A depth refugium from catastrophic coral bleaching prevents regional extinction

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Abstract. Species intolerant of changing climate might avoid extinction within refugia buffered from extreme conditions. Refugia have been observed in the fossil record but are not well documented or understood on ecological time scales. Using a 37-year record from the eastern Pacific across the two most severe El Niño events on record (1982–1983 and 1997–1998) we show how an exceptionally thermally sensitive reef-building hydrocoral, Millepora intricata, twice survived catastrophic bleaching in a deeper-water refuge (>11 m depth). During both events, M. intricata was extirpated across its range in shallow water, but showed recovery within several years, while two other hydrocorals without deep-water populations were driven to regional extinction. Evidence from the subfossil record in the same area showed shallow-water persistence of abundant M. intricata populations from 5000 years ago, through severe El Niño–Southern Oscillation cycles, suggesting a potential depth refugium on a millennial timescale. Our data confirm the deep refuge hypothesis for corals under thermal stress.

Key words: coral bleaching; coral mortality; depth refuge; eastern Tropical Pacific; El Niño–Southern Oscillation; extinction; Holocene; Millepora; refuge.

INTRODUCTION

Species can survive a changing climate by possessing traits that allow them to tolerate new conditions, adapting to new conditions, or dispersing to or existing in habitats that are buffered from the changing conditions, i.e., refugia (Ashcroft 2010, Keppel et al. 2012). Environmental refugia have been observed in the fossil record (Tzedakis et al. 2002), but are not well documented or understood on ecological time scales. In the marine environment, the impacts of global climate change, most notably warming surface waters and ocean acidification, will be governed by the ability of species to either tolerate the direct and indirect effects of changing conditions, to persist in parts of their range that are buffered from extreme conditions, or to spread outside their present range to buffered habitats. For intolerant species or populations with restricted ranges and limited dispersal potential, the extinction risk will be increased, and extinction may be unavoidable without refuges.

Coral reefs present one of the clearest demonstrations of how climate change threatens to push species to population contractions and extinctions. Shallow-water reef-building corals lie perilously close to their upper thermal tolerance limits, and many species are exceedingly susceptible to bleaching and mortality (Glynn 1996, Marshall and Baird 2000, McClanahan 2000, Loya et al. 2001). Prolonged periods (weeks) with water temperatures $\pm 1^\circ$C above monthly maximum means lead to light-induced stress within the photosystems of dinoflagellate symbionts (Symbiodinium). This stress results in expulsion or digestion of Symbiodinium from the coral host, leading to reduced algal densities, and the visual manifestation of bleaching (Lesser 2006). Once bleached, negative energy states in the coral host can result in starvation and susceptibility to secondary stressors that induce mortality (Thornhill et al. 2011).

Large-scale thermal disturbances on shallow-water coral reefs have led to extreme reductions in species abundance, including local extirpations (Loya et al. 2001), but in some cases, corals lost from a habitat during a bleaching event have since recovered (van Woesik et al. 2011). One mechanism by which thermally sensitive coral species may endure increasing sea temperatures is by surviving in deeper-water refugia (Glynn 1996, Riegl and Piller 2003). This allows for recolonization of the affected habitats after the disturbance has passed (Bongaerts et al. 2010). To date, however, the deep-water refugium concept has never been conclusively demonstrated because shallow-water populations persisted, albeit in a reduced abundance, and could have provided larvae that led to the species-level resilience.
Milleporid hydrocoral species of the Indo-Pacific have been shown to be extremely sensitive to high thermal stress (Marshall and Baird 2000, McClanahan 2000, Glynn et al. 2001). Three milleporid species known from the continental eastern tropical Pacific (ETP) were restricted in distribution to the Gulf of Chiriquí, Panamanian Pacific, and have recently experienced severe population fluctuations and crashes as the result of bleaching-induced mortality related to positive phases of the El Niño–Southern Oscillation (ENSO; i.e., El Niño). The vertically plating Millepora platyphylla, Hemprich and Ehrenberg, 1834, was driven to regional extinction in the ETP during the strong El Niño event in 1982–1983 (Glynn and de Weerdt 1991). The foliose Millepora boschmai de Weerdt and Glynn, 1991, was also severely affected (Glynn and de Weerdt 1991), but was eventually found to have survived through 1983, with a known population of fewer than 10 colonies (Glynn and Feingold 1992, Anonymous 2003). This vestigial population was eventually eliminated during the equally strong 1997–1998 El Niño event, representing a second regional extinction within the milleporid genus that coincided with a high thermal anomaly (Razak and Hoeksema 2003, Glynn 2011). These species had very small populations prior to regional extinctions (Glynn and de Weerdt 1991).

