Thermal Refuges and Refugia for Stony Corals in the Eastern Tropical Pacific

17

Tyler B. Smith, Juan L. Maté, and Joanna Gyory

Abstract

Refugia could provide the essential conditions for coral and coral reef persistence in the marginal eastern tropical Pacific Ocean (ETP) by allowing corals to avoid extinction after disturbance events and by maintaining populations that can rapidly recolonize disturbed habitats. The low diversity and restricted ranges of ETP corals make them vulnerable to seawater warming caused by positive phases of the El Niño-Southern Oscillation (El Niño). However, at spatial scales ranging from individual colonies (<10 m) to regions, (>100 km) there are areas or habitats that avoid stress or support corals that are more resistant to stress or with the capacity to recover rapidly. These habitats may form a network of refugia that ensures coral persistence through severe disturbance. This chapter explores evidence for the existence of refugia at multiple spatial and temporal scales across the ETP, with recent examples showing refugia may be common and perhaps even necessary for many species to survive the highly fluctuating environment in this eastern Pacific tropical ocean basin.

Keywords

El Niño-Southern Oscillation • Coral bleaching • Extinction • Resistance • Recovery

17.1 The Concept of Refuges and Refugia

Refuges and refugia are environments that are buffered from acute or chronic disturbance and stress that negatively affect organisms. These environments promote survival of species in an ecosystem that has otherwise become hostile. In this chapter we will follow the convention of Keppel et al. (2012) who distinguished refuges and refugia based on spatial and temporal scales (summarized in Fig. 17.1). At smaller scales, **refuges** (singular: refuge) provide protection from disturbances in three-dimensional space ranging from centimeters to hectares and across time on scales ranging from minutes to years. Refuges can also provide advantages in biotic interactions, such as competition or predation. For example, an associational refuge might deter herbivory on a palatable alga by its close spatial association with a chemically defended plant species. Thus, refuges are related to physiological and ecological spatiotemporal scales. **Refugia** (singular: refugium), however, are "habitats that components of biodiversity retreat to, persist in and can potentially expand from under changing environmental conditions" (Keppel et al. 2012). Thus, refugia are associated with larger scales of kilometers and millennia, and are related to evolutionary spatiotemporal scales.

There are three core processes that control the formation and importance of refuges and refugia, (1) reduction or

---

T.B. Smith (✉) · J. Gyory
Center for Marine and Environmental Studies,
University of the Virgin Islands, #2 John Brewers Bay,
St. Thomas, US Virgin Islands, 00802, USA
e-mail: tsmith@uvi.edu

J. Gyory
e-mail: tubularia@gmail.com

J.L. Maté
Smithsonian Tropical Research Institute, Apartado
0843-03092Balboa, Ancón, Republic of Panamá
e-mail: matej@si.edu

J. Gyory
Department of Ecology and Evolutionary Biology, Tulane
University, New Orleans, LA 70118, USA

P.W. Glynn et al. (eds.), *Coral Reefs of the Eastern Tropical Pacific*,
Coral Reefs of the World 8, DOI 10.1007/978-94-017-7499-4_17

absence of stressful conditions that lead to mortality (**avoidance**), (2) the promotion of conditions that favour **resistance** to disturbance, and (3) enhancement of conditions that lead to faster and more complete **recovery** before the next disturbance. The localized reduction of stressful conditions is the most obvious factor in forming refugia, since an area of space or period of time where the stress does not exist would be de facto a refuge. However, for a refuge to scale to a refugium the avoidance must be "reliable" (West and Salm 2003) and occur frequently enough with a given disturbance to support the persistence of a species. What is less obvious is that there exist conditions that enhance biological resistance to disturbances. An example would be two reef zones where mean thermal stress is equal, yet one area exhibits higher background temperature variability that acclimatizes corals to periods of high temperature stress and thus conditions corals to be more resistant to high mean water temperatures (McClanahan et al. 2007; Davis et al. 2011; Guest et al. 2012). Lastly, enhancement of resistance to pulse disturbances, such as thermal stress, can facilitate robust populations to face the next disturbance, as they may have undergone selection for more resistant coral host and endosymbiont *Symbiodinium* genotypes that might influence greater future resistance (Baker et al. 2004; D'Croz and Maté 2004; Guest et al. 2012; see Chap. 13, Baker et al.). Only resistance, not recovery, is possible for continuous press disturbances (Bender et al. 1984), such as ocean acidification. In press disturbances there is no period during which the population is released from constant pressure to decline in abundance. Therefore, the creation of refugia under press disturbance may demand a greater role of the first two core processes of avoidance and promotion of conditions that enhance resistance.

Refugia for corals are important for preventing extinction and increasing resilience. In the purest sense refugia allow species to avoid local, regional, or global extinction. The focus on extinctions and global scales may be why refugia have received relatively little attention in marine science, since the threat of global extinction for marine species with open populations is widely considered to be comparatively low relative to aquatic and terrestrial species (McKinney 1997). However, we also take a more general view of refuges as demographic buffers that can promote species-level resilience and, perhaps, ecological resilience (Holling 1973) by protecting local, regional, and global sexual and asexual reproductive pools. This view may be more generally applicable to refuges in coral reef regions across the tropics where extinction is not likely (Hughes et al. 2014).

