

Extinction debt of Galápagos foundational coral associates: ENSO-related cold-water bleaching triggers community biodiversity loss and turnover

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Abstract

During a cold La Niña period (August 2007-January 2008) in the central Galápagos archipelago, 70% of *Pocillopora* finger corals were bleached across three long-term monitoring sites, affording an opportunity to examine the impact of El Niño Southern Oscillation-related temperature anomalies on the persistence of these corals and their associated community of fish and mobile macroinvertebrates. Using a time series empirical approach, we tagged and tracked the fate of 96 coral heads and their associates. When surveyed in July 2008, live (recovered) and dead corals supported similar levels of randomized observed species richness and Chao 1 estimated species richness. Whereas richness on the surviving live corals remained fairly stable, Chao 1 estimated richness on dead corals underwent a nearly 50% increase between July and January 2009, thereafter declining to 50% of originally surveyed richness by February 2010. This nonlinear change in species richness was largely due to influx and decline in opportunistic generalists including pencil urchin bioeroders, gastropod snails, and hermit crabs that colonized dead corals and fed on sessile invertebrates and algae that had initially recruited to dead and undefended coral substrate. Thus, dead corals retained high overall species richness until live corals had recovered; after which richness declined as dead corals eroded and disappeared (July 2011). Live corals attracted a less speciose but stable assemblage of mutualistic xanthid crabs and fishes that increased in abundance over time with the recovery and growth of live coral tissue. Overall, three physical features of the finger coral habitats (coral vital status, total surface area, and maximum branch length) predicted the number of species associated with each colony. The delayed diversity loss of associated species following La Niña disturbance to a foundation species represents a local extinction debt of 32-49-month duration. A better understanding of the scale of extinction debt in foundational marine ecosystems is needed to quantify the breadth of impacts of climate oscillations on biodiversity and ecosystem functioning.

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Should the manuscript be accepted, the data supporting the results will be archived in an appropriate public repository (Dryad, Figshare, or Hal) and the data DOI will be included at the end of the article.

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Abstract

During a cold La Niña period (August 2007-January 2008) in the central Galápagos archipelago, 70% of *Pocillopora* finger corals were bleached across three long-term monitoring sites, affording an opportunity to examine the impact of El Niño Southern Oscillation-related temperature anomalies on the persistence of these corals and their associated community of fish and mobile macroinvertebrates. Using a time series empirical approach, we tagged and tracked the fate of 96 coral heads and their associates. When surveyed in July 2008, live (recovered) and dead corals supported similar levels of randomized observed species richness and Chao 1 estimated species richness. Whereas richness on the surviving live corals remained fairly stable, Chao 1 estimated richness on dead corals underwent a nearly 50% increase between July and January 2009, thereafter declining to 50% of originally surveyed richness by February 2010. This nonlinear change in species richness was largely due to influx and decline in opportunistic generalists including pencil urchin bioeroders, gastropod snails, and hermit crabs that colonized dead corals and fed on sessile invertebrates and algae that had initially recruited to dead and undefended coral substrate. Thus, dead corals retained high overall species richness until live corals had recovered; after which richness declined as dead corals eroded and disappeared (July 2011). Live corals attracted a less speciose but stable assemblage of mutualistic xanthid crabs and fishes that increased in abundance over time with the recovery and growth of live coral tissue. Overall, three physical features of the finger coral habitats (coral vital status, total surface area, and maximum branch length) predicted the number of species associated with each colony. The delayed diversity loss of associated species following La Niña disturbance to a foundation species represents a local extinction debt of 32-49-month duration. A better understanding of the scale of extinction debt in foundational marine ecosystems is needed to quantify the breadth of impacts of climate oscillations on biodiversity and ecosystem functioning.

Keywords : species richness, foundation species, climate oscillations, temperature anomalies, coral bleaching, generalists, specialists

Main Text

Introduction

Habitat-forming foundation species such as trees, grasses, salt marshes, mangroves, kelp, seagrasses and corals have a disproportionately large influence on other species through provisioning of shelter or food (Dayton & Hessler 1972), and by enhancing associated species diversity (Witman 1985) and multiple ecosystem functions (Ellison et al. 2005, Angelini et al. 2015). Although foundation species and mutualisms can serve to buffer the effects of disturbances on natural communities (Witman 1987, Ellison et al. 2005, Altieri et al. 2007), anthropogenic impacts are reducing the abundance and distribution of foundation species (Osland et al. 2013) and decreasing the diversity of associated flora and fauna (Byrnes et al. 2011, Sorte et al. 2017), thereby threatening community resilience and functioning (Chapin et al. 1997, Duffy et al. 2015, De Boeck

et al. 2018). Yet many aspects of whole-community changes associated with disturbance-driven losses of foundation species remain poorly understood, especially related to the timing, pattern, and magnitude of associated species loss (Stella et al. 2011, Thomson et al. 2015). Importantly, changes in species abundance or diversity of communities associated with foundation species may not occur immediately after a disturbance, resulting in extinction debt, or a significant time delay prior to the disappearance or local extinction of a species from a particular habitat patch (Tilman et al. 1994, Kuussaari et al. 2009, Watts et al. 2020). Problematically, assessing post-disturbance community-wide biodiversity loss before extinction debt has been paid could lead to incorrect estimation (usually an underestimation) of the number and types of associated species vulnerable to local extinction (Hanski & Ovaskainen 2002, Watts et al. 2020).