A third species, the branching Millepora intricata Milne-Edwards and Haime, 1860, is widespread throughout the Indo-Pacific and is both a short- and long-term “loser” among stony corals after thermal stresses, experiencing high rates of bleaching-related mortality (McClanahan 2000, Loya et al. 2001) and low rates of recovery (van Woesik et al. 2011). In the Panamanian Pacific, shallow-water populations of M. intricata were also severely affected during the 1982–1983 and 1997–1998 El Niño events, but have since partially recovered. It has been suggested that these corals may have survived in a deep-water refuge and expanded to shallow reefs between disturbances (Glynn et al. 2001, Glynn 2011); however, the data to test this assumption has never been compiled and analyzed systematically and the mechanisms supporting a potential refugium have not been evaluated. In addition, the subfossil record of shallow-water milleporid populations in the ETP has not been examined to understand if populations have persisted across periods of severe ENSO activity in the past. We investigated the response of M. intricata to extremely high sea temperature anomalies with 37 years of coral population data covering deep and shallow habitats across its range in the Gulf of Chiriqui, ETP. We used this ecological data set to test the hypothesis that M. intricata survived in a deep refugium over two modern El Niño climatic events and recruited from the survivors to the shallow habitat in the interdisturbance period. We also evaluated the presence of Millepora intricata and its congeners in the subfossil record. We used the palaeoecological data to test the hypothesis that M. intricata was able to persist over severe El Niño climatic disturbances in the past. Our results show how M. intricata avoided regional extinction over recent large-scale thermal disturbances within a depth refugium, a strategy that may have allowed this species to persist throughout the Holocene.

**Materials and Methods**

To test the hypothesis that use of a depth refugium increases the likelihood of persistence in the face of climatic perturbations, we compared patterns of persistence of three species that differed in their depth distributions at two temporal scales: an ecological scale (~40 years) and a paleoecological scale (~5000 years).

**Study system**

Modern populations of Millepora spp. were studied between 1973 and 2010 across the known former or extant range of M. boschmai, M. intricata, and M. platyphylla in the Gulf of Chiriquí, Republic of Panama (Fig. 1). Long-term study sites were established at Uva Island (Contreras Islands; 7.81461° N, 81.75895° W) in 1973 and at Perro Island (Secas Island group; 7.95318° N, 82.01037° W) in 1975 (see Supplement). These sites were typically assessed on at least an annual frequency over the study period (range between samplings: 1–46 months), for a total of 52 observations.

**Depth distributions of milleporids**

The depth distributions of milleporid species in the ETP were derived from numerous observations compiled from published reports and observations of the authors. Two species that were driven to regional extinction after El Niño climatic perturbations had former depth ranges in the ETP of 3–5 m (M. platyphylla) and 2–10 m (M. boschmai) (de Weerdt and Glynn 1991; P. W. Glynn, personal observation). The third species, M. intricata, is known as a depth generalist with populations in the Gulf of Chiriqui that occur from 1 to 25 m (T. B. Smith et al., personal observation).

**Patterns of persistence: ecological time scale**

To test whether occupation of deepwater refugia by a coral species enhances persistence through climatic perturbations and recolonization of shallow-water habitats over an ecological time scale (40 years), we compared population trends from 1973 to 2010 for two species that differed in their depth distributions. Observations of the presence or absence of Millepora spp. colonies were compiled from field data and observations of the authors taken throughout the Gulf of Chiriquí between 1973 and 2010 (see Supplement). In 1983, during the first observed El Niño event in the region, presence/absence of Millepora spp. colonies was recorded at the two study reefs during October, after the majority of coral mortality had occurred, and shallow-water presence was represented by a single living colony <2 cm long at Perro Island. After both El Niño events,
targeted surveys were used to search for surviving *Millepora* spp. colonies in multiple shallow-water habitats in the three major island groups of the Gulf of Chiriquí (Coiba, Contreras, and Secas Islands), where *Millepora* spp. were previously observed. Estimates of the survey area after the 1997–1998 ENSO were ~18% of the total potential shallow-water range of *M. intricata* (60 km search area out of 330 km of available subtidal bedrock or reef area habitat, estimated in GIS ArcView 9.2 [Esri, Redlands, California, USA]). However, the percentage of area searched likely underestimates the completeness of the search, since the areas where surveys were concentrated are known to be the highest-quality shallow-water habitat (judged by abundance) for milleporids in the Gulf of Chiriquí (P. W. Glynn, personal observation), and none were found in shallow water immediately after the 1997–1998 ENSO.

