

## **Title**

Early successional trajectory of benthic community in an uninhabited reef system three years after mass coral bleaching

## **Authors**

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## **Abstract**

Severe thermal stress events occurring on the backdrop of globally warming oceans can result in mass coral mortality. Tracking the ability of a reef community to return to pre-disturbance composition is important to inform the likelihood of recovery or the need for active management to conserve these ecosystems. Here, we quantified annual, temporal changes in the benthic communities for the three years following mass coral mortality at Jarvis Island—an uninhabited island in the Pacific Remote Islands Marine National Monument. While Jarvis experienced catastrophic coral mortality in 2015 due to heat stress resulting from the 2015/16 El Niño, significant annual shifts were documented in the benthic community in the three years post-disturbance. Macroalgal and turf dominance of the benthos was temporary—likely reflecting the high biomass of herbivorous reef fishes post-bleaching—giving way to calcifiers such as crustose coralline algae and *Halimeda*, which may facilitate rather than impede coral recovery. By 2018, indications of recovery were detectable in the coral community itself as juvenile densities increased and stress-tolerant genera, such as *Pavona*, exceeded their pre-disturbance densities. However, densities of *Montipora* and *Pocillopora* remain low, suggesting recovery will be slow for these formerly dominant taxa. Collectively, the assemblage and taxon-specific shifts observed in the benthic and coral community support cautious optimism for the potential recovery of Jarvis Island’s coral reefs to their pre-disturbance state. Continued monitoring will be essential to assess whether reassembly is achieved before further climate-related disturbance events affect this reef system.

## Introduction

Episodic high temperatures occurring on a backdrop of a globally warming ocean have led to increasing and widespread mass coral bleaching events (Hughes et al. 2018). Bleaching events can have catastrophic impacts on the coral community depending on the extent and severity of the event, although impacts vary greatly among taxa (Darling et al. 2013). For taxa that survive bleaching, colony size structures often become truncated due to high mortality in large colonies (McClanahan et al. 2008; Buglass et al. 2016; Hughes et al. 2019). This loss of large-sized adult brood stock can reduce fecundity, dampen larval recruitment, and impair community reassembly to the same pre-disturbance assemblage (Buglass et al. 2016; Hughes et al. 2019). Hence, tracking changes in the relative abundance and sizes of coral colonies post-disturbance can offer meaningful insights into the trajectory of coral community recovery (Johns et al. 2014).

Understanding which biotic and abiotic conditions enable coral communities to rebound rather regime shift to macroalgal dominance can also inform predictions of recovery (Graham et al. 2015; Gouezo et al. 2019). Both Steneck et al. (2019) in the Eastern Caribbean and Gouezo et al. (2019) in Palau found similar negative effects of algal abundance and positive effects of parrotfish on coral recovery. As benthic turfs impede successful coral recruitment (Vermeij and Sandin 2008), diverse herbivore assemblages can help reduce algal dominance following a disturbance and shift the benthic assemblage towards states that are beneficial to corals recruitment (Williams et al. 2019). Juvenile density and larval connectivity were positive drivers of recovery for some taxa like *Acropora* following mass bleaching (Gouezo et al. 2019). Likewise, in the Seychelles, Graham et al (2015) found greater density of juvenile corals and herbivorous fishes, as well as structurally complexity and deeper waters to favor coral recovery.

Thus, quantifying factors such as juvenile coral density, coral size structure, benthic cover, and herbivory in the years following the disturbance can be useful to inform a reef's recovery trajectory.

Uninhabited islands and atolls within Northern Line Islands (NLI) host coral- and predator-rich ecosystems (Brainard et al. 2005; Sandin et al. 2008). Due to their remote location, reefs around these islands have been protected from negative local human impacts likely conferring greater resilience to global climate change (Sandin et al. 2008). Jarvis Island is the southernmost of the NLI and ringed by a forereef. Low generic richness of coral at Jarvis compared to other islands within the NLI and recent connectivity modeling of coral larval dispersal suggest relative isolation for the region at large and Jarvis in particular (Brainard et al. 2005; Wood et al. 2014). Jarvis is exposed to equatorial and topographic upwelling locally intensified on the northern side of the island (Gove et al. 2006). During El Niño events, upwelling is dampened and temperatures increase, causing thermal stress that can result in episodic coral bleaching. Jarvis has experienced El Niño-driven thermal stress every five years since 1960, but has shown decadal-scale stability in coral cover until the 2015/16 El Niño (Barkley et al. 2018; Brainard et al. 2018). Prior to the 2015/16 El Niño, the forereef was dominated by *Montipora* and *Pocillopora* corals and hosted a stable biomass of herbivorous reef fishes (Brainard et al. 2019). Surveys immediately following the 2015/16 El Niño documented a >98% decline in hard coral cover and a >95% decline in coral colony density across all depths (e.g., 0–30m), island sector (e.g., upwelling and non-upwelling), and coral taxa surveyed (Vargas-Ángel et al. 2019). Surveys in 2017 revealed a benthic assemblage dominated by algal turf, no change in coral cover from 2016, and an absence of formally dominant *Montipora* colonies---yet also documented an increase in juvenile *Pavona* colonies (Vargas-Ángel et al.

2019). Continuing to track the recovery trajectory of Jarvis's reef three years post-bleaching--- including which algal functional groups have persisted, whether additional juvenile corals have established, and if herbivore biomass remains intact---offers needed insight into whether Jarvis's reefs can recover from mass bleaching naturally.

The National Coral Reef Monitoring Program (NCRMP) collects long-term monitoring data at several islands within the central Pacific to assess island-scale trends in coral reefs communities. Here we build on the temporal patterns of cover and colony density analyzed in Vargas-Ángel et al. (2019) by extending the time series analysis into 2018 and including analysis of colony size and biomass of two herbivorous fish functional feeding groups to better understand the trajectory of Jarvis's reefs three years post-bleaching. Specifically, we assess annual change in the benthic community across depth and upwelling sectors in the three years following the mass bleaching event to determine if temporal recovery proceeded equally across space. We asked whether turf algae persisted to dominate the benthos at Jarvis across all depths surveyed (0–30m), or if the community continued to shift annually towards a composition more amenable to coral recovery. We then assessed temporal changes in coral colony density (for adults and juveniles) and colony size to gain insight into the likelihood of coral community re-assembly and recruitment. Lastly, we assessed temporal change in the biomass of two functional groups of herbivorous fish based on feeding mode and evaluated the response of the benthic community to the observed variation in herbivore biomass.

## Methods

NCRMP benthic cover, coral, and reef fish community surveys at Jarvis Island were conducted before (April 2015) and after (May 2016, April 2017, July 2018) the peak of the 2015/16 El Niño event. NCRMP employs a stratified random sampling design to select random survey sites on hard bottom substrates within each of three depth strata: shallow (0-6 m), mid (>6-18 m), and deep (>18-30 m). Bathymetric and habitat maps were generated from 2006 multibeam surveys at Jarvis (Brainard et al. 2019). Random sites were allocated independently within each depth strata in proportion to the amount of hard-bottom reef habitat within the strata, yielding an unbalanced sampling effort across depths. To maximize data collection at this remote location, a fish survey team and a coral survey team dove simultaneously at separate sites (Fig. 1). Dive teams would navigate to each random site's GPS coordinates, take a depth reading at the surface, and descend to that depth to begin surveying. At coral sites, adult coral colonies were surveyed at four, fixed interval segments (2.5 m<sup>2</sup>) along a 30 m belt transect (for details, see Winston et al. 2020, PIFSC 2018a,b). Adult colonies ( $\geq 5$  cm) were identified to genus and maximum diameter was measured to the nearest cm. Juvenile coral colonies (< 5 cm diameter) were surveyed within three fixed interval segments (1 m<sup>2</sup>) along the transect, identified to genus and measured for maximum diameter. Site-level adult and juvenile colony densities (indiv. m<sup>-2</sup>) were calculated from summed segment counts. At fish sites, a pair of divers surveyed the fish assemblage using a stationary-point-count method (for details, see Ayotte et al. 2015, PIFSC 2018c). Each diver identified, enumerated, and estimated the total length of fishes within a visually estimated 15 m diameter cylinder with the diver stationed in the center. Fish biomass (g m<sup>-2</sup>) was calculated for each fish from length measurements using species-specific conversion factors, and biomass was averaged among cylinders. Herbivore biomass was summed as

scraper/excavator versus browser/grazer at each site to determine changes in biomass varied by feeding mode (based on published feeding type and diet studies of each herbivore species). At both benthic and fish survey sites, divers took benthic images for calculating benthic cover to maximize the size of this dataset. Images were taken along a 30m transect at 1 m intervals using a camera positioned 1m above the benthos. Images were analyzed using CoralNet (Beijbom et al. 2015) with 10 random points per image identified to the functional group level including: coral, crustose coralline algae (CCA), encrusting macroalgae (EMA), *Halimeda*, fleshy macroalgae, algal turf (TURF), and sediment. Sediment cover remained consistently low ( $\leq 1\%$ ) from 2015 to 2018 and was not included in the analysis. A total of 72 benthic cover, 28 coral, and 39 fish surveys were completed in 2018 as part of the NCRMP time series at Jarvis Island. The benthic cover sample size exceeds that of the coral community and fish community combined as some dives were aborted after benthic photos were taken due to underwater conditions that prevented accurate fish or coral surveys. Sample sizes for all survey years are provided in Table S1.