Extinction debt occurs across diverse taxa associated with a range of foundation species, though it remains poorly understood in marine ecosystems. For example, the probability and timing of local extinction differs across taxonomic groups, life history traits, and in the relationship between associated species and the focal habitat created by a foundation species (i.e., habitat specialists, generalists) (Kuussaari et al. 2009, Hylander & Ehrlén 2013, Watts et al. 2020). The time to species loss after disturbance also depends on the size of the focal habitat created by the foundation species and on the intensity of disturbance (Hylander & Ehrlén 2013). However, as compared with plant-dominated terrestrial ecosystems, these and other aspects of extinction debt remain poorly understood for marine ecosystems (Kuussaari et al. 2009). Simulations of extinct debt in coral reefs (for communities of 40 coral species) suggest that extinction debt of associated invertebrates and fish was up to seven times higher relative to that of terrestrial forests (Tilman et al. 1994) for the same level of disturbance (Stone et al. 1996), potentially due to the high diversity of associated species of invertebrates and fish (Idjadi & Edmunds 2006, Stella et al. 2011, Canizales-Flores et al. 2021). Concerningly, given dramatic declines in coral reefs due to climate-change related ocean warming, acidification, and disease (Wellington et al. 2001, Hoegh-Guldberg & Bruno 2010, Pandolfi et al. 2011, Glynn et al. 2017), extinction debt of coral-associated species could lead to underestimates of the pace and extent of marine biodiversity loss (Kuussaari et al. 2009).

Severe climate events can serve as natural field experiments for examining the effects of climate change-related disturbances on marine foundation species and associated species diversity (Byrnes et al. 2011, Sorte et al. 2017), which may also be used to better understand extinction debt in marine ecosystems. The El Niño Southern Oscillation (ENSO) is a global climate event characterized by anomalously warm (El Niño) and cold (La Niña) temperature fluctuations in Pacific ocean temperatures (Holmgren et al. 2001, Trathan et al. 2007), which are characterized by temperature anomalies that have increased in intensity and duration with climate change (Cai et al. 2015), contributing to declines in foundational kelps, seagrasses, and corals (Dayton et al. 1992, Campbell et al. 2011, Hughes et al. 2017). The growing appreciation that the frequency and or magnitude of extreme climatic events is increasing with global climate change underscores the importance of investigating links among environmental stress, foundation species and diversity change.

The Galápagos Archipelago is a place of unique marine biodiversity that has been repeatedly subjected to extreme ENSO events, systematically reducing coral cover (Glynn et al. 2018) and likely threatening coral- and reef-associated species (Edgar et al. 2010). Sustained high temperatures during the ENSO warming phases of 1982-1983 and 1997-1998 resulted in widespread loss of foundational scleractinian corals (95% and 27% declines in cover, respectively) (Glynn 1984, Glynn et al. 2001). Heavy bioerosion of dead corals eliminated much of the reef matrix, replacing patchy coral reefs with scattered coral heads (Glynn 1984, Glynn et al. 2001). Ongoing ENSO-related cold and warm phases (2007 La Niña, 2010 El Niño) resulted in further stress-related coral bleaching and death (Glynn et al. 2017, 2018). These ENSO events dramatically affected many coral species, the most common of which are habitat-forming finger corals (family Pocilloporidae), which typically host a diverse assemblage of invertebrates and fishes (Abele 1976, Glynn 1984, Hickman 1999). These coral-associated species were likely negatively affected by declines in continuous coral cover (Edgar et al. 2010), as well as potentially by ENSO-related temperature anomalies (Glynn et al. 2018). However, the effects of ENSO events on coral-associated community diversity and diversity-function relationships have yet to be assessed, as is any evidence of whole-community extinction debt in the Galápagos.

In this study, we examined the effects of a coral bleaching event in the Galápagos Islands triggered by a cold-water anomaly during the 2007-2008 La Niña on structurally complex *Pocillopora* spp. corals and on the communities of mobile macroinvertebrates and fishes associated with them. By measuring changes in the communities, we used a time series (July 2008, January 2009, July 2009, February 2010) empirical approach to investigate extinction debt (Kuussaari et al. 2009, Ridding et al. 2021). We tracked the extent of coral bleaching was first surveyed in January 2008 and the general fate of the finger coral habitats over a 49-month period starting in August 2007 and ending in July 2011 (Figure S1). This period of time included two additional ENSO-related temperature events: a La Niña (2008-2009) and an El Niño (2009-2010, United States National Oceanic and Atmospheric Administration, National Environmental Satellite Data and Information Service, NOAA/NESDIS, https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php). Despite another La Niña occurring from October 2008-April 2009 and an El Niño from June 2009-April 2010, these live corals did not bleach subsequent to the 2007-2008 La Niña (J. Witman and O. Rhoades, pers. obs.), suggesting that the 2007-2008 La Niña cold-water anomaly and bleaching triggered the loss of most of the coral heads.

We addressed the following questions: 1) How did a La Niña-related cold-water anomaly and associated coral bleaching alter the availability and quality of finger coral habitats? 2) Did coral bleaching reduce associated species richness, and 3) if so, was there a time lag in associated species loss and diversity changes (extinction debt) in the communities inhabiting corals? 4) Post-bleaching, did the community structure of associated invertebrates and fishes (species abundance, composition) differ between dead versus live (recovered) finger corals? Finally, 5) what attributes of the live and dead foundational finger coral habitats predicted the species richness of the associated community? Here we use the term extinction to refer to local extinction, which is the disappearance of a species from a habitat patch (Kuussaari et al. 2009, Watts et al. 2020), and not as a reference to regional or global species' extinctions.