The ETP may be especially reliant on refuges for long-term persistence of coral species and coral ecosystems. Extreme environmental heterogeneity in the ETP ranges on scales from colonies to reefs, habitats, islands, and regions (Fig. 17.1). While this is certainly not unique for coral reefs anywhere, the ETP is different from most regions due to the presence of mesoscale upwelling, cold currents that impinge from high latitudes, and a shallow upper mixed layer (10–30 m depth). The mixed layer here is defined as the depth from the surface to the depth of active mixing due to turbulence caused largely by local wind forcing, and has been formalized as a change of temperature of 0.2 °C from a near surface value (de Boyer Montégut et al. 2004). In fact, the ETP has some of the shallowest and strongest upper pycnoclines (vertical density gradients) globally, largely because of the shallow thermocline (Fiedler and Talley 2006; see Chap. 3, Fiedler and Lavín). The shallow thermocline and thin upper mixed layer bring cool, nutrient rich water close to the surface and increase the frequency and intensity of upwelling at multiple scales (within reef to regional domains) (D'Croz and O'Dea 2007). Other oceanographic factors associated with the thin upper mixed layer, such as salinity, water column productivity (e.g., concentration and turnover of phytoplankton, zooplankton, and particulate organic matter), and dissolved oxygen create the potential for a mosaic of conditions over relatively small horizontal and vertical areas. Within this diversity of environmental conditions lie multiple refuges that are buffered from acute and chronic disturbance or precondition coral resistance to stress and disturbance.

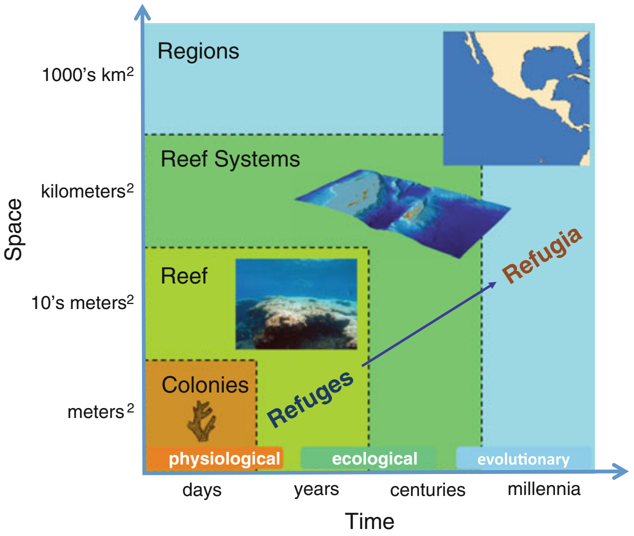

Fig. 17.1 Spatiotemporal scale across which refuges scale to refugia

In our view, refuges in the past have been critical in controlling the modern fauna of ETP coral reefs. The coral fauna of the ETP is more vulnerable to extinctions than most of the other coral reef-supporting areas of the globe because populations are regionally separated from the central and western Pacific Ocean across the Eastern Pacific Barrier (Baums et al. 2012; see Chaps. 5 and 16, Glynn et al., and Lessios and Baums respectively) and within the ETP are sparse and widely separated. Many coastal and oceanic habitats in the ETP are unfavorable for reef and coral growth, restricting available habitat and ranges of occurrence. Examples include, the sedimentary dominated systems of the Pacific Central American Faunal Gap (Springer 1958; Reyes Bonilla and Barraza 2003), areas with a high concentration of dissolved carbon dioxide (Manzello 2010), hard-bottom habitats below the regionally shallow thermocline, and areas of intense upwelling (Glynn 2003). In addition, there is a relatively high degree of endemism within the scleractinian fauna of the ETP (Glynn and Ault 2000). Thus, restricted environments for coral growth could increase the risk of global extinction for ETP endemics and regional extinction among pan Indo-Pacific species in the ETP (Glynn 2011; Harnick et al. 2012). Both prospects reduce ecological redundancy and can render the ecosystem more susceptible to disturbance (McCann 2000; Loreau 2010). In addition, even the regional loss of a species can reduce genetic diversity and the potential for speciation. This may be particularly important in the ETP, where evidence suggests that species have low gene flow with the western Pacific across the Eastern Pacific Barrier, a condition that fosters endemic genotypes (Baums et al. 2012).

In this chapter we focus primarily on refuges and refugia from thermal disturbance, since coral habitats in the ETP have been shown to be particularly susceptible to high and low temperature extremes (Glynn et al. 2001; Glynn and Fong 2006; see Chap. 8, Glynn et al.). However, this discussion could apply equally to other stressors, such as ocean acidity, that are dealt with fully in other chapters (see Chap. 18, Manzello et al.) and will be referenced only briefly in this chapter. In addition, because refuges and refugia are largely ecological and biogeographic topics that are intimately concerned with space and time, we organize our chapter along spatiotemporal scales (low to high). However, we use spatial scales to divide our sections.

