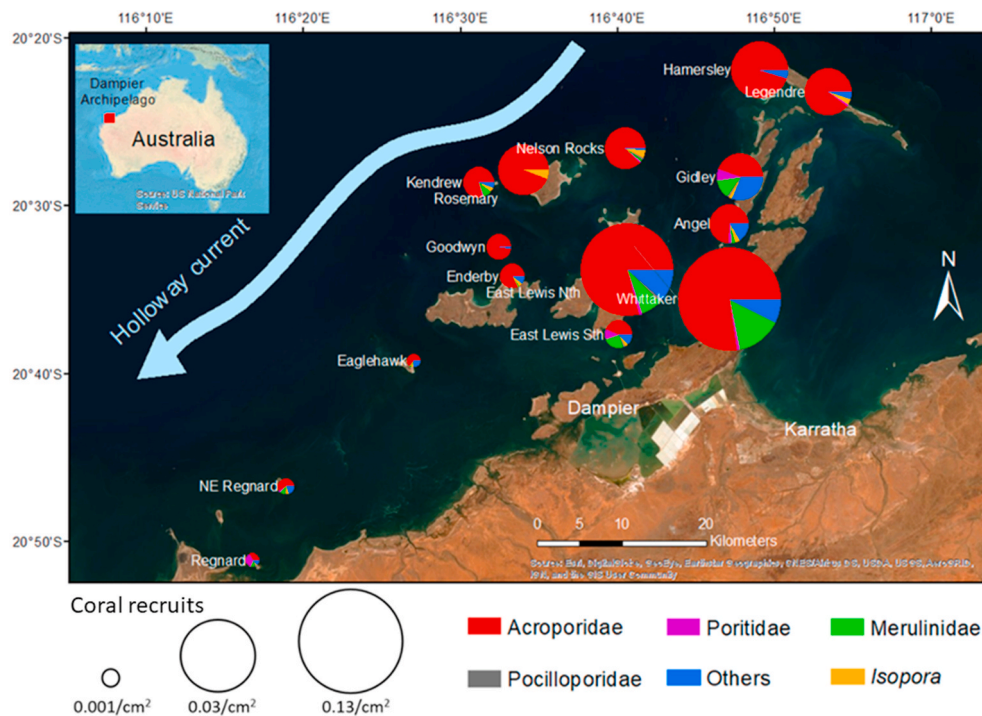
Fig. 1. Location, mean density, and composition of coral recruits at the 15 reefs within the Dampier Archipelago between 2015 and 2017. Symbol size represents the mean recruitment density (individuals/cm^2) and colours show the different coral groups. The blue arrow represents the predominant flow direction of the Holloway current. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

(Blakeway et al., 2013; Moustaka et al., 2019). Coral recruitment patterns throughout the region are poorly understood; however, a recent review of coral reproductive patterns in Western Australia suggest that between 60% and 70% of coral species occurring within the Dampier Archipelago spawn during the austral autumn (March–April) (Gilmour et al., 2016).

2.2. Spatial and temporal patterns in recruit abundance

The abundance of coral recruits was recorded annually from 2015 to 2017 at 15 reefs within the Dampier Archipelago (Fig. 1). Reefs were selected throughout the Dampier Archipelago such that they were well distributed spatially, encompassed a range of dispersal model predictions (low, medium and high predicted recruitment) (Feng et al., 2016) and supported well-developed coral assemblages (i.e., >10% cover and >10 coral genera; authors pers obs.). At each reef, 15 unglazed terracotta tiles ($11 \times 11 \times 1$ cm) were deployed on stainless steel mounting plates (Babcock and Mundy 1996) and distributed randomly within an area of approximately 10×10 m. Individual tiles were deployed at a constant depth within each reef, with a target depth range of between 6 and 9 m. However, due to a lack of well-developed coral assemblages at 6–9 m at Enderby Is, Regnard Is, Hammersley, East Lewis South and Nelson Rocks (i.e., >10% cover and >10 genera), tiles at these reefs were deployed at a depth of 4 m. To minimise movement and/or dislodgement of the tiles, care was taken to ensure that the tiles were attached to the solid reef matrix and free from abrasion by macroalgae. Tiles were deployed four weeks prior to the predicted autumn coral spawning (over 4 days in February or March) and then retrieved eight weeks after the spawning period (over 2 days in May or June). On retrieval, organic material was removed from the tiles using chlorine bleach and the tiles were dried and examined under a stereo microscope following Mundy (2000). The abundance and family of coral recruits on each tile was recorded, with recruits allocated to one of six groups (Acroporidae, Merulinidae, Pocilloporidae, Poritidae, *Isopora* spp and 'other') based on the distinguishing characteristics described in Babcock