Methods

Subtidal temperatures were recorded at 10-minute intervals during the La Niña period (NOAA/NESDIS, https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php) by Onset Tidbit™ loggers placed at 6 and 15 m depth at two of the three study sites: Baltra (00 24.705 S, 090 16.482 W) and Guy Fawkes (00 29.964 S, 090 30.773 W). No temperature data is available for the third study site Rocas Beagle (00 24. 797 S, 90 37.685 W), due to logger malfunctioning at this site. However, temperatures were also recorded at 15 m depth at an additional reference site, Cuatro Hermanos (00 84.787 S, 090 74.908 W), located 40 km southwest of Guy Fawkes to provide insight into the spatial scale of the cold-water event. Bleaching of *Pocillopora* corals during cold water events has been recorded at temperature thresholds of 19°C in the Gulf of California (Paz-García et al. 2012), while temperatures of 18.5-19°C stressed *P. verrucosa* in lab experiments (Rodríguez-Troncoso et al. 2013). Sustained cold water temperatures well-below reported thresholds of 16°C (11 and 12°C, respectively) resulted in widespread bleaching and mortality of many scleractinian coral species along the Florida reef tract (Lirman et al. 2011, Kemp et al. 2011). We thus considered the 2007-2008 Galápagos temperature records for the amount of time (i.e., hours and days) that temperatures were less than or equal to one or both of two cold-water thresholds identified in the literature (16°C and 18°C), which serve as conservative indicators of the low temperature stress to *Pocillopora* colonies (Table 1). In addition to our temperature loggers, we also obtained information regarding the cold-water plume from the NOAA Coral Reef Watch (Fig. S2, extracted from NOAA/NESDIS, <https://coralreefwatch.noaa.gov>).

As part of our bi-annual biodiversity monitoring surveys we observed substantial bleaching of finger (Pocilloporidae) and massive (Poritidae, Pavonidae) corals in the central Galápagos Archipelago. This coral bleaching occurred during a 5-7-month window, between June 2007 (when bleaching was not present) and January 2008 (when it was first observed) (Figure S1). To address our research questions, we first counted using SCUBA the number of finger coral colonies that were alive, bleached or dead in January 2008 in 2-3 large plots (30 x 5 m) at 6-12 m depth at each of the three aforementioned study sites. In July 2008, we marked dead and live (recovered) finger coral colonies with numbered plastic tags at 4-15 m depth across larger areas (approximately 600 m²) than the initial survey plots at these sites. Tagged corals (potentially

including *P. verrucosa*, *P. capitata*, *P. damicornis*, *P. eydouxi*, *P. meandrina*) were aggregated at the genus level (*Pocillopora*) due to the difficulty of identifying them to species, as the coral calcium carbonate structure of many dead corals had degraded. A total of 96 discrete *Pocillopora* coral heads were tagged and successfully tracked across all time-series surveys at the three sites (Baltra, n=29, Guy Fawkes, n=31, and Rocas Beagle, n=36).

We surveyed the fish and mobile macroinvertebrates (1.0 cm total body length or larger) associated with the tagged corals in July 2008, January 2009, July 2009, and February 2010. A diver slowly approached each tagged coral (at a short distance) and first identified and counted all visible fishes sheltering within, swimming in and out of, or hovering over the coral head. We only counted fishes within 10 cm of coral branches, with the exception of juvenile damselfish, which were included in fish counts but were often slightly further from coral heads. The diver then approached the coral more closely and identified all cryptic fishes (e.g., blennies and gobies) and mobile macroinvertebrates (e.g., crustaceans, echinoderms, and gastropods). One observer (O. K. Rhoades) conducted all the *in situ* counts to maintain the consistency of methodology and species identifications. Gastropods were identified with the assistance of local experts at the Charles Darwin Research Station. We did not census mobile invertebrates smaller than 1 cm total body length, nor did we survey sessile invertebrates or algae that recruited onto the dead corals.

The size of each tagged coral head was measured as the 2D surface area from an overhead photograph of the colony taken with a quadrapod camera framer (Witman 1985) designed to hold a Nikonos camera, a 15 mm lens corrected for barrel distortion and two strobes. Colony photographs were taken perpendicular to the substrate to obtain a standard overhead view in a 0.25 m² photo quadrat. We also surveyed the maximum branch length per coral head. Surveys of the communities associated with each finger coral head were conducted at a separate time and during a different dive from photographing of coral area (to avoid potentially disturbing and displacing fishes from corals with photography equipment and additional SCUBA divers), and at midday (to avoid confounding diurnal differences in associated community composition with variation in associated composition over time), on a single day at each time point to avoid recounting fish moving among adjacent coral habitats.

During the initial bleaching survey in January 2008, and on the four subsequent sampling periods (July 2008 - February 2010), we recorded the status of tagged corals as live if they had at least 50% cover of live tissue. For dead corals, we recorded if they had eroded, broken apart into rubble, or completely disappeared. A final survey was conducted in July 2011 at all three sites by J. Witman to only determine the persistence of the tagged, dead corals.

Statistical analyses

We compared the richness of coral-associated macrofauna on live and dead corals over time, first of all surveyed macrofauna, as well as each for fishes and mobile macroinvertebrates, separately. We calculated randomized observed species richness ('observed species richness') of the community associated with finger coral heads by constructing randomized Species Accumulation Curves (SACs), calculating the mean SAC and its standard deviation from random permutations of the data, or subsampling without replacement (Gotelli & Colwell 2001). We also calculated Chao 1 estimated species richness ('Chao 1 estimated richness') for the entire community, fishes and mobile invertebrates, of coral heads using the Chao 1 estimator, a non-parametric species estimator for abundance data (Chao et al. 2009), including 95% confidence intervals based on the actual Chao estimator (Colwell & Elsensohn 2014).