17.2 Intra-colony Refuges (Scales Less Than a Meter)

Within a single coral colony there may exist areas with differential resistance to bleaching-related mortality during thermal stress events. Such resistance favours partial colony mortality over whole colony mortality, which can be critical in preserving extant genotypes and jump-starting recovery. Many coral colonies can have morphologies that create heterogeneous environmental conditions, or microhabitats, that respond differently to stressors such as seawater warming (Brown et al. 2002). For example, because light is frequently a co-factor with thermal stress in initiating the bleaching response, factors that reduce light can reduce the severity of bleaching (Lesser 1997). Intra-colony shading is often influenced by colony morphology. Massive, branching, foliose, and encrusting (following substrate contour) colony morphologies often possess shaded surfaces where light stress is reduced. The empirical response of many ETP corals to bleaching (Glynn et al. 2001) shows that shaded areas can confer some resistance to bleaching, even though shaded surfaces may contain different endosymbiont clades that might be more sensitive to thermal stress even at reduced light levels (Baker et al. 2008). In addition, mosaic patterns of bleaching and mortality often occur even when there is no corresponding intra-colony microhabitat identified (Glynn et al. 2001). This suggests differences in symbiont type within colonies, with differing susceptibilities to heat stress (Rowan et al. 1997). Heterogeneous water velocity around corals may also create intra-colony thermal refuges. Higher water velocities around colony surfaces can reduce the height of the free boundary layer that limits diffusion and advective supply, therefore increasing the stripping of oxygen radicals (Nakamura and van Woesik 2001) or increasing the supply of heterotrophic food sources (Sebens et al. 1998). One would expect that more exposed colony surfaces would benefit from increased water velocity, but these areas may also be more exposed to increased light, making the benefit of increased water flow at the colony scale less clear.

Microhabitat refuges, and related partial instead of total colony mortality, can be a potent mechanism leading to recovery of corals after disturbance. Rapid recovery of surviving tissues has been seen in many ETP coral species after massive thermal mortality events (Glynn et al. 2001; Glynn and Fong 2006). In 1997–98 species such as *Gardineroseris planulata*, *Pavona varians*, *Pavona clavus, Porites lobata* or *Porites evermanni*, all showed intra-colony variation in bleaching and mortality that led to partial rather than whole colony mortality. In the case of *G. planulata*, upper colony surfaces suffered severe bleaching and mortality, whilst colony sides bleached but survived (Fig. 17.2). In addition, poritid corals with deep tissue reserves in their porous skeletons have been known to be resistant to whole colony mortality as these tissues can survive bleaching events and re-emerge to colony surfaces (Baker et al. 2008; van Woesik et al. 2012a). Furthermore, broadcasting zooxanthellate corals in the ETP, which includes all scleractinian species except *Porites panamensis*, can rapidly recolonize areas through sexual reproduction after thermal disturbances, suggesting reproductive mode may play a role in resilience (Glynn and Colley 2008).

Thus, species-specific traits determine the impact of changing climatic conditions upon coral survival (Loya et al. 2001; van Woesik et al. 2011; Smith et al. 2013) and hence their long-term survival and ability to recover (Darling et al. 2012; van Woesik et al. 2012a). Understanding traits that

Fig. 17.2 Colonies of *Gardineroseris planulata* showing characteristic pattern of upper surface mortality caused by top bleaching during 1997–98 El Niño. Sides of colonies served as intra-colony refuges that allowed colony survival. Recovery is occurring through regrowth onto damaged colony tops (Uva Is Panama, September 16, 2002; ~6 m depth; credit: T Smith)

determine intra-colony refuges will improve predictions of coral community response to future thermal disturbances.

17.3 Intra-reef and Inter-reef Refuges (Scales of 10–1000s of Meters)

The effects of thermal stress at reef and inter-reef scales can be heterogeneous due to interacting bio-physical processes that enhance the three core processes related to avoidance, resistance, and recovery. True reef frameworks include biologically produced carbonate build-ups elevated above the bedrock. Here we use the term “reef” to include coral communities growing on bedrock or incipient carbonate frameworks, since these habitats are likely to surpass the numbers and areal occurrence of true reef frameworks in the ETP (Guzmán et al. 2004). Intra-reef refuges include vertical depth refuges that have unique features and are treated separately in the following section.

As with coral colonies, the reef is a mosaic of heterogeneous physical conditions, some with the ability to change coral exposure or response to disturbance and stress. Also, similar to the scale of colonies, factors that increase the variance of temperature and light conditions (see below) will tend to create more persistent refuges with a greater potential to form refugia, whilst biological interactions that favour recovery, such as decreased competition for substrate, may be inconsistent from one disturbance to the next. The various mechanisms suggested in this section are not unique features of ETP reefs, so this section applies more broadly to intra-reef and inter-reef refugia globally.

Temperature means, maxima, and diel variation can differ greatly within and between reefs on scales of tens of meters to tens of kilometers (Davis et al. 2011; Gorospe and Karl 2011), and during thermal stress events this could lead to both areas of avoidance and areas where tolerance may be increased (Pineda et al. 2013). Areas of avoidance could occur where temperatures are normally lower within and between reefs, such as microhabitats subject to vertical mixing; and the flushing of fore-reef zones or near areas with tidally induced pumping of deep cool water and other localized sources of upwelling (Glynn and Stewart 1973; Riegl and Piller 2003). However, mechanisms that cool these areas would need to be persistent during thermal stress events and maintain temperatures sufficiently below bleaching thresholds to prevent thermal stress. During regional sea warming events that induce bleaching these areas may lose their benign characteristics and experience the regional warming, either because they are exposed to the open ocean where temperatures are elevated or because the thermocline is depressed. Furthermore, in order for areas of thermal stress avoidance to provide long-term refugia at the intra- and inter-reef scale, processes that cause cooling would need to be “reliable” or long-lasting over multiple stress events (West and Salm 2003). For example, Pineda et al. (2013) suggested that a cold-core eddy lowered sea surface temperatures and protected exposed outer shelf reefs in a section of the Red Sea in 2010, providing a spatially explicit refuge from thermal stress. But, cold-core eddies are not normally permanent features and may not always be present during thermal stress events, in which case there would not be a long-term refugium. Lastly, since corals in cooler areas occupy mild thermal environments, they may not have been previously exposed to elevated temperatures, and therefore may show less tolerance (Oliver and Palumbi 2011). Thus, high thermal stress avoidance mechanisms at the reef and inter-reef levels may be relatively rare.