et al. (2003). Acroporidae, Merulinidae and Poritidae recruits were classified as spawners and Pocilloporidae and *Isopora* recruits were classified as brooders, as per the dominant reproductive modes described in Gilmour et al. (2016). Due to logistical and weather constraints, all 15 tiles were unable to be retrieved from all locations in all years (see electronic supplementary material, Table S1), in which case reefs were only included in the analysis if more than 10 tiles were retrieved that year.

Spatial and temporal patterns in the abundance of coral recruits were examined using permutational multivariate analysis of variance (PERMANOVA for Primer v7©, Anderson 2008). Differences in total coral recruitment was investigated among reefs and years using a 2-way PERMANOVA. Differences among years (2015, 2016, 2017) for each coral group (spawners, brooders and coral families) were investigated using 1-way PERMANOVA's with pair-wise comparisons to identify in which years recruitment differed for each coral group. *Isopora* were not examined separately due to low numbers. PERMANOVA's were based on a Bray Curtis dissimilarity matrix of square-root transformed abundance data. Differences in the rank order of reefs among years were tested using a Friedman Rank test using the mean density of recruits per reef (cm^{-2}) in XLSTAT 2020.

2.3. Predictors of coral recruitment

Generalised additive mixed models were used to assess the relative importance of local (local total hard coral abundance, local brooder abundance, local spawner abundance, reef complexity, substrate type, depth) and mesoscale variables (dispersal model, total hard coral abundance, brooder abundance, spawner abundance, turbidity, mean sea surface temperature (SST)) on coral recruitment (see electronic supplementary material, Table S2). A full-subsets approach was used to fit all possible combinations of variables, whilst limiting models to three explanatory variables to avoid difficulty in interpreting results (Kleiber and Zeileis 2008; Fisher et al., 2018). Reef and year were included as random effects to increase the inferential power of the model (Harrison

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2014). Response data (i.e. density of coral recruits) was not transformed as selecting an appropriate error distribution (in this case a tweedie distribution) accounted for non-normal data distribution. Predictor variables were transformed to reduce the skewness where appropriate. Models containing variables with correlations exceeding 0.28 were excluded to avoid issues with collinearity among predictor variables (Graham 2003; Fisher et al., 2018). The model with the lowest Akaike Information Criteria corrected for small sample size (AICc) was selected as the best model and other models within two AICc (ΔAICc<2) of the 'best' model were considered. R^2 values across the full set of models were used to provide an indication of the predictive power of the model and an index of variable importance across the full set of models was calculated by summing the AICc weights for all models containing each variable (Burnham et al., 2011). Statistical analyses for identifying predictors of spatial variation in coral recruitment were conducted using the R language for statistical computing (version 3.6.3), and the FSSgam (version 1.11), gamm4 (version 0.2–6) and mgcv (version 1.8–31) packages (Wood 2011; Fisher et al., 2018; Wood and Scheipl 2019).

2.4. Larval dispersal model

Predicted numbers of coral larvae that were competent to settle were obtained for the Dampier Archipelago using a two-dimensional larval dispersal model on a 1 × 1 km grid (see Feng et al., 2016). The larval dispersal model is based on the three dimensional Regional Ocean Modelling System hydrodynamic model (ROMS; Marchesiello et al., 2003) and provides predictions of the total number of competent coral larvae settling each year across a 1 × 1 km grid by incorporating hydrodynamics with the development and settlement characteristics of larvae from a typical broadcast spawning coral (i.e., *Acropora millepora*, Feng et al., 2016). Coral recruitment predictions were obtained for the 15 study reefs for the years 2015–2017 from the grid point closest to the study reef; hereafter referred to as dispersal model predictions. A known limitation of the dispersal model predictions is the lack of consideration of variability in coral density on individual reefs, with equal numbers of larvae released on reefs throughout the model domain (see Feng et al., 2016 for details). For this reason, we incorporated coral cover metrics at varying spatial scales in our predictors of coral recruitment.