## Data Analysis

We conducted permutational multivariate analyses of variance (PERMANOVAs) on site-level data to test the effect of depth strata, upwelling sector, and year on the post-bleaching recovery composition of (a) benthic cover, (b) adult coral, and (c) juvenile coral communities. Two, 2-factor PERMANOVAs were run for each community (Year\*Depth; Year\* Zone) as fixed factors in a fully crossed design as sample size limitations in the NCRMP monitoring dataset prevented running a three-way PERMANOVA (Table S1). Coral cover was square root transformed and adult coral densities fourth-root transformed prior to analysis to reduce the influence of dominant taxa. PERMANOVAs were performed on zero-adjusted Bray-Curtis

dissimilarity matrices using Type III sum of squares due to the unbalanced design ( $n = 999$  permutations). As PERMANOVA is sensitive to differences in dispersion for unbalanced designs, all factors were evaluated for homogeneous dispersion using the PERMDISP2 procedure (Anderson 2006). Pairwise comparisons with Holm's correction were run for each significant factor identified by PERMANOVA to determine how community composition changed across factor levels ('pairwise adonis2' function; Arbizu 2020). Nonmetric multidimensional scaling (NMDS) was used to visualize multivariate patterns in the data. We then fit generalized linear models (GLMs) followed by Wald tests to assess annual changes in specific components of the benthic cover (logit-transformed, family: gaussian; Warton and Hui 2011), coral density (square root transformed, family: Poisson), and herbivore biomass by grazing type (square root transformed, family: Poisson). The Wald test evaluates the null hypothesis that all coefficients associated with a particular regression term (i.e., survey year) are zero; a survey design-based version of Kruskal Wallis was used if the response variable did not meet assumptions of homogeneity of variance (Lumley 2004). GLMs were run using the 'survey' package in R which allows for sample weighting (calculated as the inverse of the selection probability) and stratification (by depth) to account for the NCRMP survey design (Lumley 2020). For the four coral genera that increased in density following the mass bleaching event (*Pavona*, *Leptoseris*, *Pocillopora*, and *Psammocora*), we used log-transformed colony size data for all colonies  $\geq 1$  cm to evaluate changes in mean size across the four years. Mean size was analyzed using ANOVA or its non-parametric equivalent if genera did not meet assumptions of normality and homogeneity of variance. Lastly, we used a distance-based redundancy analyses (db-RDA) to examine the post-bleaching relationship between the benthic cover assemblage and herbivore biomass ( $n = 157$ , collocated fish and benthic cover data; Legendre and Andersson



1999). As with the PERMANOVA, the analysis was run using the ‘vegan’ package (Oksanen et al. 2019). All analyses were run in R version 3.6.3 (R Core Team 2020).

## Results

In the three years following the 2015/16 El Niño event, the benthic assemblage transitioned through a series of algal dominated communities with each year differing significantly from one another (Fig. 2; Table 1a; all pairwise adonis,  $p < 0.003$ ). Benthic composition also differed among depth strata and upwelling sectors. However, the lack of a significant interaction with year indicates that temporal changes in the benthos post-bleaching have occurred uniformly across all depths and sectors. Multivariate dispersion was consistent among years, indicating the annual differences observed are indeed due to shifts in the benthic community composition rather than dispersion (PERMDISP,  $F_{2,189} = 1.79$ ,  $p = 0.17$ ). In May 2016, encrusting macroalgae (primarily the calcifying alga, *Peyssonnelia*) was the most abundant benthic functional group at Jarvis accounting for nearly 50% of cover, but decreased significantly to ~ 30% cover in the following years (Fig. 3). In 2017, turf cover increased to 36% and replaced encrusting macroalgae as dominant benthic functional group but declined significantly in 2018 to pre-bleaching turf cover (i.e., 24%). By 2018, CCA became the dominant functional group, reaching nearly 40% cover—a significant increase over all other years. Fleshy macroalgae declined significantly from 9% in 2017 to only 2% cover in 2018, while the calcareous macroalgae, *Halimeda*, increased in 2018 to 6% cover compared to < 1% cover in all prior survey years. Despite these annual shifts in the algal communities at Jarvis Island, coral cover remained low (< 2%) after the El Niño (Fig. 3).

By 2018, adult colony density reached 15% of the pre-bleaching density (2015: mean =  $7.26 \pm 0.80$  SE colonies  $m^{-2}$ ; 2018: mean =  $1.12 \pm 0.26$  SE colonies  $m^{-2}$ ) and juvenile density had recovered to 31% of pre-bleaching levels (2015: mean =  $0.68 \pm 0.16$  SE colonies  $m^{-2}$ ; 2018: mean =  $0.21 \pm 0.0$  SE colonies  $m^{-2}$ ). This increase in 2018 was led by four genera: *Pavona*, *Leptoseris*, *Psammocora*, and *Pocillopora* (Fig. 4), reflecting a significant shift in both the adult and juvenile coral assemblage compared to 2016 (Table 1,  $p = 0.003$ ). The adult coral assemblage also varied with depth, but these differences were consistent over time. The juvenile assemblage did not vary by depth, but did exhibit temporal differences by sector such that densities were higher in the upwelling zone in 2017 ( $p = 0.003$ ) but this pattern reversed by 2018 (Fig. S1). *Pavona* densities were significantly higher in 2018 than in 2016 for both adults and juveniles, driven by increases in *P. chiriquiensis*, *P. duerdeni*, and *P. varians*. Densities of *Leptoseris*, *Psammocora*, and *Pocillopora* also increased by 2018; however, these changes were only significant for *Psammocora* juveniles. Mean colony size for these four genera in 2018 were significantly smaller than pre-bleaching colony means in 2015, reflecting both the increase in smaller colonies and a truncation in the overall size structure for *Leptoseris*, *Psammocora*, and *Pocillopora* (Table 2). However, increases in juvenile *Pavona* densities from 2016 to 2018 were coupled with persistence of large colonies in the population. *Montipora*—the most abundant genera in 2015—remained conspicuously rare in 2018 with only two small (<10cm diameter) adult colonies  $m^{-2}$  were measured and no juveniles observed (Table S2). Similarly, while some massive *Porites* colonies survived the mass bleaching event (Barkley et al. 2018), none of these colonies were encountered within the transect surveys in 2018. Several surviving colonies were observed outside the study sites exhibiting variable partial mortality (Fig. S2a).

The herbivore community comprised 12% of the total fish biomass at Jarvis Island in 2015. Total herbivore biomass remained stable throughout the four survey years ( $F_{3,153} = 0.61$ ,  $p = 0.61$ ), though temporal differences at the functional group level were observed. In 2018, scraper/excavator biomass increased by > 50% over pre-bleaching levels in 2015 ( $F_{2,92} = 3.84$ ,  $p = 0.025$ ), led by greater biomass of two parrotfishes: *Calotomus carolinus* and *Scarus tricolor*. Collectively, these two species comprised 26% of the scraper/excavator biomass and 12% of the total herbivore fish biomass in 2018. Browser/grazer biomass was variable in the three years post-bleaching but not significantly different from pre-bleaching values ( $F_{2,92} = 2.13$ ,  $p = 0.13$ , Fig. 5). This temporal variability in the herbivorous fish biomass explained only 8% of the variation in the benthic cover from 2015-2018, and was best explained by scraper/excavators, not browser/grazers (db-RDA, Table S3).