We also compared the composition of coral-associated macrofauna on live and dead corals over time by performing a Principal Components Analysis (PCA) using raw abundances of coral-associated macrofauna as the response variables and treating each individual coral head in each survey as an individual sample. The PCA algorithm used unweighted singular value decomposition on values fitted using unweighted linear regression of chi-transformed data (Legendre and Legendre 2012). We then calculated Euclidean dissimilarities in composition using multiscale bootstrapped resampling.

Finally, we assessed the attributes that predicted associated richness by constructing linear mixed effects

models of associated richness per coral head, first for all macrofauna, and then each for fishes and mobile macroinvertebrates. Overhead surface area of the coral colonies and maximum coral branch length were treated as fixed effects, individual coral heads and sites included in the model as random intercepts, and time was treated as a random slope.

We ran mixed effects models using the lme4 R package (Bates et al. 2015), we ran rarefaction (species accumulation curves) and principal components analysis using the vegan R package (Oksanen et al. 2020), and we calculated Chao 1 total estimated richness using the SpadeR package (Chao et al. 2016). All statistical analyses were conducted using R software (version 3.6.2, R Core Development Team 2017).

Results

Temperature

Minimum temperatures at two of the study sites ranged from 13.9°C at Guy Fawkes (at 15 m) to 16.3°C (at 6 m) depth at Baltra, and were similarly low (14°C) at the Cuatro Hermanos reference site (Table 1A). Temperatures were at or below the threshold of 18°C for *Pocillopora* bleaching for 6.3 to 34.3 days at Baltra (6 m) and Guy Fawkes (15 m) respectively (Table 1B). At Guy Fawkes, the subtidal environments experienced the colder bleaching threshold of 16°C or lower for less than 1 hour at 6 m, but this time period increased to 54.6 hours at 15 m depth. Temperatures were colder at the Cuatro Hermanos reference site, where they were 18°C or lower for 59.5 days and 16°C or lower for 5.3 days (Table 1B).

Satellite images of minimum sea surface temperatures (SST) confirmed our temperature logger data and depicted a cold-water plume moving northwest along the South American Coast and deflecting offshore to reach our study area in the central Galápagos. During August-October 2007 the minimum SST of 15-20°C occurred (Figure S2). This was likely the origin of the cold water that led to coral bleaching, given that we recorded substantial temperature declines at 6 and 15 m depth during this same time period (Figure 1). By January 2008, the minimum SST had increased to 20-25°C (Figure S2).

Effects of ENSO-related cold-water anomalies on finger corals

After the 2007-2008 La Niña bleaching, a minority of bleached corals recovered their pigmentation and survived, while most corals died and eroded (Figure 2A). When surveyed 6-13 months post-bleaching in July 2008 (Figure S1), only 24% (n=26) of surveyed *Pocilloporaspp.* colonies had fully recovered their color, 6% had partially recovered live tissue, but experienced at least 25-75% tissue loss, and 69% (n=75) of all bleached coral colonies (as in Figure 2C) had died and were colonized by mobile and sessile invertebrates, fish and algae (as in Figure 2D). Subsequent monitoring between July 2008-February 2010 revealed that 3% (n=3) of corals had visibly eroded, 14% (n=15) had detached from the substrate and broken into coral rubble, and 12% (n=13) had completely disappeared, with their fragments likely washed away by currents. Over this survey period, live corals (560-616 cm²) had not lost overhead surface area, whereas dead corals (419-474 cm²) had lost an average of 13% overhead surface area and were on average 24% smaller than live corals (Figure 2B). All finger corals that had initially bleached and died at the beginning of the study in January 2008 had disintegrated by July 2011 (Figure 2B). Over the survey period, the live corals did not bleach or deteriorate subsequent to the 2007-2008 La Niña (J. Witman and O. Rhoades, pers. obs.).

Post-bleaching shifts in coral-associated species richness

Randomized observed species richness (Figure 3) and Chao 1 estimated species richness (Figure 4) of associated species varied significantly across certain time points and/or between live and dead corals. In July 2008, which was 6-13 months post-bleaching and within the 2007-2008 La Niña period, live and dead corals supported similar observed (20-21 species) and Chao 1 estimated (40-41 species) total species richness (Figures 3A, 4A). However, observed total species richness on dead corals increased to 25 species in January 2009 relative to July 2008 (including seven fishes and 19 macroinvertebrate species), and then it declined thereafter until February 2010 (Figure 3A). By contrast, observed total species richness (and observed fish richness) on live corals was initially higher in July 2008 (and higher than on dead corals in July 2008) and

comprising 20 species (including 9 fishes and 11 macroinvertebrate species), decreased in January 2009, and remained stable through February 2010 (Figure 3A-B).

Across all sampling dates, Chao 1 mean estimated total richness was 16-41 and 16-61 total species (Figure 4A), 4-10 and 5-16 fish species (Figure 4B), and 10-21 and 8-73 invertebrate species (Figure 4C) associated with live and dead corals, respectively. Similar to observed species richness, between July 2008 and January 2009, Chao 1 estimated total and invertebrate species richness on dead corals underwent a nearly 50% increase, from 41 to 61 total species richness and from 25 to 73 invertebrate richness, then declined significantly to 25 total and 20 invertebrate species richness in July 2009, and ultimately to 16 total and 8 invertebrate species richness in February 2010 (Figure 4A&C). By contrast, Chao 1 estimated total and invertebrate species richness on live corals did not significantly differ across most time points, and fluctuated from 41 to 24 to 35 total species and 21 to 21 to 18 invertebrate species from July 2008 to July 2009, but it significantly declined to 16 total and 10 invertebrate species richness in February 2010 (Figure 4A&C). By contrast, Chao 1 estimated fish richness declined over time on dead corals (from 16 to 7 to 5 to 9 species) and live corals (from 10 to 4 to 7 to 5 species), and in July 2008 it was significantly higher than in any other time periods (Figure 4B).