More reliable features in shallow water that would promote avoidance of bleaching conditions and provide potential refugia might be microhabitats shaded by permanent structures and areas subject to strong currents (West and Salm 2003). Light can vary within and among coral reefs due to shading from reef structures, such as erect macroalgae or coral canopies, and nearby terrain such as cliffs and overhanging structures. In addition, water column light attenuation (e.g., turbidity) and cloudiness (Glynn 1996; Brown 1997; Mumby et al. 2002) can reduce irradiance. West and Salm (2003) suggested that shading by subtidal structures and adjacent terrain might be a highly reliable factor that reduces bleaching, whereas turbidity and cloud cover may have low reliability. Water flow that flushes toxins or transports nutrients and food may also differ in its reliability; permanent features, such as tidal and ocean currents, are highly reliable, whereas transient and variable features, such as wave action, tidal range, and wind-driven currents, will be less reliable.

Although long-term avoidance from thermal stress might be rare on the intra- and inter-reef scale, processes that increase tolerance to warming may promote refuges and refugia. For example, slowing of water flows and ponding of water on reef flats, back reef lagoons, and embayments can lead to greater diel warming of water masses interspersed with tidally induced flushing and cooling (Davis et al. 2011; Pineda et al. 2013). This leads to greater variability in daily temperatures, consistent transient exposure to water temperatures greater than the surrounding ocean, and a higher mean temperature. Experimental and empirical evidence show that corals exposed to greater mean, maximum and variable temperatures can be more resistant to bleaching or bleaching-related mortality during heat stress (McClanahan et al. 2007; Bellantuono et al. 2011; Oliver and Palumbi 2011; van Woesik et al. 2012b), and at the inter-reef scale corals exposed to greater temperature variability are more resistant to declining growth during and after heat stress (Castillo et al. 2012). The cause of this effect is not known, but higher temperatures experienced by corals in warmer or variable environments may "frontload" genes for tolerance to high thermal stress (Barshis et al. 2013), with genetic responses that correspond to acclimation and adaptation (Palumbi et al. 2014), or cause shifts in symbiont types (Baker et al. 2008).

Reef flats and back reefs in the ETP may act as refuges from the worst effects of thermally induced coral bleaching mortality. Reef flats experience higher light and more variable temperatures, with higher mean and maximum/minimum values, than surrounding reef areas. These physical regimes might precondition corals for tolerance to conditions that cause bleaching (Fig. 17.3; Davis et al. 2011), potentially forming a refugium for coral species that can develop increased tolerance. Similarly, back reef zones with lagoons or impounded water experience restricted flow that allows greater diel heating and may precondition corals to resist thermal stress (van Woesik et al. 2012b). In addition, lagoons backed by land are often made turbid due to run-off and accumulation of particulate matter (sediments and particulate organic matter) and nutrient enrichment of phytoplankton communities. Turbidity was increased by about 0.2 NTUs in the lagoon at the Uva Island study reef during one of our surveys in 2010, although phytoplankton enrichment (i.e., higher chlorophyll concentration) was not observed during this period (Fig. 17.4).

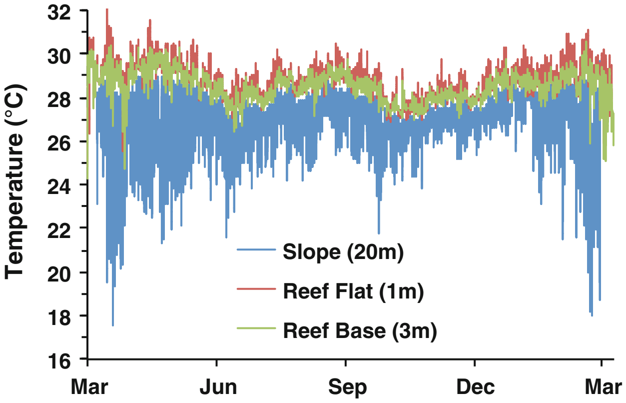

Fig. 17.3 Benthic temperature records at three reef habitats/depths at Uva Is reef, Panama from January 2003 to April 2004. Methods as in Smith et al. (2014)