The percentage cover of *M. intricata* and *M. platyphylla* was estimated between 1975 and 2010 from permanent chain transects (Rogers et al. 1983) along the fore reef within long-term sites at Uva Island and Perro Island at depths between 2 and 5 m. The percentage cover of *M. intricata* and *M. platyphylla* was zero in permanent transects after 1983 and up to 2010; therefore the entire data set was broken into two components and tested separately. (1) To test the hypothesis that shallow-water populations of *M. intricata* and *M. platyphylla* changed over the entire time period, the percentage

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**Fig. 1.** (A) Study sites in the Gulf of Chiriquí, Republic of Panama, with an expanded view of the Secas and Contreras island groups (blue boxes) with the focal study reefs indicated (red boxes). (B) The Perro Island study reef in the Secas Islands, and (C) the Uva Island study reef in the Contreras Islands. Brown areas indicate the reef flat. Bathymetry profiles derived from single-beam sonar surveys kriged in GIS (Esri ArcView 10.0; data courtesy of B. Riegl, Nova Southeastern University).
cover among years from 1973 to 2010 was compared with a nonparametric Wilcoxon signed-rank test. (2) To test the hypothesis that shallow-water populations of *M. intricata* and *M. platyphylla* had stable populations prior to the onset of severe modern ENSO events, changes in percentage cover among years prior to the 1982–1983 El Niño (when cover was nonzero) were tested separately with repeated-measures analysis of variance (ANOVA).

To establish that shallow-water recruits were absent after El Niño disturbance and the time point at which they reappeared, recruits were tracked within recruitment plots at each study reef. The Uva reef, “North plot,” 1300 m², was sampled 14 times from 1993 to 2010. The “South plot,” 1400 m², was sampled 12 times from 1993 to 2010. The “20-m² plot” was sampled 21 times from 1984 to 2010. The “1-m² plots” (N = 11) were sampled 12 times from 1994 to 2010. Perro reef, a 20-m² plot, was sampled 21 times from 1984 to 2010. Recruits as small as ~5 mm in length were detectable by this method. All recruitment plots were arrayed along the fore-reef crest and base (west–northwest facing; Fig. 1).

To test the hypothesis that *M. intricata* had reestablished abundant shallow-water populations and maintained deep-water populations ~11 years after the 1997–1998 El Niño, the density of *M. intricata* was also recorded across depths in 2 m or 4 m wide belt transects (N = 150) in March 2010 at Uva and Perro Island reefs. Transects were deployed along depth isobaths (shallow reef, 3–10 m; deep reef, 13–18 m; all depth measurements relative to mean low water) with a random number of fin kicks separating each transect (a minimum of 3 m). Most transects were 10 m in length; however, due to limited time at Perro Island, we surveyed 10 50–200 m long transects below 13 m depth in order to cover the majority of the deep-slope habitat. Statistical results showed no difference between densities in deep and shallow habitats with or without the longer Perro Island transects (t test comparing densities in depth habitats: df = 138, F = 0.89, P = 0.348). Densities of *M. intricata* were normally distributed, and variances were homogeneous. Data were compared with a two-way ANOVA with site and reef habitat (depth range) as fixed factors (α = 0.05), testing the hypotheses that recovery varied between sites and that shallow and deep populations showed different densities. To determine the size of the 2010 population and the progress toward recovery at the two long-term study sites, the total abundances of *M. intricata* in shallow- and deep-reef habitats at the two study reefs were estimated by multiplying the density estimates by total area of reef habitat, which was calculated in GIS (Esri ArcView 10.0).