Differences in coral-associated species on live and dead corals

Principal component analysis (PCA) of the entire community of fish and mobile macroinvertebrates associated with the finger corals indicated that the overall species composition of the communities differed significantly between live and dead corals (Figure 5A, see Figure S3 for explanation of PCA species scores). Species composition also differed among certain time points, especially between the first time point (July 2008) relative to other time points for live corals and dead corals, and between the last time point (February 2010) relative to other time points for live corals (Figure 5A). Live corals were characterized by high PC1, which increased across time points, and was strongly correlated with the presence of mutualistic xanthid crabs *Trapezia ferruginea* and *Trapezia digitalis* (Figure S3A). Dead corals were characterized by lower values of PC1, which was strongly correlated with the presence of the pencil urchin *Eucidaris galapagensis* (Figure S3A). Relative to the latter points, earlier time points were characterized by lower PC2 values, which were strongly correlated with the presence of the pencil urchin and juveniles of the ring-tailed damselfish *Stegastes beebei*, as well as a speciose assemblage of opportunistic snails (Figure S3B).

Live and dead corals exhibited strong overlap in fish assemblages (Figure 5B), but particular differences in the community of associated invertebrates (Figure 5C-D). With respect to coral-associated fishes, live and dead corals were dominated by two territorial and residential fish species: the coral hawkfish *Cirrhitichthys oxycephalus* and the juvenile ring-tailed damselfish *Stegastes beebei*; though the abundance of these species varied seasonally, and ultimately declined by 65% and 90%, respectively (particularly on dead corals) between July 2008 and February 2010 (Figure 5B). Other common species at certain time points (e.g., *Ophioblennius steindachneri* in July 2008 and *Lythrypnus gilberti* in January 2009 on dead corals and *Thalassoma lucasanum* in July 2008 on live corals) also exhibited high seasonal variability in abundance (Figure 5B).

With regards to coral-associated invertebrates, dead corals hosted opportunistic and predatory macroinvertebrate species, dominated by the pencil urchin *Eucidaris galapagensis*, hermit crabs (Figure 5C), and a rich assemblage of 16 species of gastropods, especially two species of *Engina* as well as *Muricopsis zeteki*, which increased between July 2008 and January 2009 (Figure 5D). The abundance of pencil urchins on dead corals increased initially by 100% (21 to 42 individuals) between July 2008 and January 2009, and then declined by 62% between January 2009 and February 2010 (Figure 5C). Pencil urchins were observed feeding directly on the calcium carbonate structure of dead and occasionally bleached live coral tissue, while gastropods and hermit crabs were frequently observed feeding on the sessile invertebrates (barnacles, sponges, ascidians, bryozoans) that had colonized dead coral skeletons (O.K. Rhoades, pers. obs.). By contrast, the coral-associated invertebrates on live finger corals were dominated by hundreds of mutualistic xanthid crabs (*Trapezia spp.* including *Trapezia ferruginea* and *Trapezia digitalis*) (Figure 5C). The total number of mutualistic crabs increased by 300% (71 to 284 individuals) between July 2008 and February 2010 (Figure 5C). Gastropods were considerably (10 times) more abundant on dead corals relative to live corals (Figure

5D).

Relationships between coral habitat attributes and associated species richness

Three physical attributes of finger coral habitat structure: coral status (live/dead) ($p < 0.0001$), overhead surface area ($p = 0.0025$) and maximum coral branch length ($p = 0.0005$), predicted the number of species associated with the corals (Table 2). Ordinary Least Squares (OLS) regression analysis indicated that total species richness was positively and linearly related to the top surface area of the colonies, although the significance and strength of these relationships varied between live and dead corals and across time points (Figure 6). Species-area relationships were significant for live corals across all time points (Figure 6, bottom panel), whereas they were only significant for dead corals for the two latter time points (Figure 6, top panel). Surface area also explained a greater proportion of total variation in species richness for live versus dead corals ($r^2 = 0.26$ to $r^2 = 0.62$ versus $r^2 = 0.15$, respectively, Figure 6). The richness of coral-associated macrofauna increased by 14-22 species per a projected 1.0 m^2 increase in live coral surface area across time points, and by 18 species per a projected 1.0 m^2 increase in dead coral surface area (Figure 6). Tighter species-area relationships on live corals were driven by fishes ($r^2 = 0.47$ to $r^2 = 0.58$) relative to invertebrates ($r^2 = 0.19$ to $r^2 = 0.29$). For dead corals, richness of associated species was poorly predicted by coral surface area for both fishes ($r^2 = 0.08$ to $r^2 = 0.14$) and invertebrates ($r^2 = 0.06$ to $r^2 = 0.14$) (Figure S4A-B).

Species richness of the associated community was also predicted by the length of live finger coral branches (Figure S5). The richness of coral-associated macrofauna increased in live corals by 8-25 species per a projected 1.0 m increase in coral branch length at three of four time points ($r^2 = 0.29$ to $r^2 = 0.43$). On the other hand, branch length of dead finger corals showed either a weak positive ($r^2 = 0.21$, July 2009) or weak negative ($r^2 = 0.17$, February 2010) relationship with species richness of the associated community (Figure S5 top panel).