17.4 Depth Refugia (Vertical Scales of 10s of Meters)

Near-surface conditions in the ETP have the potential to create relatively shallow depth refuges and refugia compared with other tropical regions (Glynn 1996; Riegl and Piller 2003; Bongaerts et al. 2010; Smith et al. 2014). Because in most locations in the ETP the oceanographic conditions limit the formation of true light-dependent deep coral formations (i.e., mesophotic coral reefs; Hinderstein et al. 2010), in this chapter we refer to deeper or deep corals as any colonies deeper than shallow water coral or coral reef formations, typically >5–12 m. In areas without large-scale upwelling, the upper mixed layer depth, from the sea surface to the top of the first thermocline, is between 10 and 30 m (Table 17.1, Fig. 17.4). The typically thin upper mixed layer in the ETP has the potential to lower temperatures at modest depths compared with western ocean basins in the Pacific and Atlantic, increasing the chance to avoid thermal stress. In addition, avoidance of bleaching with depth may be enhanced by light attenuation, which can be substantial in many areas of the ETP because of productive and turbid waters. Furthermore, a prominent and dense chlorophyll maximum layer with high abundance of phytoplankton is associated with the bottom of the upper mixed layer (D'Croz and O'Dea 2007) where vital plant nutrients sequestered below the pycnocline in deeper waters are exposed in the photic zone. The tropical chlorophyll maximum layer may be associated with increased pelagic food (Leichter and

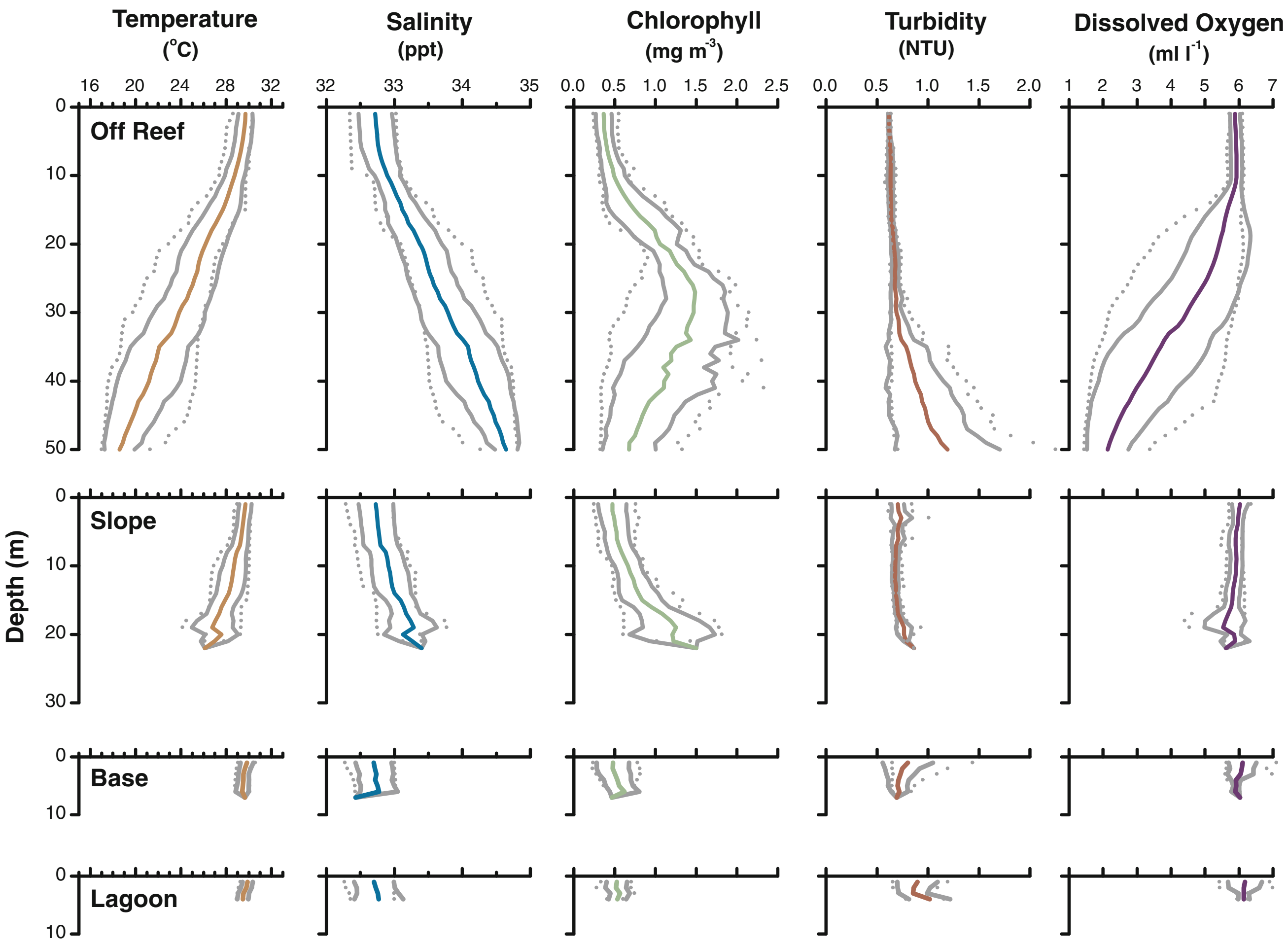

Fig. 17.4 Vertical and horizontal structure of water column bio-physical properties of Uva Island reef system, Gulf of Chiriquí, Republic of Panama, taken from oceanographic CTD casts. Locations of casts are from top to bottom, off-reef (n = 11), reef slope (10), reef base (9), and backreef lagoon (8). Data are means, standard deviation and min/max from 1 m depth bins. Data recorded from March 14 to 22, 2010 with a Seabird 25 sensor package; methods in Smith et al. (2014)

Genovese 2006) that could provide heterotrophic subsidy for bleached corals and improve recovery (Grottoli et al. 2006).