2.5. Percent cover of hard coral and reef complexity

Percent cover of live scleractinian (hard) corals and reef structural complexity were measured annually at increasing distance from the study reefs (3 spatial scales): 5 m, 200 m and 15 km. Within 5 m of the recruitment tiles, estimates of percent coral cover were obtained from high resolution photographic mosaics of the substratum. A GoPro4™ was used to capture overlapping images of the substratum (≈200 images per site), which were then combined to construct a two-dimensional photo mosaic with the structure from motion software Agisoft™ (Pedersen et al., 2019). Forty photos were randomly selected from each photomosaic and the percent cover of scleractinian (hard) coral recorded using six fixed points per photograph using the software Transect Measure (www.seagis.com.au). Reef complexity was estimated using the ratio of linear distance to the contoured surface distance of a 10 m length of chain carefully moulded to the reef surface within the 10 × 10 m study area (following McCormick 1994).

To estimate percent cover of hard coral at larger spatial scales (i.e., within 200 m and 15 km of the recruitment tiles) coral cover was quantified along replicate 50 m transects. At each reef three transects were situated at fixed locations (permanent markers) with the first transect commencing immediately adjacent the recruitment tiles. Transects were oriented end-to-end (separated by 5 m), parallel to the reef edge and along the same depth contour as the recruitment tiles. Transects were surveyed at least once annually, with transects at six reefs surveyed twice in the same year (January and May 2015 and 2017) and percent cover and reef complexity of all transects averaged for that year. Photographs were taken by divers at 1 m intervals along each transect (50 photographs per transect) at a height of ~0.5 m above the substratum (~0.28 m² per photo). Forty photos were randomly selected within each transect and the percent cover of scleractinian (hard) coral genera recorded using six fixed points per photograph using the software Transect Measure (www.seagis.com.au). Points were evenly spaced across the height and width of the image to provide a mean point density of approximately 14 points per m², sufficient to provide reliable descriptions of percent coral cover from photo transects (Dumas et al., 2009). Corals were assigned to genera using the updated coral taxonomy from Richards (2018) and then assigned as either broadcast spawners or brooders using the dominant reproductive mode described in Gilmour et al. (2016). Percent cover of corals and reef complexity within 200 m and 15 km of recruitment tiles was calculated by averaging all percent cover and reef complexity measurements within 200 m (3–6 transects) and 15 km radius (6–24 transects) of each study reef for each year (See Table S1 for further details).

2.6. Environmental data

Environmental data were collected for each reef using a combination of techniques. Mean KD490 (diffuse attenuation coefficient at 490 nm KD2 algorithm; hereafter referred to as turbidity) and degree heating weeks (DHW) were retrieved from NOAA's ERDDAP data server (Dataset ID: nesdisVHNSQkd490Daily and NOAA_DHW, respectively; see S5 for details). KD490 represents the MODIS diffuse attenuation coefficient at 490 nm with a KD490 value of 0.1 equating to an attenuation depth of 10 m. Higher KD490 values generally reflect higher turbidity, lower water clarity and more rapid attenuation of light with increasing depth but is susceptible to overestimation in shallow water due to bottom interference (Zhao et al., 2013). Water depth was recorded by divers at each reef to the nearest 0.5 m and adjusted for current tidal conditions using tide tables sourced from the Australian Bureau of Meteorology. http://www.bom.gov.au/oceanography/projects/ntc/wa_tide_tables.shtml.

3. Results

3.1. Temporal and spatial patterns in recruit densities

Mean densities of coral recruits varied among reefs (PERMANOVA, reef: p = 0.001) from a low of 0.0002 recruits cm⁻² in 2016 at Regnard to a high of 0.273 recruits cm⁻² at Whittaker Island in 2017 (Fig. 2; ESM Table S3). Recruit densities varied widely among years (PERMANOVA, year: p = 0.001, ESM Table S3), the lowest density occurring in 2015 and the highest in 2017 (Figs. 2 and 3a), increases being largely consistent among reefs (PERMANOVA, reef x year: p = 0.067, ESM Table S3). Despite the large variability in recruitment among reefs the rank order of recruitment among reefs was consistent among years (Friedman, χ2 = 4.9, df = 2, p = 0.086; ESM Table S4). Recruitment was typically highest at Whittaker Island (0.12 recruits cm⁻²) and East Lewis North, with some of the highest rates of recruitment across the study period recorded at these reefs in 2017 (Fig. 2). Conversely, coral recruitment at Eaglehawk, Regnard, NE Regnard and Enderby Islands did not exceed 0.008 recruits cm⁻² across the three years (Fig. 2).