## Discussion

In the aftermath of mass bleaching events, persistence of macroalgae often results in phase shifts to algal-dominated reefs rather than coral recovery (Graham et al. 2015). However, the 2018 benthic transition from algal turf to CCA dominance at Jarvis marks a different change. Under the relative dominance model, when both herbivory and nutrient levels are high, CCA is predicted to dominate (Littler and Littler 1984). Similar rapid increases in CCA post-bleaching have been reported in remote reefs in Western Australia (Gilmour et al. 2013), the Phoenix Islands (Obura and Mangubhai 2011), and the Chagos Archipelago (Benkwitt et al. 2019), where the benefits of isolation include high densities of herbivorous fish. Benkwitt et al. (2019) attributed nutrient inputs from seabirds along with herbivory as drivers of high CCA and

*Halimeda* cover in shallow, protected backreefs in the remote Chagos Archipelago two years after a mass bleaching event. Jarvis similarly possesses many of these attributes including an intact herbivore population, locally intensified upwelling, minimal human impacts, and hosts the most significant seabird colony in the Pacific (Rauzon et al. 2011). However, the deeper reefs and low rainfall at Jarvis compared to the Chagos Archipelago likely make seabird nutrient subsidies a minor player compared to upwelling derived nutrients. Immediately following the 2015/16 El Niño, seabird counts declined at Jarvis, and unlike the El Niño events of 1982/83 and 1997/98, a strong La Niña—which typically fuels robust phytoplankton blooms—did not follow the 2015/16 event (Brainard et al. 2018). Lack of upwelling and depressed seabird abundances may have created a nutrient-poor environment in which *Peyssonnelia* was a more opportunistic space occupier than other nutrient-limited fleshy macroalgae. Turf algae became dominant in 2017, suggesting increased nutrient availability (Vermeij et al. 2010), potentially from the return of upwelling. By 2018, herbivore biomass was the highest recorded during this study (330 kg ha<sup>-1</sup>)—exceeding the Indo-Pacific post-bleaching recovery thresholds of 258 kg ha<sup>-1</sup> identified by Graham et al. (2015)—and CCA and *Halimeda* replaced turf algae as the dominant benthic substrate.

Juvenile densities were low in both 2016 and 2017 when *Peyssonnelia* and then turf dominated the benthos. While turf algae can be a dominant space holder on reefs capable of overgrowing coral recruits (Vermeij et al. 2010), *Peyssonnelia* has recently been hypothesized to similarly outcompete juvenile corals for space (Stockton and Edmunds 2021). At Jarvis, the benthic transition from *Peyssonnelia* and algal turf to a CCA dominance in 2018 has conceivably bolstered coral recruitment success, coinciding with the observed increase of juvenile colonies (Diaz-Pulido et al. 2009). High CCA cover may come with some consequences for coral

recovery. While CCA is generally an inferior spatial competitor to corals (Barott et al. 2012), particularly thick-crust CCA can inhibit growth and survivorship of coral recruits (Jorissen et al. 2020) and can outcompete some adult coral taxa (Buenau et al. 2011). Indeed, thick-crust CCA was observed overgrowing adult corals suffering from partial mortality at Jarvis (Fig. S2c). CCA is more widely viewed as a positive component of the benthos, facilitating coral larval settlement and metamorphosis (Morse et al. 1988; Tebben et al. 2015) and solidifying reef structure (Setchell 1930; Littler and Littler 2012). Qualitative visual assessments of substrate complexity at Jarvis Island indicate that complexity in 2018 equals that from 2015 (Fig. S3) despite the loss of live coral over this period. This stability in substrate complexity may be due to the ability of CCA to calcify over dead coral skeletons, preserving the complexity of the substrate by limiting erosion. Similar observations were made in the Phoenix Islands post-bleaching, where thick crusts of CCA coated dead coral skeletons but the shape of the colony was still readily identifiable to genera (Obura and Mangubhai 2011). However, in the NLI substrate complexity declined at Kiritimati following mass mortality induced by the 2015/16 heat stress event based on detailed quantitative assessments using structure from motion photogrammetry techniques (Magel et al. 2019). NCRMP is adopting photogrammetry methods into their monitoring approaches to be better poised to accurately quantify temporal changes in structural complexity over time at Jarvis in the near future.

Herbivory can influence whether a reef recovers from bleaching or regime shifts to an algal-dominated state (Graham et al. 2015). However, associations between benthic composition and herbivorous fishes can vary by feeding type, underscoring the value of quantifying specific functional groups of herbivores in coral reef habitats (Heenan and Williams 2013). At Jarvis, scraper/excavator biomass increased significantly in 2018, co-occurring with increases in

juvenile coral densities and CCA. Such increases in large bodied excavators have been associated with increases in coral cover in American Samoa (Heenan and Williams 2013), as their feeding behavior is thought to clear space for coral larval settlement thereby facilitating recruitment (Mumby and Steneck 2008). However, Traçon et al. (2013) found juvenile coral density to be negatively correlated with the biomass of scraping and excavating herbivores across the Great Barrier Reef. These differences may be attributable to differences in functional group assemblage among these Pacific regions or the differential role of herbivores in facilitating or inhibiting coral recruitment depending on the dominant benthic assemblage on a given reef. Clearly, there is value in determining the mechanisms and conditions in which scraping and excavating herbivores support recruitment, especially in reef habitats recently impacted by mass bleaching.

In the aftermath of mass bleaching at Jarvis Island in 2015/16, our results uncover early indications of coral recovery. Vargas-Ángel et al. (2019) found no evidence of depth or thermal refugia from bleaching impacts. Three years after bleaching, we similarly found no evidence of greater recovery on deeper reefs, as suggest by Graham et al. (2015) or higher coral cover in the upwelling sector where nutrients are more abundant. However, increases in juvenile recruitment were evident in the upwelling sector a year earlier than detected in the non-upwelling zone. By 2018, juvenile densities were more than two times higher in the non-welling zone, which may indicate poor survivorship in the upwelling sector or high variation in recruitment in both time and space. Although adult coral density and cover has remained low overall in the three years after bleaching and the previously dominant *Montipora* extirpated, different genera (including *Pavona*, *Psammocora*, and *Leptoseris*) have increased by 2018 to exceed their pre-bleaching densities. These are stress-tolerant genera that share fundamental life history characteristics (i.e.,

cryptic, domed/plating morphologies, small reproductive size, large corallites) which enable them to survive warm water disturbances better and possibly recover more rapidly (Darling et al. 2012). Similar results were reported after mass bleaching in the Maldives in 1998 and the Chagos Archipelago in 2015, whereby the dominant *Acropora* and *Pocillopora* genera suffered widespread mortality while remnant *Pavona* persisted and successfully recruited post-disturbance (Loch et al. 2004; Pisapia et al. 2016; Sheppard et al. 2017). Juvenile coral densities at Jarvis rebounded to ~ 30% of pre-bleaching levels by 2018 lead by four genera: *Pavona*, *Psammocora*, *Leptoseris*, and *Pocillopora*. This increase in juvenile corals aligns with the significant decrease in mean colony size observed for these genera. While greater juveniles in the population are unlikely to result in large impacts in total coral cover--- collectively these four genera account for only 0.26% of the live cover observed in 2018---the significant increase in juvenile density suggests coral recovery is underway at Jarvis despite coral cover being very low. *Montipora* recruits remained absent (perhaps unsurprisingly given the lack of adult colonies), yet *Pocillopora* juveniles were present in low numbers despite the truncation in adult colony size structure (Fig. S2b), indicating viable larval recruitment and the potential of recovery for this formerly dominant taxa. Similarly, massive adult *Porites* colonies did survive the mass bleaching event at Jarvis (Barkley et al. 2018) though at low densities, suggesting recovery is possible for this genera in the future but likely very slow (Pisapia et al. 2016). In Kanton Lagoon, hard coral cover recovered to 53% of the pre-bleaching cover after 13 years. This recovery was dominated by plating Acroporids that were nearly eliminated in the 2002 bleaching event, suggesting that even low densities of adult broodstock can play a critical role in community recovery. Interestingly, these recovering Acroporids were more bleaching resistant to high water temperatures (Mangubhai et al. 2018). Survivorship of select *Porites* and *Pocillopora* colonies at

Jarvis may be enough to spur recovery of these taxa over the coming decade and confer resistance to future thermal stress.