Suitable substrata for the formation of coral reefs is limited in many parts of the ETP. With the exception of oceanic islands, ETP carbonate reef build-ups are typically shallow structures with frameworks forming in less than 10 m depth (Glynn 1976, 2000). Thus, depth refuges in neritic reefs below 10 m will mostly consist of coral communities formed of isolated colonies growing on bedrock or coralliths on unconsolidated substrates. Since coral communities may cover larger areas and host more total hard coral populations than true structural coral reefs (Guzmán et al. 2004), they may be particularly important in determining where refuges or refugia form.

In addition, cooler conditions with depth during periods between El Niño events are necessary but not sufficient evidence to demonstrate that these habitats are refuges or refugia. The thermocline is often deepened by 5–10 m during El Niño conditions in the ETP (Enfield 2001; Fiedler and Talley 2006), which has the potential to erase any thermal buffering. Thus, there may be variability in the cooling provided in depth refuges over El Niño conditions, both from location to location and within a single location over multiple thermal stress events (i.e., reliability), and this may limit the potential for depth refugia. For example, the handful of studies that presented data on temperature with depth during the 1997–98 El Niño in the eastern Pacific showed temperature was isothermal or up to 3.0 °C cooler at 7–30 m depth [Champion Island, Galápagos (Wellington et al. 2001); Devil's Crown, Galápagos (Feingold 2001); Bahía Culebra, Costa Rica (Jiménez et al. 2001)]. An understanding of the processes that control the upper ocean vertical temperature structure during thermal stress events in different regions is lacking both empirical observations and mechanistic studies, and is an area of needed investigation.

Table 17.1 Locations and characteristics of coral community and coral reef environments in eastern tropical Pacific Ocean and their potential to support deep refugia populations

Country	Location	Conditions	Mixed layer depth (m)	Deeper coral species	Max. depth (m)	Source
Chile	Easter Is.	Oligotrophic	80?	Cyva, Lesc, Leso, Poda, Pove, Polo	>50	Glynn et al. (2003); Hubbard and Garcia (2003)
Colombia	Island: Gorgona Is.	Mesotrophic-Eutrophic (upwelling)	7–40	Pagi, Polo, Psspp, Pava	<20	Zapata and Vargas-Ángel (2003); Giraldo et al. (2008); K. Mejía, C. Muñoz, and F. Zapata, pers. comm.
Colombia	Malpelo Is.	Oligotrophic	30	Polo, Poca, Pacl, Pava, Gapl,	>30	Birkeland et al. (1975); Zapata and Vargas-Ángel (2003)
Costa Rica	Island: Caño Is.	Oligotrophic	20*	Polo, Psspp, Poel, Pagi	<22	Guzmán and Cortéz (1989)
Costa Rica	Coastal: Bahía Culebra, Golfo de Papagayo	Eutrophic (upwelling)	0–20	Lepa, Pacl, Pagi, Pava, Poel, Polo, Popa	<20	Jiménez et al. (2001), Cortés and Jiménez (2003)
Costa Rica	Coastal: Bahía Culebra – Pta. Gorda, Península de Nicoya	Mesotrophic	20*	Lepa, Pacl, Pagi, Poel Polo, Popa, Pava	<20	Cortés and Jiménez (2003)
Costa Rica	Cocos Is.	Oligotrophic	13–30	Lesc, Pala, Psam, Gplan, Pvspp	>35	Bakus (1975); Guzmán and Cortés (2007), J. Cortés pers. comm.
Ecuador	Galápagos Iss. North	Oligotrophic-Mesotrophic	15–30	Cyel, Pagi, Pava, Polo, Pacl	>40	Glynn and Wellington (1983); Banks et al. (2009); T. Smith, unpub. data
Ecuador	Galápagos Iss. West: Deep populations not known	Eutrophic (upwelling)	0	Pagi, Polo	5	Glynn and Wellington (1983); T. Smith, unpub. data
Ecuador	Galápagos Iss. East and South	Mesotrophic-Eutrophic (upwelling)	0–25	Cycu, Didi, Psspp, Pagi, Pocl, Polo	25	Glynn and Wellington (1983); T. Smith unpub. data
El Salvador	Coastal: Deep populations not known	Mesotrophic	20*			Reyes-Bonilla and Barraza (2003)
France	Clipperton Atoll	Oligotrophic	30–40*	Polo, Lpap[?]	>50	Glynn et al. (1996)
Mexico	Coastal: Deep populations not known	Mesotrophic-Eutrophic (upwelling)	20–30		<10	Reyes Bonilla (2003), Carriquiry and Reyes-Bonilla (1997)
Mexico	Revillagigedo Iss.	Oligotrophic	20–30*	Polo, Pavona	30	Reyes-Bonilla pers. comm.
Panamá	Island: Secas Iss., Contreras Iss., Coiba Island group	Mesotrophic	12–25	Cycu, Gapl, Miin, Pach, Pacl, Pagi, Polo, Pava, Lapa	27	Maté (2003), Authors, unpub. obs.
Panamá	Island: Pearl Iss., Deep populations not known	Mesotrophic-Eutrophic (upwelling)	0–20		<10	Maté (2003)

Areas are subdivided by country, locations, productivity, depth of mixed layer, species in deep habitats, and depth ranges from 12 m to deepest record of scleractinian coral occurrence