Temporal differences in coral recruitment among years (Fig. 3a) were largely driven by increases in broadcast spawning corals (Acroporidae and Merulinidae) that had substantially higher recruitment in 2017 compared to 2015 and 2016 (Fig. 3c–e). In contrast, brooders and Pocilloporidae groups recruited in highest densities in 2016, while Poritidae recruited in similar densities across all years (Fig. 3b,f,g; ESM Table S5).

3.2. Predictors of recruitment

Percent hard coral cover (15 km) and turbidity were the best
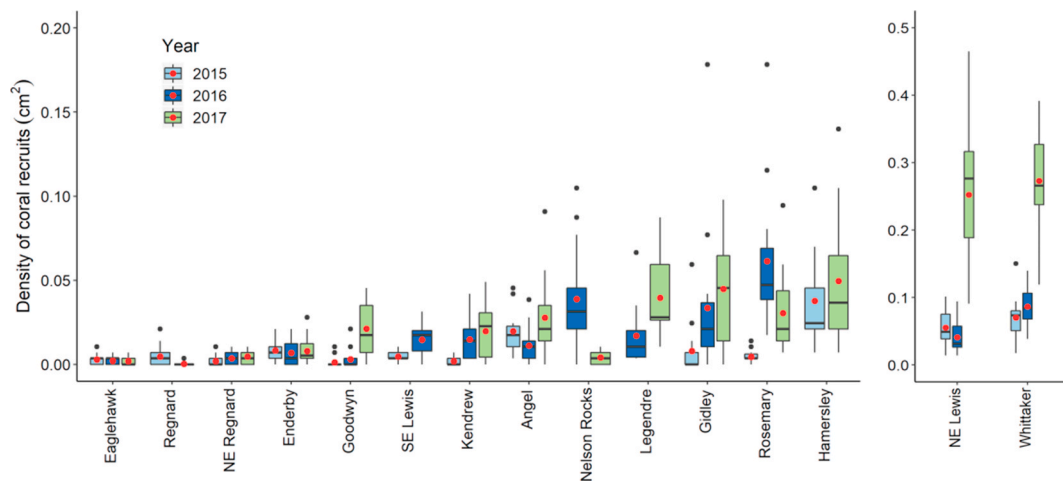
Fig. 2. Box plots showing the mean (red dot), median (horizontal line), quartiles and outliers (box and black dots) of recruitment density (individuals/cm²) in 2015, 2016 and 2017 at the 15 reefs throughout the Dampier Archipelago. Reefs are ranked in order from lowest to highest mean recruitment density. Due to logistical and weather constraints, all 15 tiles were unable to be retrieved from Regnard Is, South East Lewis Is, Nelson Rocks, Legendre Is. and Hammersley all years, resulting in recruitment data for two years. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)
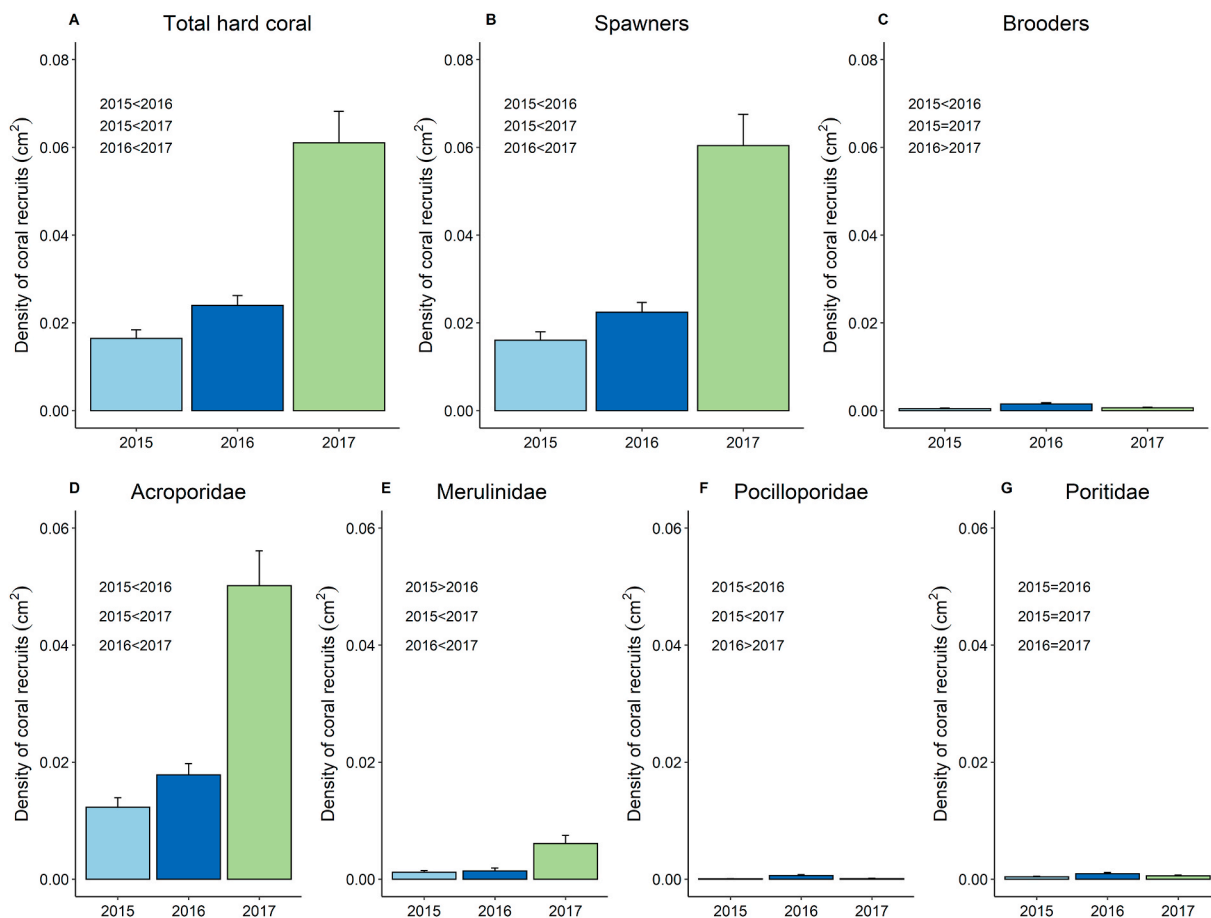