The monitoring datasets analyzed here are highly resolved in time and space, allowing us the unique opportunity to detect bleaching response at annual time scales in a relatively pristine ecosystem. However, they are limited in their ability to assign causality to the temporal changes observed. At Jarvis, we considered which processes may have worked together following the 2015/16 El Niño event to shift the benthic community from macroalgae and turf to calcifier dominance in order to further develop mechanistic hypotheses warranting future study. Collectively, our observations of increased CCA cover, declines in turf and macroalgal cover, high herbivore biomass, and increased density of stress-tolerant corals provide reasons for optimism. However, the future trajectory of this reef system is uncertain. CCA may continue to cement and stabilize the complex reef framework, facilitate continued coral recruitment supported by high herbivore biomass, and advance on a trajectory towards coral recovery. Alternatively, isolation may impede recovery at Jarvis. Coral recovery is influenced by larval supply and successful post-settlement survivorship (Gouezo et al. 2019; Hughes et al. 2019). In the absence of remnants, *Montipora* and *Acropora* recovery will largely depend on larval import, protracted by the island's remoteness and isolation (Wood et al. 2014). Due to limited larval connectivity, recruitment may remain heavily reliant on local reseedling for the near future, slowing the reestablishment of the former dominant reef framework building taxa (i.e., *Montipora* and *Pocillopora*). Without large gains in coral cover, Jarvis may experience a gradual degradation of reef complexity via bioerosion and wave energy, disrupting the current stability in the total herbivore biomass (Graham et al. 2007; Pratchett et al. 2008). However, coral recovery on other isolated Indo-Pacific reef systems has taken upwards of 12 years post-bleaching



(Gilmour et al. 2013; Graham et al. 2015; Mangubhai et al. 2018; Gouezo et al. 2019) and our data only reflect up to the three-year mark. Yet, the increased frequency and intensity of El Niño events may further stress the system before comprehensive recovery can occur. Taken together, the myriad of possible outcomes underscores the need for continued long-term monitoring at Jarvis in order to inform scientists and resources managers whether these early signs of recovery will translate into the return of a coral dominated ecosystem.

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## Tables

Table 1. PERMANOVA results for assessing temporal change in (a) benthic cover, (b) adult coral, and (c) juvenile coral assemblages by depth and by upwelling sector. Two, 2-factor PERMANOVAs were run for each assemblages (Year\*Depth; Year\* Zone) as fixed factors in a fully crossed design.

### a) Benthic cover

	<b>Df</b>	<b>SS</b>	<b>MS</b>	<b>F.Model</b>	<b>R<sup>2</sup></b>	<b>p</b>
Year	2	1.612	0.806	28.862	0.220	<b>0.001</b>
Depth	2	0.466	0.233	8.338	0.064	<b>0.001</b>
Year*Depth	4	0.131	0.033	1.172	0.018	0.309
Residuals	183	5.109	0.028	0.698		
Year	2	1.612	0.806	27.503	0.220	<b>0.001</b>
Sector	1	0.208	0.208	7.107	0.028	<b>0.002</b>
Year*Sector	2	0.048	0.024	0.817	0.007	0.566
Residuals	186	5.449	0.029	0.745		

### b) Adult colony density

	<b>Df</b>	<b>SS</b>	<b>MS</b>	<b>F.Model</b>	<b>R<sup>2</sup></b>	<b>p</b>
Year	2	0.872	0.436	3.621	0.071	<b>0.002</b>
Depth	2	1.248	0.624	5.182	0.102	0.095
Year*Depth	4	0.401	0.1	0.833	0.033	0.582
Residuals	81	9.754	0.12	0.795		
Year	2	0.872	0.436	3.589	0.071	<b>0.001</b>
Sector	1	0.878	0.878	7.226	0.072	<b>0.001</b>
Year*Sector	2	0.32	0.16	1.317	0.026	0.201
Residuals	84	10.205	0.121	0.831		

### c) Juvenile colony density

	<b>Df</b>	<b>SS</b>	<b>MS</b>	<b>F.Model</b>	<b>R<sup>2</sup></b>	<b>p</b>
Year	2	0.928	0.464	4.812	0.098	<b>0.001</b>
Depth	2	0.226	0.113	1.174	0.024	0.294
Year*Depth	4	0.468	0.117	1.214	0.05	0.271
Residuals	81	7.81	0.096	0.828		
Year	2	0.928	0.464	4.933	0.098	<b>0.001</b>
Sector	1	0.148	0.148	1.578	0.016	0.171
Year*Sector	2	0.455	0.227	2.417	0.048	<b>0.041</b>
Residuals	84	7.901	0.094	0.838		

Table 2. Colony size data from 2015-2018 for the four most abundant coral taxa observed post-bleaching. Post-hoc results based on adjusted p-values are shown for annual differences mean colony size.

Genera	Year	N	Colony Size			Post-hoc Result
			Range	Mean	SE	
<i>Pavona</i>	2015	305	2-102	18.3	0.9	2015 > 2018
	2016	44	3-100	19.5	3.2	
	2017	124	2-200	21	2.3	
	2018	187	1-210	18.2	1.9	
<i>Psammocora</i>	2015	110	2-45	13.6	0.9	2015, 2016 > 2018
	2016	27	5-80	19.7	3.4	
	2017	33	2-60	13.9	2	
	2018	56	1-45	10.1	1.2	
<i>Leptoseris</i>	2015	55	3-68	13.8	1.3	2015, 2016 > 2018
	2016	29	5-32	13.1	1.2	
	2017	21	3-20	11	1.2	
	2018	42	2-22	8.2	0.7	
<i>Pocillopora</i>	2015	1,557	2-105	17.9	0.3	2015 > 2017, 2018
	2016	18	4-63	14.6	3.2	
	2017	18	2-60	12.8	3.2	
	2018	33	3-42	10.6	1.4	