**Patterns of persistence: paleoecological time scale**

To test the hypothesis that *M. intricata* has persisted in the Gulf of Chiriqui through intense ENSO cycles during the latter part of the Holocene, whereas *M. boschmai* and *M. platyphylla* did not, the presence of subfossil populations of *Millepora* spp. were assessed in 5–6 m vertical push-cores from two study reefs in the Gulf of Chiriqui: Uva Island (five cores) and Canales de Tierra Island (five cores). Each core was first divided into 5-cm intervals for processing. To isolate subfossil *Millepora* skeletons from the core material, carbonates >2 mm in longest diameter were separated from the sedimentary matrix with a sieve. These carbonates were then cleaned using high-pressure water and sorted to genus. Where possible, *Millepora* fragments were classified to species level using the descriptions of Razak and Hoeksema (2003) and de Weerdt and Glynn (1991). Where species-level identification was not possible due to taphonomic degradation or because the sample was too small, the skeletons were classified as *Millepora* spp. Within each core, *Pocillopora* spp. and *Gardineroseris planulata* fragments were dated using a combination of standard 14C analysis (Beta Analytic, Miami, Florida, USA) and accelerator mass spectrometry (National Ocean Sciences AMS facility at Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, USA). We also dated seven of these same corals with U-series dating (University of Minnesota) to constrain the local reservoir correction for the radiocarbon ages through the late Holocene. The radiocarbon dates were then calibrated according to the local reservoir correction using Calib 6.0 software (Stuiver et al. 2005, Toth 2013). For consistency, we used only the calibrated radiocarbon dates, and not the U-series dates, to create age models for each core. This age model allowed us to estimate the ages of individual milleporid fragments. Although the 95% confidence interval of our calibrated radiocarbon dates could be as high as several hundred years, our age models still provide a reasonable estimate of the occurrence of milleporids in the Gulf of Chiriqui over a millennial timescale. Complete methods on core sampling, processing, and dating are described in Toth et al. (2012) and Toth (2013).

**Patterns of biophysical conditions between shallow and deep reef habitats**

To test the hypothesis that biophysical conditions of the shallow and deep habitats differ, and that conditions that are potentially ameliorative to thermal stress, but also potentially inimical to coral fitness at periods between El Niño events, occurred in the deep-water habitat, vertical water column profiles and benthic temperature data were collected. A Seabird 25 CTD was used to measure vertical profiles of temperature, dissolved oxygen, chlorophyll (*Wetlabs EcoFLNT* [Wetlabs, Philomath, Oregon, USA]), and photosynthetically active radiation (PAR; *LICOR* 400 [LICOR, Lincoln, Nebraska, USA]). Low levels of dissolved oxygen and light could potentially limit growth of milleporids in the deep-water habitat, whereas lower temperatures, low light, and high water
column chlorophyll (a proxy for heterotrophic subsidy) could protect corals during El Niño conditions. Casts were made between 14 and 22 March 2010 (N = 54) and distributed in transects from off-reef to on-reef areas at Uva Island at depths of 1–70 m. Data were averaged into 1 m depth bins for each cast and used to calculate the bin mean, standard deviation, and minimum/maximum values among all casts. The extinction coefficient of PAR was calculated (Lalli and Parsons 1997) using three casts made directly over deep *M. intricata* communities (18 m) at Uva Island. Benthic thermistors (Hobotemp v2 [Onset Corporation, Bourne, Massachusetts, USA]) recorded data at 30-minute intervals at 4 and 18 m depth from 12 March 2005 to 20 January 2010 at the Uva Island study site.

**Fitness of Millepora intricata in shallow- and deep-reef habitats**

Our observations suggested that in near-reef, deep-water habitats, colonies of *M. intricata* reduced in size compared to shallow-water habitats. Additionally, whereas shallow-water populations of *M. intricata* were attached to the substrate and formed part of the reef framework, deep-water populations generally formed as unattached colonies. To test the hypothesis that *M. intricata* in the depth refugium had reduced fitness relative to shallow colonies, sizes and growth rates of *M. intricata* were measured. Sizes of *M. intricata* in shallow and deep water were recorded in order to track growth as part of recovery and to determine if deep populations exhibit limitations to maximum size. The sizes of the largest *M. intricata* colonies were recorded at both study sites starting in 1983, although some years were not sampled, and the sizes of deep (>12 m depth) colonies were measured only once in 1989 after the 1982–1983 El Niño event, and then more frequently in 2000 after the 1997–1998 El Niño event.