Fig. 3. Mean density of recruits (+SE) observed in 2015, 2016 and 2017 at the 15 reefs throughout the Dampier Archipelago between 2015 and 2017 for (a) total recruitment (b) total spawners (c) total brooders (d) Acroporidae, (e) Merulinidae (f) Pocilloporidae and (g) Poritidae. Y-axis scales for Acroporidae, Merulinidae, Pocilloporidae and Poritidae are adjusted to illustrate yearly variations.

predictors of total coral recruitment density over the three years, though there were several other models that had similar explanatory power (Fig. 4, ESM Table S6). Percent hard coral (15 km) was a particularly good predictor of total coral recruitment and was included in all of the top models (ESM Table S6). Highest coral recruitment densities were

observed on reefs with greater mesoscale hard coral cover, low turbidity and high dispersal model predictions (ESM Table S6, Fig. S1).

The best predictors of recruitment for the spawners and Acroporidae were the mesoscale variables hard coral cover (15 km), turbidity and the dispersal model (Fig. 4), with trends between these groups and best
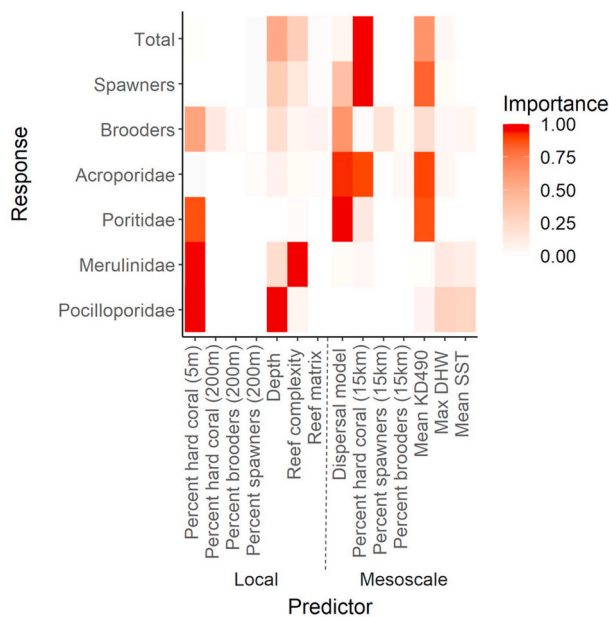
Fig. 4. Variable importance across the full subset of generalised additive mixed models of coral recruitment in the Dampier Archipelago. DHW = Degree Heating Weeks, SST = Sea Surface Temperature.