## Figures

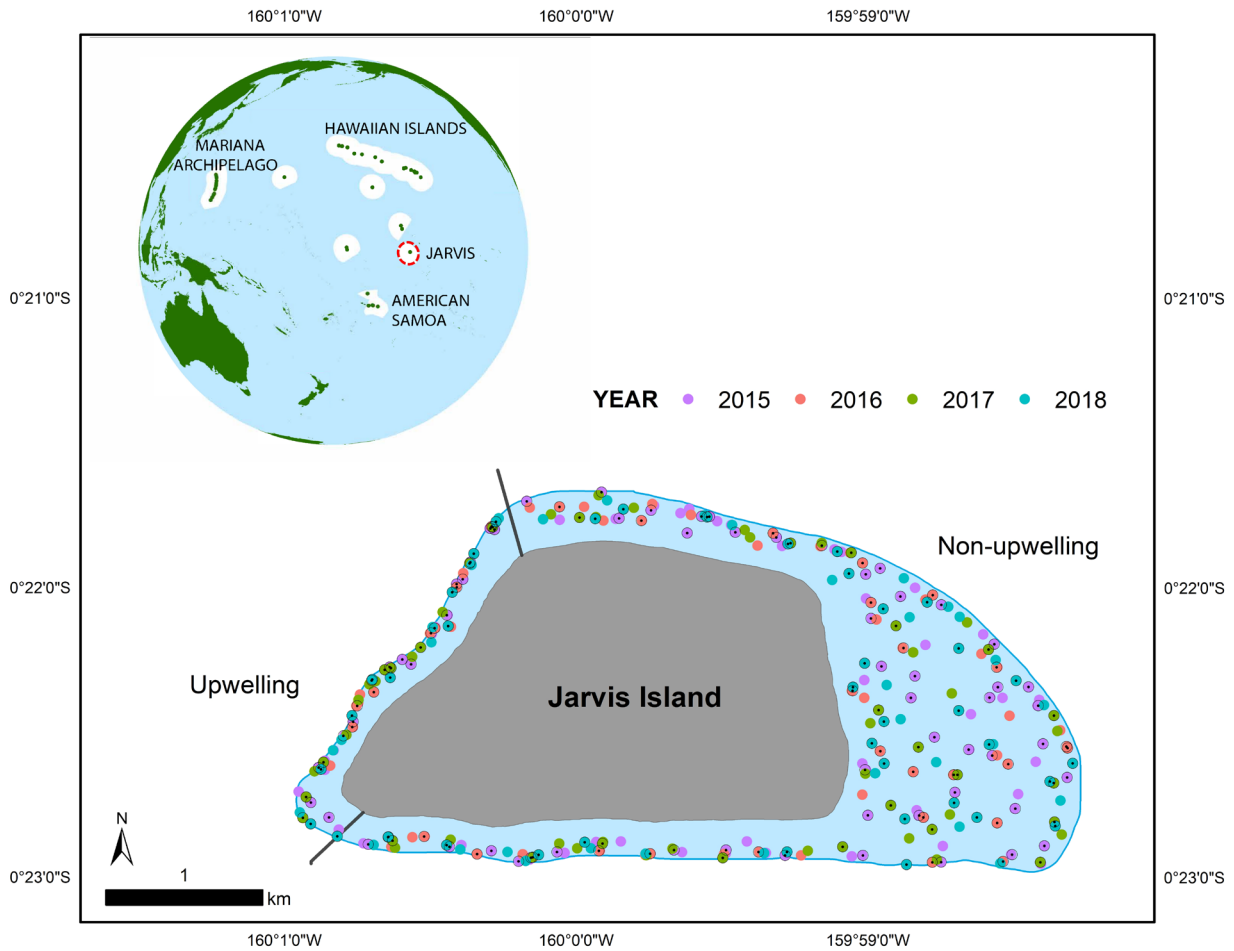


Figure 1. Benthic cover survey sites by year (2015–2018) at Jarvis Island in the central Equatorial Pacific. West facing ‘upwelling’ sector and ‘non-upwelling’ sector are demarcated. Sites with black centers denote fish SPC survey locations; sites without denote coral demographic survey locations.

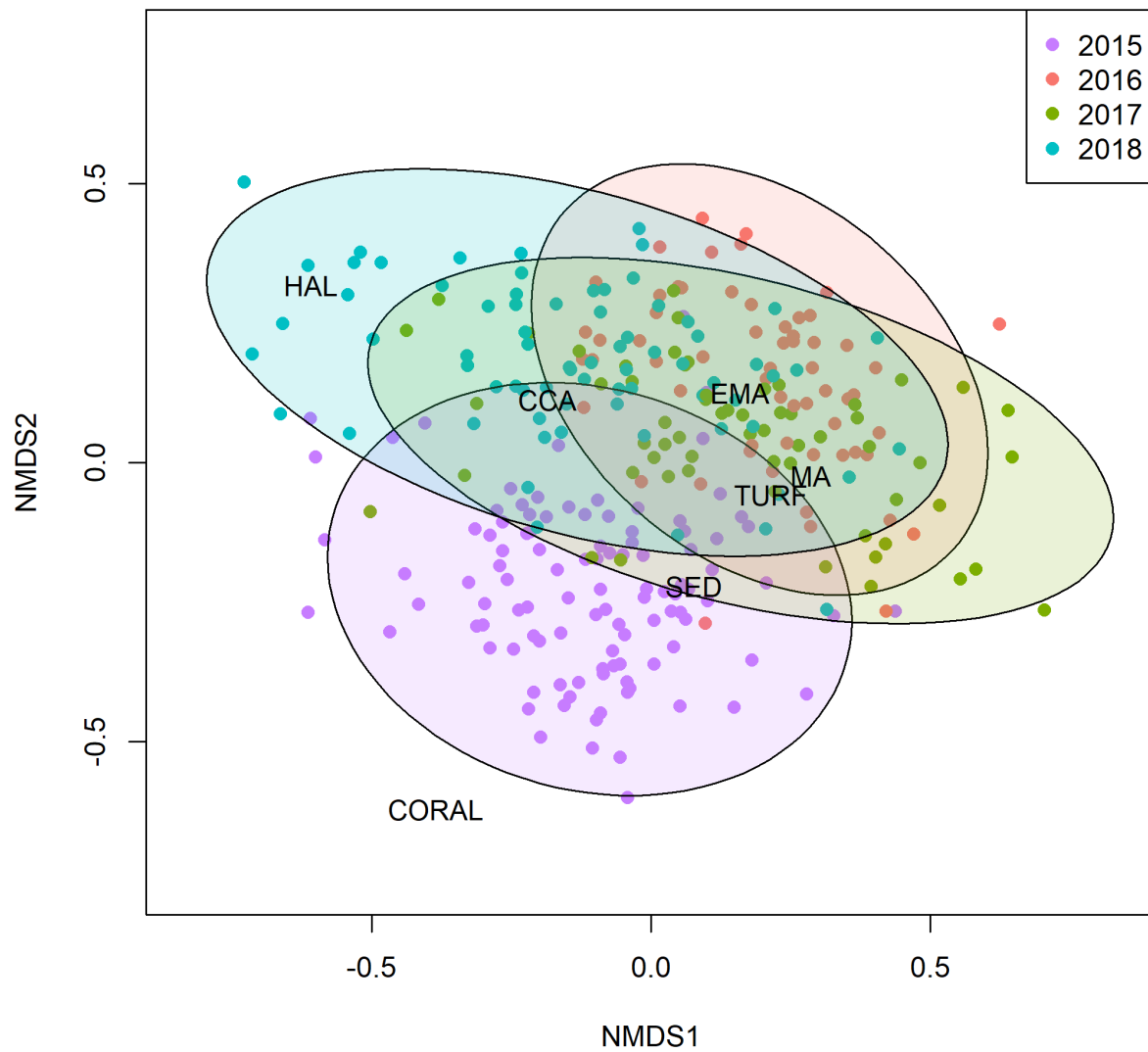


Figure 2. Nonmetric multidimensional scaling (NMDS) plot showing benthic cover vectors and shaded 95% confidence ellipses around the community centroid for each survey year post-bleaching. HAL: *Halimeda*; CCA: crustose coralline algae; EMA: encrusting macroalgae; MA: fleshy macroalgae. Stress value = 0.13.