Discussion

Strikingly, nearly 70% of *Pocillopora* corals bleached and died between August 2007 and July 2008 at our three study sites in the Galápagos, which coincided with the 2007-2008 La Niña-related cold-water anomaly. This represents a major loss of live coral foundational habitat for associated fishes and mobile macroinvertebrates. Nevertheless, dead coral colonies were still able to retain the ecosystem function of hosting high species richness of associated fish and mobile macroinvertebrates for more than two years after the disturbance. However, the species composition of these assemblages (and particularly of invertebrates) significantly varied between mutualistic xanthid crabs on live corals to opportunistic and predatory pencil urchins, hermit crabs, and gastropod snails on dead corals, and shifted over time on live and dead corals. This shift in associated species composition was likely due to changes in structure and provisioning of food on coral tissue, and loss or growth of live coral tissue. Furthermore, the speciose and opportunistic associated assemblage on dead corals ultimately declined in richness due to erosion and disappearance of complex coral structure, and likely led to loss of coral-associated richness after 32-49 months.

Cold water effects on corals

Our observations suggest that an ENSO-related cold-water anomaly led to bleaching and death of finger corals. The bleaching period coincided with the arrival of a plume of cold water ($15\text{-}20^\circ\text{C}$ minimum SST) flowing up the west coast of South America, arriving in the central Galápagos during October 2007. During this time period, corals were exposed to temperatures at or below published cold water thresholds for coral bleaching, including 18°C for up to 34 days and 16°C or less for 2.3 days at Guy Fawkes (15 m depth). Temperatures at Baltra (15 m) were at or below the 18°C threshold for 18.8 days. As expected, temperatures decreased with depth from 6 to 15 m. Longer periods of unusually cold water occurred at the reference site Cuatro Hermanos (where corals are rare) likely related to the presence of stronger upwelling currents relative to those at Guy Fawkes or Rocas Beagle (Witman et al. 2010).

In general, cold-water coral bleaching has received less attention than warm water bleaching, although it can cause extensive coral mortality. For example, (González-Espinosa & Donner 2020) documented cold-water

coral bleaching at 14 sites in the Eastern Tropical Pacific alone from 1998 -2017. One of these events was reported from the northern islands of Darwin and Wolf in the Galápagos where bleaching of three coral species (*Porites lobata*, *Pocillopora spp.* and *Pavona clavus*) occurred in 2007 when SST were 16°C (Glynn 2009, Glynn et al. 2017), which was likely caused by the same La Niña event reported in this study. Given that climate models predict that the frequency of extreme La Niña events and associated cold-water anomalies will increase with climate warming (Cai et al. 2015), our study suggests that more attention should be paid to the consequences of coral bleaching caused by low temperatures.

Coral-associated richness

Our study of *Pocillopora* colonies in the central Galápagos rocky subtidal ecosystem contribute to the growing number of studies that show that finger corals host a diverse assemblage of fish and invertebrates. Our surveys showed that recently recovered *Pocillopora* colonies supported up to 20 observed species (randomized observed species richness), and up to 41 total estimated species (Chao 1 estimated species richness), including nine known fishes and 11 known mobile macroinvertebrate species. Dead colonies of the same Genus supported an even greater diversity of up to 25 observed species and 61 total estimated species, including seven known fishes and 18 known mobile macroinvertebrate species. Even so, these species estimates are an underestimate of the actual diversity of the entire community of associated species, since (for ethical considerations) we chose not to collect corals and exhaustively census the mobile fauna living in the interstices of the coral, or the sessile invertebrates and algae that colonized the dead *Pocillopora* colonies.

The biodiversity of communities associated with *Pocilloporacorals* has been extensively studied in other tropical regions, and the range of our estimated values of species richness (20-41 species associated with live corals depending on the mode of analysis) falls within the range (though at the lower end) of published values of *Pocillopora* communities in other regions. The seminal work of (Abele & Patton 1976) demonstrated that off the Pacific coast of Panama (close to the Galápagos study region), *Pocillopora* colony area predicted the species richness of the decapod community associated with the corals, supporting 61 total species of decapods. Subsequent work has found that 36-127 species were found associated with *Pocilloporacorals* at locations from the Red Sea to Hawaii (Britayev et al. 2017). Consequently, declines in finger coral habitats appear to represent an important loss of foundational habitat for a diverse assemblage fishes and invertebrates.

Extinction debt of coral associates

Coral associates experienced biodiversity loss multiple years after disturbance to their foundational habitat, which coincides with loss of richness in other ecosystems. Indeed, bleached and dead finger coral habitats retained high levels of species richness for 13-19 months after the bleaching disturbance occurred; in fact, species richness of mobile macroinvertebrates considerably increased during this time period. However, this trend was reversed by a significant loss of mobile macroinvertebrate richness 19-25 months post-bleaching. During the final survey of associated species, total Chao 1 estimated species richness on dead corals was significantly lower relative to corals at earlier time points, and relative to live corals at that time. Depending on how long after our initial survey (June 2007) bleaching actually occurred, and how long before our final survey (July 2011) corals disintegrated, we estimate that it took between 32 and 49 months for the bleached *Pocillopora* to disintegrate and entirely disappear, driving the species richness of associated fish and macroinvertebrates down even further, possibly to zero as their habitat was lost.