Growth rates of *M. intricata* colonies were measured at Uva Island reef between 5 August 2007 and 18 March 2010. Colonies with a maximum length of 10–20 cm were collected from 18 m depth (for the deep treatment) and 12 m depth (for the intermediate and shallow treatments). Colonies were measured along their axis of maximum length and affixed to a plastic mesh grid consisting of five colonies spaced a minimum of 30 cm apart. Three grids of five colonies each were anchored to the bottom with steel stakes at 3 m (shallow treatment), 10 m (intermediate treatment), and 18 m (deep treatment), and spaced along the isobath at intervals of >7 m. At the termination of the growth study, the maximum length of colonies was remeasured. Growth rates among depths were normally distributed and variances were homogeneous. Data were compared among depths with a one-way ANOVA and differences between depths were compared with a Tukey’s HSD test (α = 0.05).

**Results**

*Millepora intricata* was eliminated from shallow-water habitats across its known range in 1983 and 1998 (Fig. 2A, B). No colonies were found shallower than 12 m depth after either El Niño event at the study reefs, or anywhere else in the Gulf of Chiriquí on shallow coral reef, rubble, or hardbottom habitats, despite extensive searches. The cover of all milleporeid species declined significantly in permanent transects across years because cover dropped to zero after the 1982–1983 El Niño and remained zero through 2010 (Fig. 2B; χ² = 263.7, df = 28, P < 0.0001), whereas the cover of milleporeids was higher and stable prior to 1983 (F = 5.84, df = 7, 3, P = 0.088).

Over both El Niño events (1982–1983 and 1997–1998), the only known surviving colonies at the long-term study sites and other hardbottom and rubble habitats occurred in habitats deeper than 12 m (Fig. 2A). Unbleached colonies were observed as late as October 1983 at depths >12 m, whereas all shallow colonies had died. Observations of colonies deeper than 12 m were not made during the 1997–1998 El Niño event; however, the size of deep-water colonies during our first post-disturbance observation indicated that living deep colonies had survived through the respective El Niño events. The maximum diameter of colonies recorded in depths >12 m in 1989, 6.2 years after the 1982–1983 El Niño event, was 60 cm (n = 23). Assuming a maximum diameter growth rate of 7.3 cm/yr taken from shallow-water colonies (see following analysis), the age of the largest colony was 8.2 years old and at least 4 of the 23 were alive before the 1982–1983 El Niño event. In May 2000, 1.5 years after the 1997–1998 El Niño, the largest colony measured would have been 4 years old (30 cm diameter, n = 21), with an assortment of 8–12 cm diameter colonies with calculated ages as old or older than 1.5 years. These estimates are quite conservative, since deep growth rates (10 and 18 m) are less than half those in shallow water, and, therefore, ages are likely older than we have estimated here. Observations in 2011 showed that deep populations were widespread, as colonies of *M. intricata* were abundant in deeper habitats in at least six sites examined in the Gulf of Chiriquí: Perro (Secas Islands), Uva, Ridley Rock (Contreras Islands), Coibita (Coiba Island), Brincanco, La Lavadora (near Prosper Rock), La Viuda (see Supplement).

Despite the complete shallow-water extirpation of *M. intricata* in 1983 and 1998, colonies reappeared on shallow-reef habitats within three years and were relatively abundant by six years after both El Niño events (Fig. 2A). After the more intensively monitored 1997–1998 El Niño event, the first colonies of *M. intricata* at Uva Island appeared in 2001 on the fore reef slope at the lower end of the shallow depth range (8–11 m; see Supplement). *M. intricata* also disappeared within long-term recruitment monitoring plots, but subsequently reappeared in the plots via larval recruitment within
four years after each event (Fig. 2A; see Supplement). Twelve years after the 1997–1998 El Niño, there were no significant differences in colony densities between deep (>11 m) and shallow habitats from 1973 to 2010 (figure produced from data presented in the Supplement). Observations of adult colonies were divided into three categories: absent, present (low abundance of <25 total colonies observed in any area surveyed), and abundant (>25 colonies). The horizontal pink line indicates periods after ENSO disturbance when recruits of M. intricata were absent from recruitment monitoring plots, and the vertical blue lines indicate the first reappearance of recruits to plots. (B) The percentage cover of Millepora intricata and Millepora platyphylla (mean ± SE) in shallow permanent transects at Uva Island and Secas Island from 1975 to 2010 (N = 20). (C) The maximum length of M. intricata at Uva Island and Perro Island from 1973 to 2010 from shallow and deep observations.