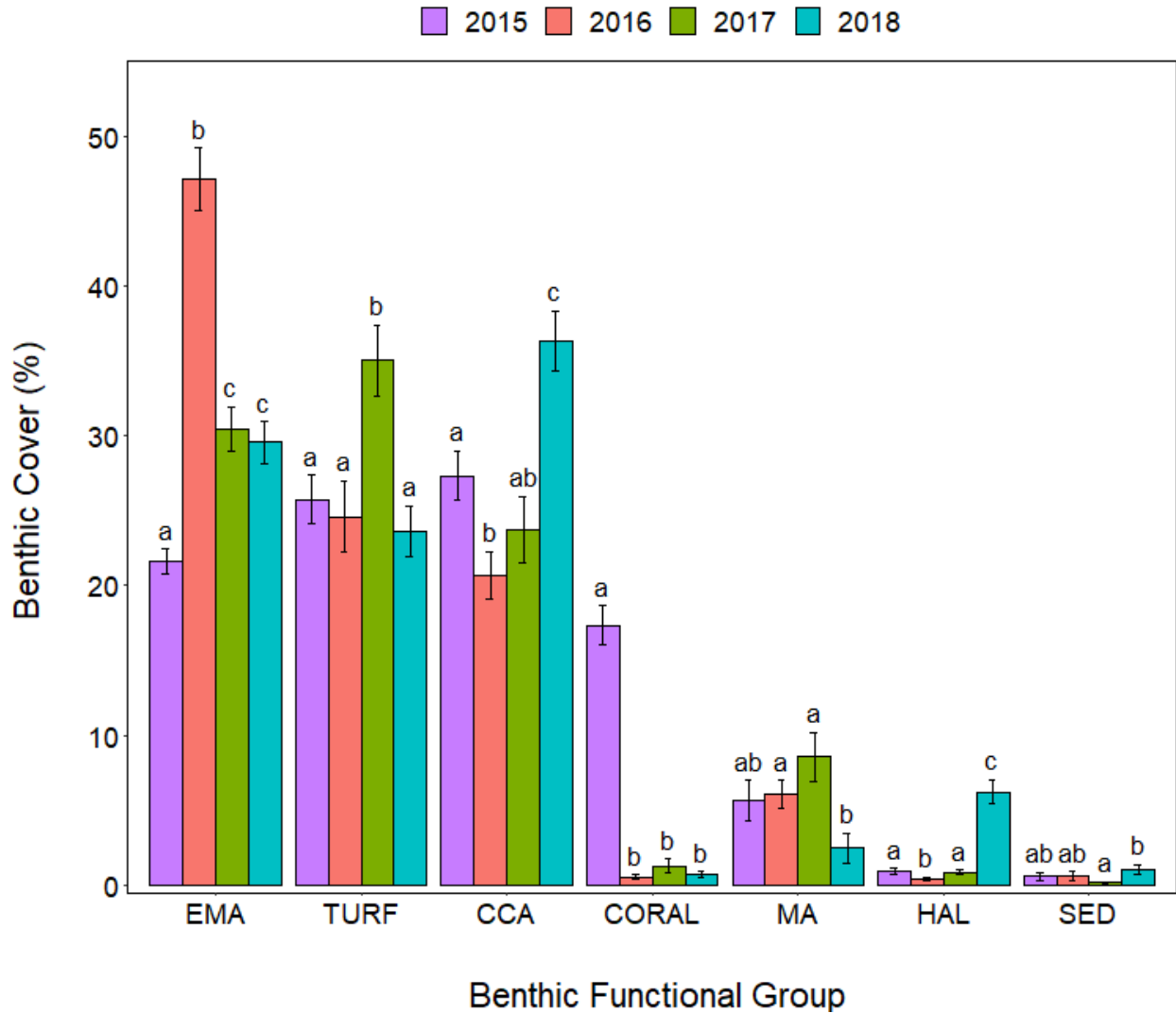


Figure 3. Change in benthic percent cover (mean  $\pm$  SE) of six benthic functional groups following the mass bleaching event following the 2015/16 El Niño (vertical gray line). For each benthic group, differing letters denote significant differences among the three post-bleaching years. The 2015 pre-bleaching data was not included in the analysis. No yearly differences were observed for coral. EMA: encrusting macroalgae; CCA: crustose coralline algae.

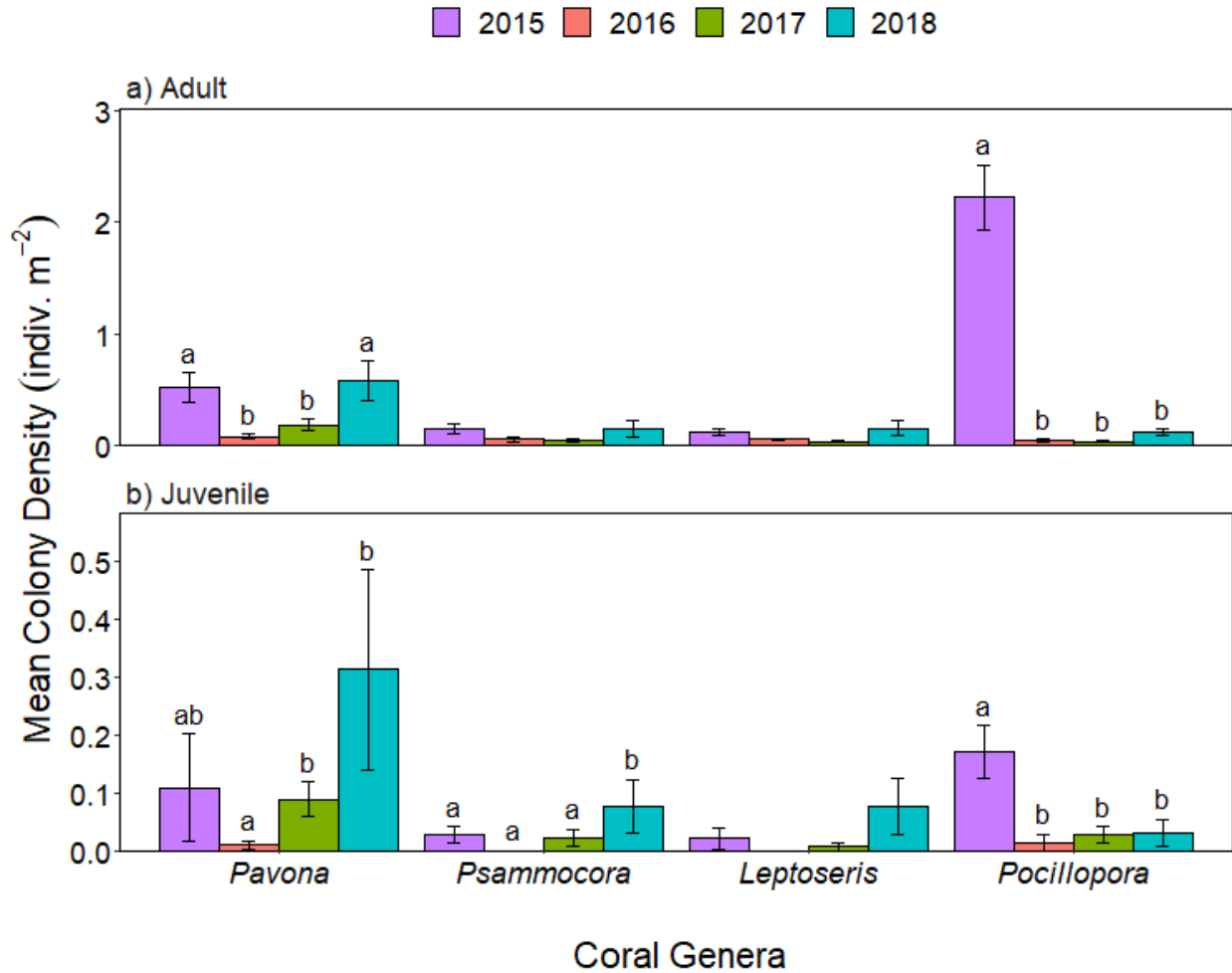


Figure 4. Mean  $\pm$  SE (a) adult and (b) juvenile colony density from 2015 to 2018 for the four most abundant genera, following the mass bleaching event following the 2015/16 El Niño (vertical gray line). For each genera, differing letters denote significant differences among the three post-bleaching years. The 2015 pre-bleaching data was not included in the analysis.

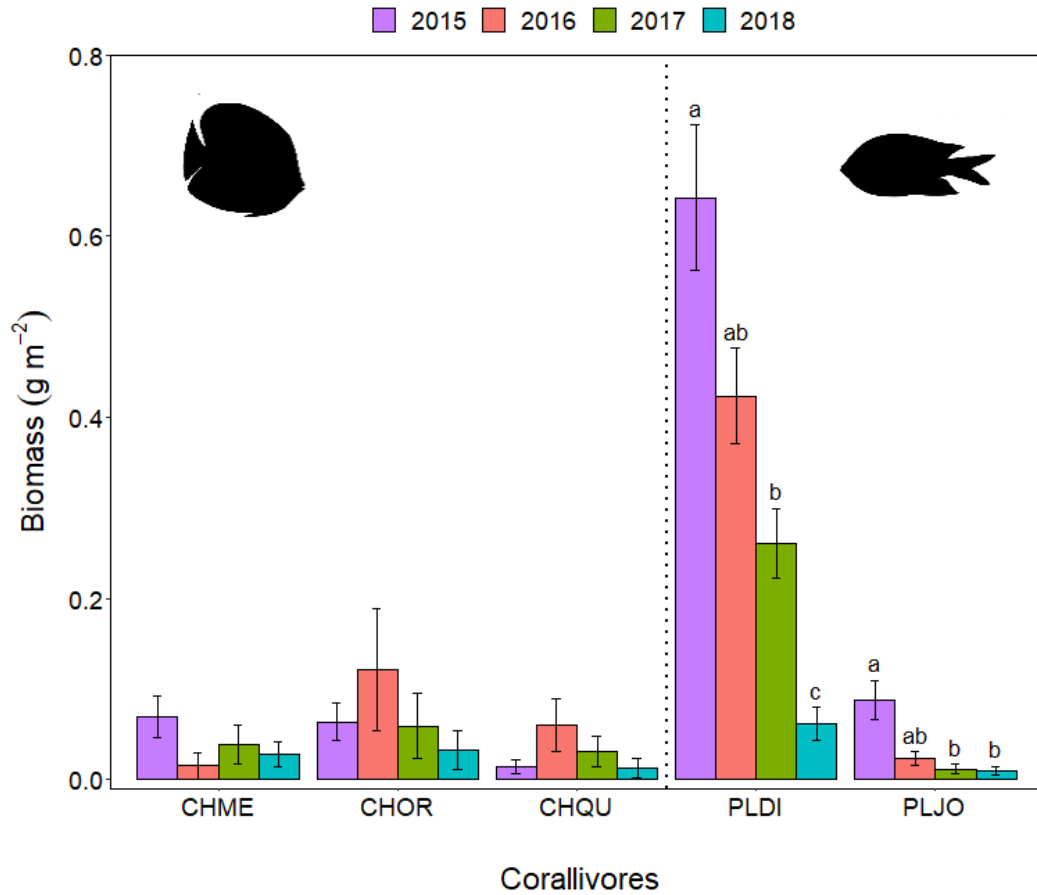


Figure 5. Mean  $\pm$  SE herbivorous fish biomass ( $\text{g m}^{-2}$ ) grouped by feeding mode from pre-bleaching event (dashed line) to the three years post-bleaching. Differing letters denote significant differences in scraper/excavator biomass among years.