Coral-associated richness on live versus dead corals

As with standing dead wood forests on land that have died due to disease or herbivorous insect attacks (Stokland et al. 2012, Seibold et al. 2015, Thorn et al. 2020), bleached and dead finger corals retained their biodiversity-enhancing function for multiple years after cold-water bleaching and death. This is both related to the habitat provided by the complex branching structure of the finger corals, as well as the food provided by sessile invertebrates and algae that rapidly recruited to and grew on the dead and undefended corals (Hadfield & Paul 2001, McCook et al. 2001). In this study, both overhead surface area and maximum branch length of *Pocillopora* corals significantly predicted the number of associated species, aligning with theory that habitat complexity is a leading predictor of species diversity (MacArthur & MacArthur 1961), and that

coral colony surface area and branch length are indicators of the habitable area or volume for associated fishes and invertebrates (Abele & Patton 1976, Britayev et al. 2017). Our study further demonstrated that live tissue area was particularly important in determining the richness of associated species; surface area (and coral branch length, to a lesser extent) accounted for a much greater proportion of the total variation in species richness on live corals versus dead corals (26-62% versus 15%). As with other recently disturbed and dead foundational habitats, live coral habitat has greater structural integrity and complexity relative to dead coral structure, such that live coral area is more representative of habitat area. Additionally, dead corals provide supplementary, ephemeral functions related to provisioning of food, which differ from the habitat and food functions provided by live corals, which attract a disproportionately rich assemblage of opportunistic coral associates.

Accordingly, the richness and composition of the associated communities differed between live and dead finger coral habitats, and these differences magnified over time. Though the composition and abundance of fishes (dominated by coral hawkfishes and juvenile damselfishes) was similar on live and dead corals, abundance was highest at the first community census and then fluctuated over time on live corals, while both fish species decreased in abundance over time on dead corals. Moreover, live and dead corals exhibited distinct assemblages of invertebrates, with symbionts and specialists occupying live corals, versus opportunistic generalists occupying dead corals, and each of these assemblages became more and more distinct as live corals recovered and grew, while dead corals simultaneously eroded into rubble and disappeared.

Species composition on recovered, live corals exhibited a shift over time toward total dominance by xanthid crabs (genus *Trapezia*), highlighting the importance of live coral habitat for this species. Trapeziid crabs are obligate residents that feed on live coral tissue while also defending corals from attack (Stewart et al. 2006, Stella et al. 2011). *Trapezia* crabs exhibited a striking increase in abundance on live corals between July 2008 and February 2010, possibly due to redistribution of individuals from recently dead to remaining live (recovered) corals, which has been found to occur after widespread bleaching (Glynn et al. 2017), according to colony size (Canizales-Flores et al. 2021). It is possible that the large increase in the number of *Trapezia* occupying the live coral habitats from July 2008 to February 2010 at the Galápagos sites reflects habitat limitation due to the reduction of live coral habitats after the bleaching-induced mortality of *Pocillopora spp.*, in addition to growth of live tissue on those colonies over time. Overall high mobility of the fish, crustacean, and echinoderm fauna associated with live and dead corals suggests that active dispersal could explain the surge of species richness in the dead coral habitats between July 2008-January 2009 and the increase in abundance of *Trapezia* crabs in live corals. Our results also suggest that a metapopulation perspective (Hanski & Ovaskainen 2002) may be a useful conceptual framework for investigating post-disturbance patterns of live and dead coral habitat occupancy, at least in this system of discrete finger corals in the Galápagos, and for tropical reefs of other regions where disturbances result in increasingly patchily and sparsely-distributed branching coral colonies.

By contrast, bleached and dead corals exhibited rapid colonization by opportunistic and transient urchins, crabs, and gastropod snails, which ultimately declined due to loss of structure. These mobile macroinvertebrates contributed to a marked, non-linear change in associated community richness; first an increase in total species richness on recently dead corals between the first two community surveys (July 2008-January 2009), and thereafter a striking decrease over the next 13 months to February 2010. These species included large numbers of the well-known pencil urchin bioeroder, *Eucidaris galapagensis*, as well as hermit crabs and a number of species of gastropod snails. These species were observed to be feeding on dead coral tissue and sessile invertebrates, which may have arrived via migration of juveniles and adults and/or larval recruitment onto undefended coral skeleton habitats. These species declined in abundance and richness over time as corals disappeared into rubble, serving to temporarily enhance overall coral-associated community abundance and richness until obligate specialists recovered on live corals.

Consequences of finger coral declines for coral specialists versus generalists

Theory predicts that extinction debt should vary depending on the degree of habitat specificity of associated species (Kuussaari et al. 2009, Hylander & Ehrlén 2013, Watts et al. 2020) with generalists characterized

as having broad habitat requirements and specialists “largely dependent on one particular habitat type” (Watts et al. 2020). Specialists with low dispersal should have relatively short duration extinction debt, while generalists with high dispersal would have the longest extinction debt, as they could utilize other habitats after a disturbance. Of the *Pocillopora* associated community of fishes and mobile macroinvertebrates, we have sufficient information on small-scale (within-habitat) distribution to estimate that at least six species can be considered largely dependent on the *Pocillopora* habitat. These include three species of *Trapezia* crabs which are known obligate *Pocillopora* mutualists (Glynn 1976, Hickman & Zimmerman 2000), the spider crab *Telephrys cristolipes* described as inhabiting finger corals in Hickman & Zimmerman (2000), the corallivorous gastropod *Babelomurex hindsii*, and the coral hawkfish *Cirrhitichthys oxycephalus*, which is frequently observed in finger corals and among black corals in the Galapagos (J. Witman, pers. obs.). As in most communities of mobile species such as birds (Watts et al. 2020), insects (Hanski & Ovaskainen 2002), and reef fishes (Kritzer & Sale 2006), the community of fishes and macroinvertebrates associated with live and dead finger corals represents a mix of habitat and food specialists and generalists. Future research to identify habitat specialist species on Galápagos reefs is needed to understand those species most vulnerable to habitat loss and to overall biodiversity loss following future temperature stress from climate oscillations.