Subfossil Millepora skeletal fragments were found within shallow reef cores from Uva and Canales de Tierra from ~5000 cal. yr BP (calibrated calendar years before 1950) to the present (Fig. 3A, B). At both sites, almost all of the milleporid skeletons we identified (60% identified to species level) were M. intricata (81% at Uva and 93% at Canales de Tierra). In fact, only 13 subfossil Millepora skeletons were identified confidently as either M. boschmai or M. platyphylla. Six of these corals could not be assigned ages with confidence because the age model for one core from Uva Island was incomplete.

Although M. intricata skeletons were abundant at both sites over the last 5000 years, M. boschmai and M. platyphylla occurred only sporadically (Fig. 3A, B). Notably, neither species was found to occur in the subfossil record during regional hiatus in reef accretion ~4100–1600 cal. yr BP (Fig. 3C; Toth et al. 2012). In
two of the cores collected at Uva Island, however, there were several records of *M. intricata* between 4100 and 1600 cal. yr BP, including one at 3150 cal. yr BP. The hiatus in reef accretion coincided with a period of high ENSO variability (Conroy et al. 2008, Koutavas and Joanides 2012), which was likely characterized both by more frequent and stronger El Niño events than any other time in the Holocene (Rein 2007, Yan et al. 2011).

Vertical profiles of water column characteristics showed changes with depth, which indicate the processes that could support a depth refugium from thermal stress, but also may cause reduced fitness for corals at depth. Strong stratification of the near-surface water column was evident at the transitional depths separating shallow and deep populations of *M. intricata* (Fig. 4). This shallow thermocline brings cool and variable temperatures to deeper depths (mean4m = 28.5° ± 0.7°C [mean ± SD], range, 23.7°–30.9°C; mean18m = 27.1° ± 1.6°C, range, 16.7°–30.3°C; Fig. 4). The thermocline at 18 m depth was associated with the chlorophyll maximum layer, with high mean and maximum concentrations of planktonic chlorophyll (Fig. 4; see also D’Croz and O’Dea 2007). In addition, the first thermocline was associated with a decline in surface-dissolved oxygen concentrations, with very low minimum levels reached by 30 m depth (Fig. 4). Light was moderately attenuated with increasing depth at the study sites, with a mean irradiance at 17 m of 23% of subsurface values and an extinction coefficient 0.1055 m⁻¹.

Post-disturbance coral growth rates were higher in the shallow habitat compared with the deep habitat. Annual increases in the maximum length of *M. intricata* after post-disturbance reestablishment was apparent throughout the shallow-water habitats at the study reefs (Fig. 2C), whereas the maximum length of corals in deeper water were stable after the 1997–1998 El Niño. Growth rates measured as the percentage change in longest linear axis of *M. intricata* were significantly higher at shallow depths and over double those achieved at 10 and 18 m depth, which were not significantly different from each other (one-way ANOVA, df = 2, 38, \( F = 15.2, P < 0.0001 \); mean3m = 59.7 ± 7.5%/yr [mean ± SE]; mean10m = 25.3 ± 5.2%/yr; mean18m = 12.6 ± 4.4%/yr). The mean change in the longest axis of shallow-water colonies was 7.3 ± 0.7 cm/yr (\( n = 14 \)).

**DISCUSSION**

In this study, we provide the first empirical evidence of a depth refugium for *Millepora intricata* and confirm depth refugia as a potential mechanism of coral survival through a severe thermal disturbance (sensu Glynn 1996, Riegl and Piller 2003). There were no colonies found in multiple shallow-water habitats during extensive searches over at least three years after two El Niño disturbances; however, deep populations persisted through these events. Given the high rates of mortality of *M. intricata* during mass bleaching thermal stress (Marshall and Baird 2000, McClanahan 2000, Loya et al. 2001), including the total mortality of the shallow-water populations in this study, we suggest that this
deep-water refugium was the mechanism that prevented regional extinction. As a corollary, because most corals of all species found in depths up to 15 m were bleached in the 1982–1983 El Niño (Glynn 1983), the narrow depth range (<10 m maximum depth) of *M. boschmai* and *M. platyphylla* ensured the absence of a depth refugium and may have predisposed these species to regional extinction.