## Supplemental Tables and Figures

**Table S1.** Sample sizes of surveys conducted for a) coral density and benthic cover across depth, sector, and years used in PERMANOVA analysis to assess post-bleaching recovery composition, and b) herbivore biomass used to examine temporal change in herbivore biomass and the post-bleaching relationship between the benthic cover assemblage and herbivore biomass

a) Coral Density and Benthic Cover

Depth	Sector	2016		2017		2018	
		Coral	Cover	Coral	Cover	Coral	Cover
Shallow	Non-upwelling	7	15	8	19	7	19
	Upwelling	2	4	3	3	3	5
Mid-depth	Non-upwelling	13	25	10	16	13	30
	Upwelling	4	7	2	9	0	6
Deep	Non-upwelling	3	7	7	9	3	6
	Upwelling	1	2	2	4	2	6

b) Herbivore biomass

Year	2015	2016	2017	2018
N	60	30	28	39

**Table S2.** Mean (SE) for adult and juvenile colony density (indiv. m<sup>-2</sup>) by coral genera. These estimates and errors were calculated incorporating sampling weights and strata given the complex NCRMP study design. As such, these values differ slightly from those presented in Vargas-Ángel al (2019) for 2015–2017 calculated using simple random sampling.

Genus	Adult				Juvenile			
	2015	2016	2017	2018	2015	2016	2017	2018
<i>Acropora</i>	0.1 (0.05)	0	0	0	0.03 (0.03)	0	0	0
<i>Coscinaria</i>	0.002 (0.002)	0	0	0.03 (0.02)	0.004 (0.004)	0	0	0
<i>Favia</i>	0.03 (0.02)	0.02 (0.01)	0.08 (0.05)	0	0	0	0.01 (0.01)	0
<i>Favites</i>	0.008 (0.006)	0.009 (0.005)	0.002 (0.002)	0.01 (0.01)	0	0	0	0
<i>Goniastrea</i>	0.001 (0.001)	0	0	0	0	0	0	0
<i>Hydnophora</i>	0.001 (0.001)	0.005 (0.003)	0.005 (0.004)	0.005 (0.003)	0	0	0	0
<i>Isopora</i>	0.002 (0.002)	0	0	0	0	0	0	0
<i>Leptastrea</i>	0.01 (0.01)	0	0.003 (0.003)	0.003 (0.003)	0.004 (0.004)	0	0.005 (0.005)	0
<i>Leptoseris</i>	0.12 (0.04)	0.05 (0.01)	0.03 (0.01)	0.16 (0.07)	0.02 (0.02)	0	0.006 (0.006)	0.08 (0.05)
<i>Montipora</i>	3.80 (0.64)	0.007 (0.005)	0 (0)	0.007 (0.007)	0.32 (0.08)	0	0	0
<i>Pavona</i>	0.52 (0.13)	0.08 (0.022)	0.18 (0.05)	0.58 (0.18)	0.11 (0.09)	0.009 (0.007)	0.09 (0.03)	0.31 (0.17)
<i>Pocillopora</i>	2.22 (0.29)	0.05 (0.01)	0.03 (0.008)	0.11 (0.03)	0.17 (0.045)	0.014 (0.014)	0.027 (0.014)	0.031 (0.024)
<i>Porites</i>	0.08 (0.03)	0.02 (0.007)	0.02 (0.007)	0.01 (0.01)	0	0	0.01 (0.01)	0 (0)
<i>Psammocora</i>	0.16 (0.05)	0.05 (0.02)	0.05 (0.02)	0.15 (0.07)	0.03 (0.01)	0	0.02 (0.01)	0.08 (0.05)

1

2 **Table S3.** Results of the db-RDA full model and partial analyses relating herbivore biomass by  
3 grazing type to benthic cover (using collocated fish and benthic cover survey data from 2015-  
4 2018, n= 157).

5

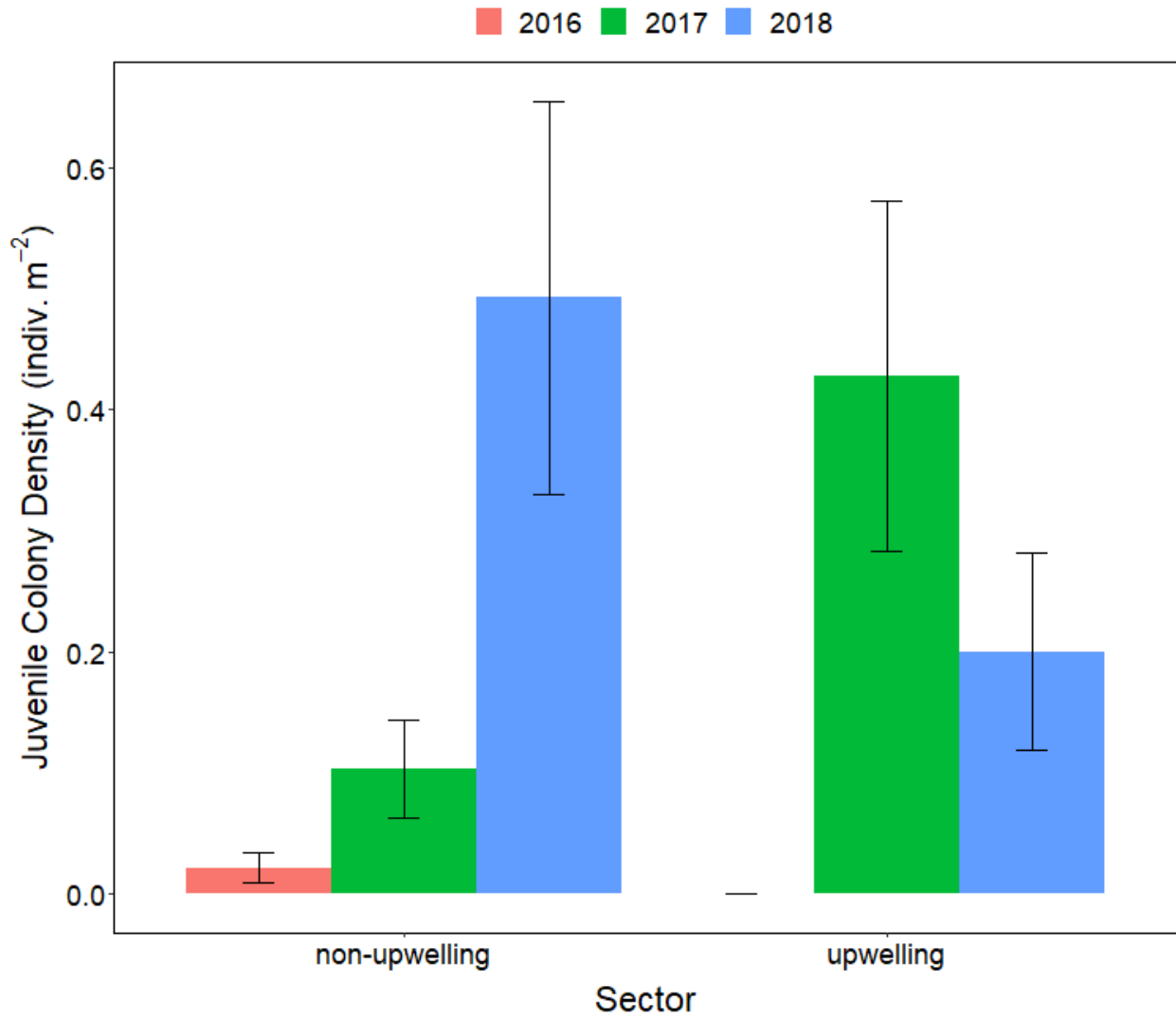
<b>Herbivores</b>	<b>% explained</b>	<b>Variance</b>	<b>Pseudo- F</b>	<b>p</b>
Full Model	8%	0.47	6.58	< <b>0.001</b>
Partial Models				
Scraper / Excavator	5%	0.42	11.58	<b>0.001</b>
Browser / Grazer	<2%	0.06	1.58	0.1