predictors being similar to those observed for total coral recruitment. In contrast, the best predictors of recruitment for brooders, Merulinidae, Poritidae and Pocilloporidae groups were a combination of mesoscale (i. e., dispersal model and turbidity) and local scale (i.e., local hard coral cover, depth and reef complexity) variables (Fig. 4, ESM Table S6). High recruitment densities of brooders, Merulinidae, Poritidae and Pocilloporidae were observed on reefs with greater than 25% local hard coral cover (5 m), whilst recruitment densities at lower coral cover were highly variable (ESM Fig. S1). Overall, mesoscale variables explained more variation in coral recruit densities than local scale variables (Fig. 4), featuring in all top models (ΔAICc<2) for all response variables with the exception of Pocilloporidae (ESM Table S6). Turbidity (i.e., KD490) was included in eight of the fourteen top models (ESM Table S6), however, the relationship between recruitment and turbidity was variable and sensitive to two outlying datapoints which represented reefs with very high turbidity (see ESM Tables S6 and 7 for further details).

4. Discussion

Despite an almost 4-fold difference in coral recruitment among years, variation in the relative rates of recruitment among reefs was temporally consistent, indicating recruitment in the Dampier Archipelago is partly deterministic and predictable. For example, two reefs in the north-east of the Dampier Archipelago (Whittaker and North East Lewis) had consistently high coral recruitment, while four reefs in the south-west of the archipelago (Eaglehawk, Regnard, North East Regnard and Enderby) had consistently low coral recruitment for all three survey years. These results corroborate previous studies which suggested recruitment patterns recur at the reef scale because oceanographic currents interact with local topography in a seasonally consistent way (Alldredge and Hamner 1980; Wolanski and Hamner 1988; Sammarco 1991; Oliver et al., 1992). Accordingly, we found that the dispersal model explained a moderate amount of the variation in recruitment, particularly for Acroporidae and broadcast spawning corals more generally. Spatially consistent patterns in the recruitment of spawners and brooders have been previously recorded in the central Indian Ocean (Adjeroud et al., 2007), the Great Barrier Reef (Sammarco 1991; Eagle et al., 2012) and the Caribbean (Sammarco 1985), while other studies have recorded

congruous spatial patterns in just brooders (Glassom et al., 2004). The limited temporal extent of our study (i.e., 3 years) prevents us from identifying drivers of variance among years, but identifying reefs with consistently high rates of recruitment relevant to other locations remains a high priority for optimising conservation outcomes, because the regular arrival or recruits to these reefs may promote quicker recovery following disturbance (Boschetti et al., 2020).

The best predictors for coral recruitment over the three years included percent hard coral (at 15 km and 5 m), indicating links between recruitment and adult abundance over different spatial scales for different coral families and reproductive modes. High recruitment of broadcast spawning corals such as Acroporidae and Merulinidae (>0.03 recruits cm^{-2} or 10 recruits per tile) occurred on reefs with greater than 35% mean coral cover within 15 km, while high recruitment of brooders, Pocilloporidae and the broadcast spawning Poritidae occurred when local coral cover (within 5 m) was greater than 25%. The importance of coral cover at differing spatial scales may be driven by the development times of larvae. Local retention of larvae (recruitment) is expected to be high in brooding taxa, as brooded larvae are capable of settlement immediately on release and often settle near conspecifics (Vermeij 2005) and closely related adults (Vermeij and Sandin 2008; Doropoulos et al., 2015). The positive relationship we observed between recruitment of brooders and local coral cover (5 m) supports this hypothesis. Similarly, the positive relationship we observed between recruitment of spawners and coral cover at mesoscales (15 km) suggests similar mechanisms may operate for more widely dispersed larvae over larger scales.