The rapid recovery of *M. intricata* after the El Niño events was most likely the result of recruitment of larvae produced by colonies in the deep-water refugium. It is unlikely that repopulation was initiated from large-scale connectivity in the Pacific, as the nearest other source populations outside the Gulf of Chiriquí lie across the Eastern Pacific Barrier (Glynn and Ault 2000), over which there is little-to-no connectivity on ecological time scales for another pan-Pacific coral, *Porites lobata*, which has the potential for long larval durations (Baums et al. 2012). Given that the source of larvae for shallow-water recolonization was likely local, the multi-year extirpations of shallow-water populations of *M. intricata* across their ETP range, and the proximity (tens of meters) of extant deeper-water populations, we conclude that shallow populations recruited from deep-water refuges. If this inference is true, the deep habitat served not only as a refuge, providing protection from regional extinction, but also allowed for partial recovery to the affected shallow habitat within a few years. To our knowledge this study provides the first demonstration of the deep refugia hypothesis (sensu Bongaerts et al. 2010), which posits a deep coral refuge as a source of larvae to degraded or extirpated shallow populations.

The hydrocoral *M. intricata* has persisted in the ETP for at least the last 5000 years despite high ENSO variability and El Niño events at least as strong as those in recent years. In fact, Rein (2007) suggested the strongest El Niño events during the Holocene occurred between 2000 and 4000 years ago, with frequent events more intense than those in either the 1982–1983 or 1997–1998 El Niño events. The active ENSO system around this time resulted in a hiatus in active reef accretion in several parts of the Pacific, including the ETP, from 4100 to 1600 cal. yr BP (Toth et al. 2012), which precluded the long-term persistence of shallow-water milleporid populations as well. *M. intricata* was much less abundant during 4100–1600 cal. yr BP compared to before and after; however, subfossil *M. intricata* did appear in some cores during this period, suggesting that this taxa may have recovered in shallow-water habitats during brief respite in El Niño disturbances. On the other hand, *M. boschmai* and *M. platyphylla* were rare throughout the record and absent from 4100 to 1600 cal. yr BP. The greater subfossil abundance and millennial-scale persistence of shallow-water *M. intricata* populations, in a region where ENSO variability was high throughout the Holocene, suggests that *M. intricata* is likely more resilient to El Niño-related disturbances than its congeners. Given the ecological evidence suggesting that shallow-water populations of *M. intricata* are just as sensitive to thermal stress as *M. boschmai* and *M. platyphylla*, the appearance of abundant *M. intricata* populations in the subfossil record gives further support to the conclusion that this species may require a depth refugium to survive strong El Niño events. If the recent changes in milleporid populations due to high thermal stress reflect past sensitivities for *Millepora* spp., then depth refuges may have facilitated persistence of *M. intricata* in the Gulf of Chiriquí throughout the Holocene. We would expect to find a continuous record of *M. intricata* populations within cores extracted from deeper portions of the reef slope where modern populations flourish. It cannot be conclusively determined from our data if *M. boschmai* and *M. platyphylla* were extirpated in the ETP through strong El Niño events of the Holocene, only to recolonize across the Eastern Pacific Barrier in the last two millennia, or if they somehow survived in the ETP over the latter half of the Holocene. However, it seems incredible that they would have survived in the ETP through the severe El Niño events 4100–1600 cal. yr BP, only to go regionally extinct within the last 40 years, coinciding with their inclusion into ecological investigation.