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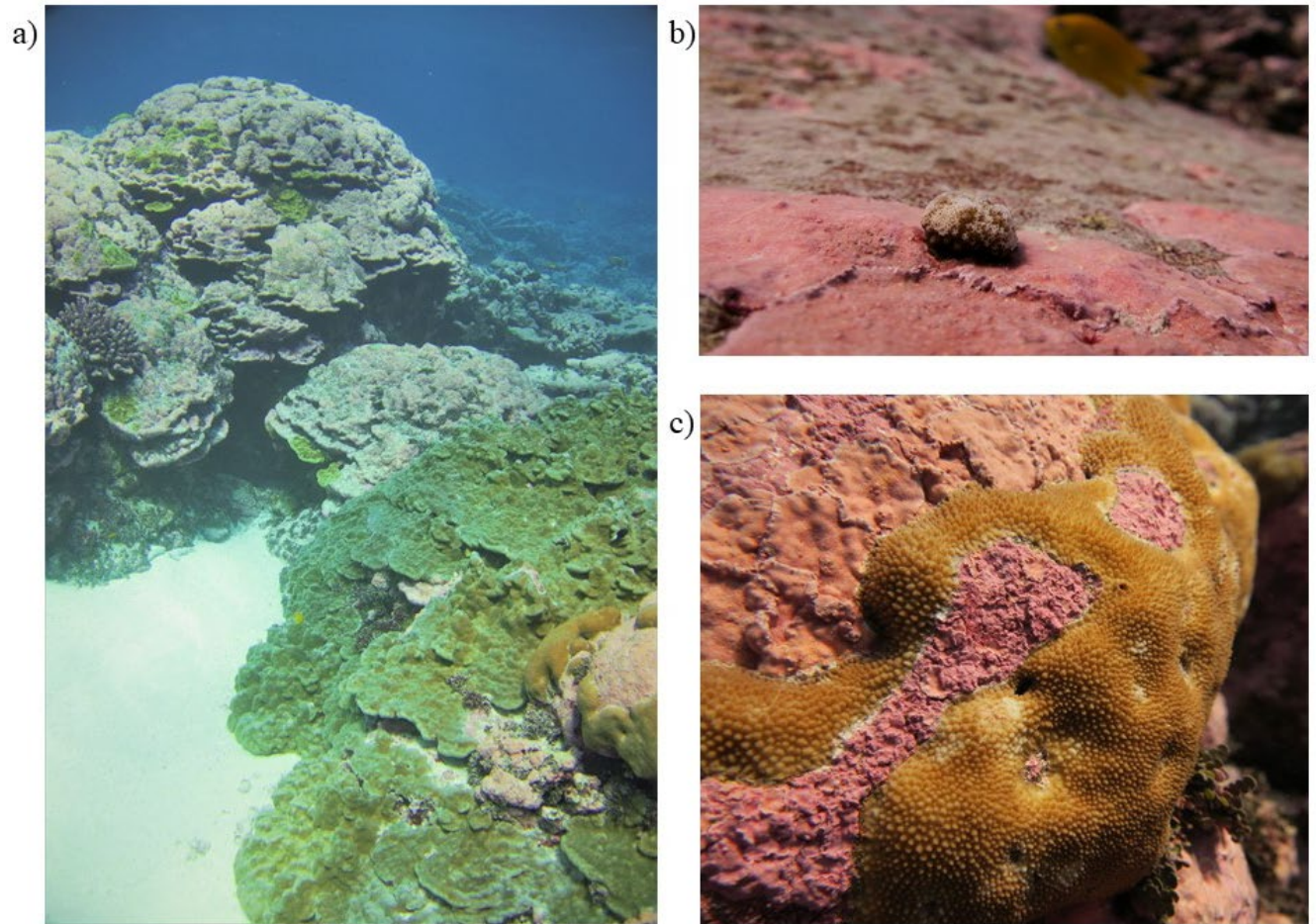


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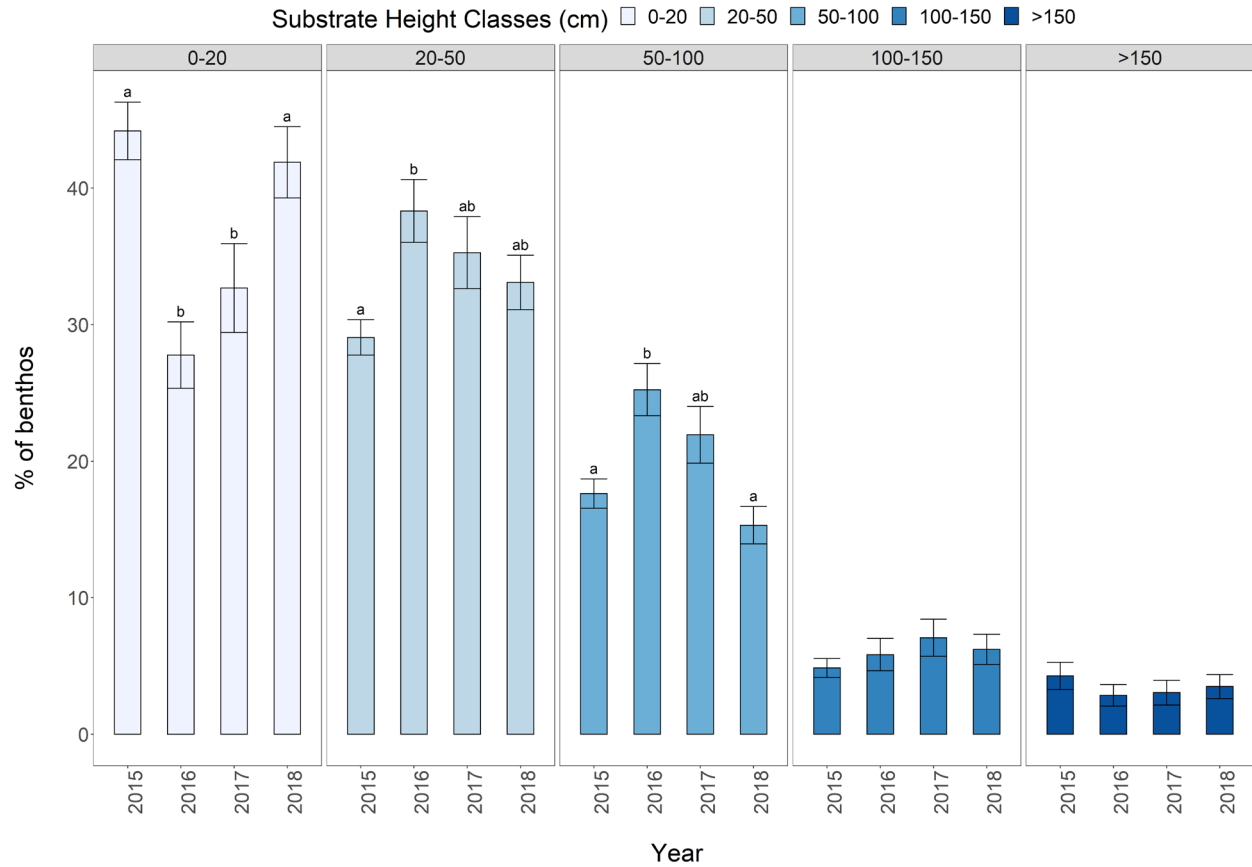
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**Figure S1.** Juvenile colony density (mean  $\pm$  SE) by sector and year following the mass bleaching event. No juveniles were observed in the upwelling sector in 2016.



13  
14 **Figure S2.** While no massive (e.g., < 2m diameter) *Porites* colonies were quantified during the  
15 2018 coral demographic surveys, several large surviving colonies were observed by divers in the  
16 shallow reef area (a), exhibiting varying ranges in partial mortality such as the live colony in the  
17 foreground and the dead colony covered in CCA in the background. Coral juveniles like this  
18 *Pocillopora* (b) were observed growing atop coralline algae, while other colonies like this  
19 *Hydnophora* (c) appear to be competing with thick crusts of coralline algae.

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24 **Figure S3.** Visual estimates of substrate complexity measured as the percent of the benthos at  
 25 each fish survey site (mean ± SE) occupied by each five classes of substrate height. Significant  
 26 differences among years for a given substrate height class are denoted by differing letters based  
 27 on Dunn's multiple comparison tests following significant Kruskal-Wallis tests. No letters  
 28 indicate no differences among years for a given class (Kruskal-Wallis,  $p > 0.05$ ).

29

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