*Mixed layer depths estimated from Fiedler and Talley (2006), Fig. 11. Data are interpolated from predominantly open ocean CTD casts and are approximated near bathymetric highs, such as islands and continental shelves

Species key: *Cycloseris curvata* = Cycu, *Cycloseris vaughani* = Cyva, *Diaseris distorta* = Didi, *Gardineroseris planulata* = Gapl, *Leptoseris papyracea* = Lepa, *Leptoseris scabra* = Lesc, *Leptoseris solida* = Leso, *Millepora intricata* = Miin, *Pavona clavus* = Pacl, *Pavona gigantea* = Pagi, *Pavona varians* = Pava, *Pocillopora capitata* = Poca, *Pocillopora damicornis* = Poda, *Pocillopora elegans* = Poel, *Pocillopora verrucosa* = Pove, *Porites lobata* = Polo, *Porites panamensis* = Popa, *Psammocora* spp. = Psspp

Highly productive eutrophic areas of the ETP are less likely to support depth refuges and refugia because conditions associated with high productivity limit suitable deeper habitats for coral growth. Eutrophic areas of the ETP (Table 19.1) range from turbid inshore locations exposed to terrestrial run-off (e.g., parts of the Gulf of Chiriquí in

Panama, Los Cóbanos in El Salvador), seasonal coastal upwelling regions (i.e., the Gulfs of Tehuantepec, Papagayo, and Panama), and continuous coastal and oceanic upwelling areas (e.g., the western and southern Galápagos, the coasts of Peru and Ecuador). When zooxanthellate corals occur in eutrophic environments, strongly attenuated incident light can reduce the maximum depths of occurrence, such as in Panama (Glynn 1976), and in these areas corals may not exist to depths that interact with the first (shallowest) thermocline. This turbidity can be increased by sediment in terrestrial run-off or upwelling-increased productivity that stimulates blooms of phytoplankton and zooplankton.

In addition, low temperature thermal stress from seasonal and continuous upwelling can limit the occurrence of deeper corals or, in the case of the Peruvian coastline, can prevent the occurrence of any zooxanthellate corals. The 20 °C isotherm often surfaces during upwelling conditions, with even more extreme temperatures in subsurface areas (Glynn and Stewart 1973; Jiménez 2001). Periods of exposure to these temperatures that last longer than a few weeks can inhibit coral growth and lead to coral mortality (Glynn and Stewart 1973; Glynn 1990; Glynn and Fong 2006). Coastal upwelling environments are present in the Gulf of Tehuantepec, Gulf of Papagayo, Gulf of Panama, and off the Ecuadorian mainland, and in these upwelling areas most corals are restricted to shallow depths (<5 m) (Glynn and Leyte-Morales 1997; Glynn 2000, 2003). At Gorgona Island, Colombia the influence of the Gulf of Panama upwelling across the larger Panama Bight likely causes periodic intrusions of cold water to shallow depths (Giraldo et al. 2008), and this may explain why deep corals are not abundant around this nearshore island (Table 19.1; F. Zapata, pers. comm.). Shallow water upwelling refuges and refugia are discussed later in this chapter.

Less productive and turbid oligotrophic areas of the ETP have been shown to support depth refugia in at least one case. In the Contreras Islands a neritic depth refugium has been shown for one species of coral. Populations of the extremely thermally sensitive hydrocoral *Millepora intricata* that are restricted to the Gulf of Chiriquí, Panama survived in depth refuges (>12 m depth) over the two most severe recent El Niño events (1982–83, 1997–98), while the two congeners *Millepora boschmai* and *Millepora platyphylla* without deep populations were driven to regional extinction in the ETP (Smith et al. 2014). Deep populations likely provided planktonic recruits for recolonization of shallow habitats after thermal stress, allowing partial recovery of shallow water populations. In the same study, reef core records indicated that *M. intricata* persisted at two reefs in Panama throughout the last half of the Holocene period (5500 BP), including over a period of heightened ENSO activity that likely generated El Niño conditions that surpassed the severity of those in 1982–83 and 1997–98 (Toth et al. 2012). Smith et al. (2014) concluded that depth refuges in the ETP were necessary for *M. intricata* to avoid regional extinction, and provided evidence of the deep refugia hypothesis (Glynn 1996; Riegl and Piller 2003; Bongaerts et al. 2010). Also, post-El Niño deep refugia hydrocoral populations were not found in structure-forming coral reefs, but were present in coral communities associated with bedrock or in corallith deposits along the deep talus slopes of coral reefs. This further suggests that zooxanthellate coral communities growing outside of true reefs form an important component of depth refugia in the ETP.

Many other areas in the ETP may also support depth refugia for certain coral species, but there are much less data. For this reason we will discuss different oligotrophic areas of the ETP and their potential to support depth refugia, which we hope will encourage further investigations in this region. In neritic environments on the continental shelf of the tropical Pacific Americas, where turbidity and cold water are not limiting, significant coral communities form at locations between 10 and 40 m, and could therefore harbour refuge populations. Deeper scleractinian corals along the continental mainland appear to be sparser than in offshore areas (Table 19.1), but the size of the extensive Central American coastline suggests that the total number of deep coral colonies could be large. Many sections along the continental mainland of the ETP show some deep coral development, particularly in Costa Rica and Panama (Table 19.1). Nearshore deep coral development, however, may be rare or lacking in Mexico and El Salvador (Reyes Bonilla 2003; Reyes Bonilla and Barraza 2003).