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Tables

Table 1 . Water temperatures (degC) per depth at the two study sites (Baltra and Guy Fawkes) and at 15 m depth of the reference site (Cuatro Hermanos) during June 2007- January 2008, including (A) summary statistics (SD=standard deviation, CV=coefficient of variation), and (B) the amount of time in hours and days at or below cold-water threshold temperatures (16 and 18degC) that are known to produce widespread coral bleaching elsewhere (see main text).

(A)

Site	Depth (m)	Recordings (n)	Mean	Min	Max	Median	SD	CV
Baltra	6	31,560	20.9	16.3	24.7	21.2	1.5	7.2
	15	31,564	20.4	15.3	24.7	20.7	1.6	7.8
Guy Fawkes	6	32,520	20.2	15.8	23.6	20.3	1.2	5.8
	15	32,518	19.6	13.9	23.4	19.8	1.4	7.1
Cuatro Hermanos	15	32,454	18.9	14	22.5	19.0	1.3	6.9

(B)

Site	Depth (m)	Hours [?] 16°C	Days [?] 16°C	Hours [?] 18°C	Days [?] 18°C
Baltra	6	NA	NA	151.5	6.3
	15	14.1	0.6	451.8	18.8
Guy Fawkes	6	0.7	NA	237.3	9.8
	15	54.6	2.3	825.3	34.3
Cuatro Hermanos	15	127.3	5.3	1428.1	59.5

Table 2 . Maximum likelihood (ML) estimates and 95% confidence intervals for linear mixed effects model of coral-associated species richness, including coral status (live/dead), coral overhead surface area, coral maximum branch length, and the interaction between coral status and surface area/branch length. Continuous predictors are centered and standardized, such that the full range of a continuous predictor is 2 units (compared to 1 unit for categorical predictors).

Predictor	ML Estimate, 95% confidence interval	Significance
Coral status (live vs dead)	0.54 (0.34, 0.75)	p<0.0001 ***
Coral overhead surface area	0.33 (0.12, 0.54)	p=0.0025 *
Coral max branch length	0.21 (0.09, 0.32)	p=0.0005 **
Coral status*Surface area	-0.22 (-0.46, 0.01)	p=0.062 (NS)
Coral status*Branch length	0.03 (-0.19, 0.26)	p=0.76 (NS)

Figure legends

Figure 1 . Composite plots of sea surface temperature regimes at Baltra, Guy Fawkes and Cuatro Hermanos (the reference site for Rocas Beagle) during the period of coral bleaching. Line color corresponds with temperatures recorded at 6 m (red) and 15 m (blue). Dashed lines correspond to the threshold cold temperatures (18°C and 16°C) that induce bleaching in *Pocilloporacorals*.

Figure 2. (A) Status of coral heads (by % surveyed with certain tissue characteristics) and (B) mean and standard error of overhead surface area of live (black) and dead (gray) coral heads across the time series (July 2008 to February 2010). Dead corals (but not live corals) were also surveyed in July 2011. (C) The same tagged coral head, surveyed in (C) July 2008 and (D) February 2010.

Figure 3 . Mean and standard deviation of species accumulation curves (SACs) of randomized observed associated species richness with live (black) and dead (gray) *Pocillopora* corals. Associated species include

(A) all surveyed species, (B) fishes and (C) mobile macroinvertebrate species. Blue and red underlining indicates La Niña and El Niño periods, respectively.

Figure 4. Means and 95% confidence intervals of Chao 1 estimated species richness of (A) all surveyed (total) species, (B) fishes and (C) mobile macroinvertebrates on live (black) versus dead (gray) corals at each survey date between July 2008 and February 2010. Note different scales on y-axis. Means with 95% confidence intervals that do not overlap the mean of the other group under comparison are significantly different (Ramsey & Schafer 2012).

Figure 5 . Species composition of coral-associated fishes and mobile macroinvertebrates surveyed on live versus dead coral heads at each survey date between July 2008 and February 2010. (A) Biplot of loadings for principal component 1 (PC1) by principal component 2 (PC2) from a principal components analysis (PCA) using abundances of coral-associated macrofauna as the response variables and treating each individual coral head in each survey as an individual sample. PC1 accounted for 24% of total variation in composition, while PC2 accounted for 15% of total variation in composition. Points refer to the community assemblage associated with individual corals, including live (square symbols) and dead (circle symbols) corals, sampled at each of four time points (represented by different colors). The ellipses show the 95% confidence regions for the mean centroids of each survey group (live or dead corals) surveyed at a specific date. Raw abundance of (B) fishes, (C) crustaceans and echinoderms, and (D) gastropods counted on live and dead corals across all survey dates. Asterisks (**) indicate species that are endemic to the Galápagos; “*other sp. Unknown 1*” and “*other sp. Unknown 2* in part (C) refer to unidentified crustaceans.

Figure 6 . Species-Area relationships, regressing estimated total richness against coral overhead surface area for individual dead or live coral heads at each survey date between July 2008 and February 2010. Regression line equations, r-squared values and p-values for significant relationships are shown. Note that dead corals did not exhibit significant S-A relationships in July 2008 and January 2009.

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