Positive stock-recruitment relationships have been observed in spawning corals following catastrophic mortality events (Gilmour et al., 2013; Lukoschek et al., 2013) with the recovery of these reefs driven by recruitment of locally sourced larvae (within 15 km). Two additional plausible mechanisms for the positive stock-recruitment relationships in the Dampier Archipelago include enhanced rates of settlement in regions with higher coral cover due to higher larval densities (Heyward et al., 2002; Suzuki et al., 2012; Doropoulos et al., 2018), and/or better post settlement survival of larvae in locations where adults are abundant due to favourable environmental conditions. Regardless of the mechanism, the links between recruitment and adult abundance over different spatial scales suggests high rates of larval retention within the Dampier Archipelago during our study period. These findings are supported by connectivity models for the region, which found high rates of larval retention within the Dampier Archipelago most years (dispersal distances <10 km) (Kool and Nichol 2015; Feng et al., 2016; Boschetti et al., 2020), and genetic studies which found generally low levels of genetic similarity between corals in the Dampier Archipelago and those located 130 km to the southwest at Ningaloo Reef (Underwood et al., 2013; Evans et al., 2018).

Numerous recruitment models have aimed to disentangle the complex nature of meso- and local-scale interactions on reefs. (Connolly and Baird, 2010; Sammarco and Andrews, 1989; Crabbe and Smith, 2003; Feng et al., 2016). Recent advances in hydrodynamic modelling (i.e. reef scale resolution, Feng et al., 2016), bathymetry mapping and the incorporation of larval behaviour characteristics into models (i.e. minimum, peak and maximum competency periods) (Connolly and Baird 2010) have resulted in substantial improvements in model predictions of coral recruitment on reefs over the last 30 years. However, our results indicate that adult abundance at both the local and mesoscales were generally better predictors of recruitment than the larval dispersal model. That said, when the larval dispersal model was combined with simple metrics such as percent hard coral cover and water turbidity, it provided good predictions of the relative abundance of coral recruits over large geographical areas. Future dispersal models may be improved through the inclusion of emerging information on the effects of other environmental variables on the behaviour and ecology of coral larvae. For example, temperature can influence pelagic larval duration of marine species, including corals (O'Connor et al., 2007), and are likely to

alter dispersal patterns as sea temperatures increase (Figueiredo et al., 2014). Given that post-settlement survival of coral recruits are likely to be dependent on local environmental conditions (Fitzhardinge 1988; Babcock and Mundy 1996; Baird and Hughes 2000; Chong-Seng et al., 2014; Evans et al., 2020), future recruitment models aiming to identify reefs with consistently high (hot-spots) and low recruitment of corals should aim to incorporate a range of local and mesoscale environmental factors.

A 375% increase in the density of recruits between 2015 and 2017 suggest that mesoscale environmental conditions became more favourable for recruitment over the study period. Inter-annual variability in patterns of coral recruitment are well documented (Harrison and Wallace 1990; Harriott and Banks 1995; Harriott et al., 1997; Hughes et al. 1999, 2019) and are typically attributed to differences in oceanographic conditions (e.g. current patterns, water temperature), adult coral abundance and/or reproductive output (Hughes et al., 2019). Consistent with the influence of large-scale hydrodynamics, we found increases in the dispersal model predictions on most reefs (13 of 15) and a strong shift toward La Niña conditions between 2015 and 2017 (see ESM Table S8). Recruitment rates of some fish, coral and crayfish are positively correlated with the Southern Oscillation Index (SOI) in coastal western Australia, with higher recruitment recorded during La Niña years, when the ENSO-influenced Leeuwin Current is stronger and sea surface temperatures higher (Pearce and Phillips 1988; Lenanton et al., 2009; Wilson et al., 2018). Connectivity models for north-western Australia have also revealed large changes in oceanographic conditions around the same time as the autumn coral spawning period, with the predominant current direction in the dispersal model changing from a north-easterly direction to a south-westerly direction in mid to late March (Feng et al., 2016). Given that the predicted time of spawning between 2015 and 2017 varied by 16 days (14 March to 2 April) it is likely that the predominant current direction differed among years and may have influenced the direction of larval dispersal and/or immediate post-settlement survival of recruits. Changes in mesoscale oceanographic conditions between 2015 and 2017 may also have led to increased fecundity of corals and subsequent recruitment (Hughes et al. 2000, 2019), but this was not measured.