The environmental mechanisms that facilitated the depth refugium for *M. intricata* were most likely reduced light and possibly factors that relate to a shallow thermocline in the Gulf of Chiriquí (12–30 m; D’Croz and O’Dea 2007). Shading reduces oxidative stress to *Symbiodinium* photosystems and delays the onset of bleaching in thermally stressed hard corals (Lesser 1997), whereas cooler temperatures provide a mechanism to avoid thermal stress. In addition, heterotrophic food inputs have the ability to favor resistance among corals that can feed on zooplankton or particulate sources (Grottoli et al. 2006). For milleporids, which are capable heterotrophic feeders (Lewis 2006), the chlorophyll maximum layer associated with the first thermocline has the potential to provide these heterotrophic subsidies (Leichter and Genovese 2006). The thermocline results in a mean temperature that is 1.4°C cooler at 18 m depth; however, there were no vertical profile data or deep temperature records at our study reefs over the two modern El Niño disturbances, when the thermocline should have been deeper (Enfield 2001). Studies in ETP coral reefs in the Galápagos (Champion Island; Wellington et al. 2001) and Costa Rica (Bahia Culebra; Jiménez et al. 2001) over the 1997–1998 ENSO showed that during months with the highest sea surface temperatures, conditions at 7–30 m depth varied between isothermal with the surface or up to 3.0°C cooler, reflecting cooling processes at depth. Thus, the depth refugium for *M. intricata* provides avoidance of light stress and may mitigate thermal stress, but the role of the deep refugium in ameliorating thermal stress or increasing resistance to mortality through heterotrophy must be investigated further.
The deep refugium of *M. intricata* may be vulnerable to long-term shifts in the frequency and intensity of disturbance (Parkos et al. 2011), because the deep environment is not completely buffered from environmental change. Furthermore, the conditions within the refugium are less favorable for colony growth than those of shallow-water habitats. Although deep habitats were somewhat buffered from El Niño conditions, bleaching and mortality of *M. intricata* still occurred in the deep refugium during each of the El Niño events. In March 1983, when all shallow milleporid colonies were already dead, deeper colonies of *M. intricata* showed about 20% bleaching, and by April 1983 many deeper colonies were bleached or had died (Glynn 1983). After the 1997–1998 El Niño, increasing population sizes of *M. intricata* in the deep habitat suggested re-expansion after mortality. For example, a handful of known colonies (<25) survived in deep depths at the two main study reefs just after 1997–1998 (Glynn et al. 2001). However, by 2010, *M. intricata* had increased in abundance in all habitats at the two study reefs. Although *M. intricata* population growth rates were high in deep habitats, individual colony growth rates were much lower at deeper depths and colonies did not tend to increase beyond a maximum size (~60 cm) that was half the maximum size recorded in shallow habitats. Thus, the lowered temperatures and attenuation of light that might enable the depth refugium during thermal events could also lead to less favorable conditions for growth. In addition, low oxygen concentrations below the thermocline have been implicated in the restriction of pelagic fishes to a thin, mixed surface layer in the ETP (Prince and Goodyear 2006). Likewise, low oxygen may restrict the growth of corals and their prey. Refugia are not a failsafe for extinction, and models of extinction need to address the demographic vulnerabilities of the refugium itself.

A deep-water refugium for high thermal stress may be the only mechanism that supports persistence through periods of elevated seawater temperatures for ultra-sensitive taxa like *Millepora* spp. This may be particularly true for species that have limited adaptive capacity for thermal stress. The second shallow-water extirpation of *M. intricata* during the 1997–1998 El Niño, 14 years following the primary disturbance, indicates limited capacity for adaptive resistance in this species, such as
may occur with symbiont shifting or shuffling (Baker et al. 2004). In refugia systems where species avoid extreme conditions, even where there are resistant survivors in the nonrefugium habitat, new recruits from the refugium that do not undergo selection cannot assist in adaptive shifts of genotypes. Populations of *M. intricata* in the refugium were only partially protected from thermal stress, and therefore may have faced some selection; however, this was clearly insufficient to cause shifts to resistant genotypes in shallow-water colonies recruited from deep water.

The empirical response of *M. intricata* to these disturbances has broad relevance to maintenance of diversity across severe disturbance events. Species that occur across heterogeneous habitats, where some microhabitats possess the biophysical capacity to mitigate stress, can utilize refugia to survive acute disturbances. In this extreme case, the shallow-water reef habitat in the Gulf of Chiriquí was nonresistant to disturbances has broad relevance to maintenance of resilience could provide the necessary demographic buffer to ensure survival of coral taxa in the future.

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**LITERATURE CITED**


**SUPPLEMENTAL MATERIAL**

**Supplement**

Summary of *Millepora* spp. observations across the Gulf of Chiriqui from 1973 to 2010 compiled from field notes and data *(Ecological Archives E095-144-S1).*