Turbidity (KD490) was among the best predictors of recruitment and showed a weak negative effect on total recruitment and the recruitment of broadcast spawning corals, particularly the Acroporidae. Turbidity is known to be critical during the early lifecycle phases of broadcast spawning corals (Jones et al., 2015), with high turbidity associated with negative impacts on egg fertilization, settlement and metamorphosis (Babcock and Davies 1991; Humanes et al., 2017). High turbidity is typical on inshore reefs in the Dampier Archipelago (Moustaka et al., 2019) and recent observations of coral recruitment 120 km to the southwest of our study found high recruitment to tiles on turbid inshore reefs (Evans et al., 2020), suggesting that the effect of turbidity on coral recruitment is variable. The lack of a strong relationship between coral recruitment and turbidity in the present study may be due to differences in coral species among sites, the insensitivity or tolerance coral species in this region to turbid water, or the use of KD490 to estimate turbidity. KD490 is a good indicator of water clarity in clear oceanic waters (Zhao et al., 2013) but is susceptible to overestimation in shallow water due to bottom interference (Zhao et al., 2013). KD490 also fails to capture information on the size and/or type of particles in the water column and the intensity of acute turbidity events (https://eastcoast.coastwatch.no aa.gov/cw_k490_hires.php), both of which can influence coral settlement and early survival (Babcock and Davies 1991; Jones et al., 2015). The relationships between coral recruitment and turbidity identified in this study were also heavily dependent on two outlying datapoints (Regnard Is. 2015, 2016). When these two datapoints were removed from the analysis turbidity was no longer included in the top models, suggesting the relationship between turbidity and recruitment was driven by extremes of turbidity. Our results therefore suggest that low to moderate levels of turbidity are unlikely to be responsible for the observed spatial variation in recruitment observed in the Dampier Archipelago.

5. Conclusions

Understanding the processes that influence the replenishment of coral populations and the scales over which they operate remains a research priority. Notable in our study is that coral recruitment followed spatially consistent patterns driven by density dependant relationships between coral recruits and adult coverage. We identified reefs with consistently high rates of recruitment relevant to other locations (i.e. recruitment hotspots), suggesting reefs in the Dampier Archipelago are likely to be both sources and sinks of coral larvae for some taxa. Coral recruit densities in the Dampier Archipelago were generally low (mean $= 0.06$ cm^{-2}) in comparison to reefs located at similar latitudes on the Great Barrier Reef (e.g. Swains reefs: mean $= 0.08$ recruits cm^{-2}, Hughes et al., 1999; Keppel Islands: mean $= 0.12$ recruits cm^{-2}, Davidson et al., 2019); however, they were high in comparison to reefs immediately to the south (Ningaloo Reef 280 km south: mean $= 0.01$–0.5 recruits cm^{-2}, Turner et al., 2018; central Pilbara 50 km south: mean $= 0.003$ recruits cm^{-2}, Evans et al., 2020). Despite this, our study suggests high rates of larval retention within the Dampier Archipelago and therefore limited capacity for reefs within the Dampier Archipelago to act as occasional sources of larvae to aid in the recovery and resilience of reefs throughout the region (see Boschetti et al., 2020). Our results reaffirm the need for improved models of coral recruitment and to manage coral populations as inter-connected networks of reefs, rather than discrete populations on individual reefs.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2021.105318.

Author contribution

Damian Thomson: Conceptualization, Methodology, Formal analysis, Investigation, Writing - Original Draft, Visualisation, Writing - Review & Editing. **Russell Babcock**: Conceptualization, Methodology, Investigation, Writing – Review, Funding acquisition. **Richard Evans** Investigation, Formal analysis, Writing- Review & Editing, **Ming Feng** Formal analysis, Writing- Review & Editing. **Molly Moustaka** Investigation, Formal analysis, Writing- Review & Editing. **Melanie Orr** Investigation, Visualisation, Writing- Review & Editing, **Dirk Slawinski** Formal analysis, **Shaun Wilson** Formal analysis, Writing- Review & Editing, **Andrew Hoey** Formal analysis, Writing- Review & Editing.

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