There are well-developed deep coral communities present at several neritic islands where waters are clearer than the adjacent continental mainland and deep temperatures are not limiting. Examples include Caño Island (Guzmán and Cortés 1989), Costa Rica; and the Secas Islands, Contreras Islands, and Coiba Island group, Panama (Glynn and Maté 1997). At Caño Island, isolated patches of *Porites lobata, Psammocora* spp., *Pocillopora elegans*, and *Pavona gigantea* occur to 22 m depth although there is a sand margin at a modest 12 m depth near the main reef. Guzmán and Cortés (1989) suggested that deeper corals growing on the reef slope (>5 m depth) had higher survival than shallow corals during the 1982–83 El Niño, which may suggest a depth refuge during this thermal stress event.

In Panama, our recent observations of non-coral, rock outcrops have revealed the presence of zooxanthellate coral communities occurring deeper than 20 m in the Coiba Iss. group, the Secas Iss., and the Contreras Iss.. In the Contreras Iss., along a rock outcrop just north of the Uva Island study reef, abundant isolated colonies of *Gardineroseris planulata*, *Millepora intricata*, *Pavona chiriquiensis*, *Pavona clavus*, *Pavona gigantea*, *Porites lobata*, and *Pavona varians* occur between 18–25 m. Similar communities have been observed around the Coiba Iss. group (Guzmán et al. 2004) and the Secas Iss. (T. Smith, unpub. observ.).

There is great potential for depth refugia at oceanic islands located far from the continent. Offshore islands and archipelagos in the far eastern Pacific exist across an enormous expanse of ocean and a diverse array of abiotic settings (Fiedler 1992; Fiedler and Talley 2006; see Chap. 3, Fiedler and Lavín), ranging from the intense upwelling of the western Galápagos Islands to the oligotrophic waters surrounding Clipperton Atoll. Islands that support light-dependent corals include the Revillagigedo Islands, Clipperton Atoll, Cocos Island, Easter Island (Rapa Nui), Malpelo Island, and the Galápagos Archipelago. Clear oceanic environments with no upwelling to moderate levels of upwelling might support refuges at depths considered mesophotic in the Western Atlantic and Pacific Ocean basins (30–150 m; Hinderstein et al. 2010). Examples include Clipperton Atoll, Cocos Island, Easter Island, Malpelo Island, and the northern Galápagos Islands (Darwin and Wolf Islands) (Table 19.1). Each of these islands supports zooxanthellate corals, including some shallow water species, to depths greater than 30 m (Table 19.1). Perhaps the most spectacular example of deep, light-dependent coral communities is found at Clipperton Atoll, and was well described by Glynn et al. (1996) who sampled high coral cover to 60 m.

There is both direct and indirect evidence that deep coral populations at oceanic islands can endure thermal stress events better than shallow reefs. Cover of *Gardineroseris planulata*, *Pavona* spp., *Pavona varians*, *Porites lobata*, and *Psammocora stellata* on two reefs at Cocos Island was higher in deeper reef areas (>9 m) than shallow areas of the same reefs, where some coral species disappeared after the 1982–83 El Niño event (Guzmán and Cortés 1992). Indeed, some of these colonies may have assisted in recolonization and recovery of shallow water areas (Guzmán and Cortés 2007). There is also direct and indirect evidence from the Galápagos Archipelago that some oceanic islands demonstrated greater coral survival in deeper areas after thermal stress. The best evidence for a depth refuge effect in an oceanic setting comes from Feingold (2001) who showed that fungiid corals at around 33 m did not bleach during the 1997–98 warming event, whereas corals present around 16 m were nearly all bleached. This study attributed the difference to both decreasing irradiance and more variable temperatures at depth caused by the intrusion of cooler water associated with the thermocline.

Coral reefs in the northern Galápagos were heavily impacted by the 1982–83 El Niño event (Glynn et al. 2009), but recent surveys at Darwin and Wolf Islands in 2012 reported extensive deep coral populations in depths greater than 20 m (Glynn et al. 2015; T. Smith, unpub. data). Coral cover peaked at 54 % in 24 m depth in Bahía Tiburón, Wolf Island, whereas coral cover at 10 m was 18.5 %. Deeper coral populations were also observed, but not quantified at Marchena Island. In the southern Galápagos at Floreana Island, cover at 20 m depth was 7.6 % and declined to 0 % at 30 m, showing a more limited potential for a deep refugium possibly related to cooler, more oligotrophic conditions (but see the discussion of fungiid survival above). At other oceanic islands, the evidence for a depth refuge is more equivocal. At Easter Island a 1–2 °C positive temperature anomaly (26–27 °C) caused some bleaching to 30 m (Glynn et al. 2003). Light-dependent corals occur much deeper (to 50+ m) at Easter Island, but their condition was not observed and coral mortality was not quantified (P. Glynn, pers. comm.).

17.4.1 Species-Specific Aspects of Depth Refuges

A prerequisite for a coral species benefitting from a depth refugium is that the species is a depth generalist. For example, it was seen that among milleporid species in the Gulf of Chiriquí that those species without a deep population were driven to regional extinction in the ETP, whereas *Millepora intricata* was able to survive in deep zones over two extreme El Niño disturbances (Smith et al. 2014). Not only does *M. intricata* survive in deep areas but it also seems to be abundant at depth. This is important, since mortality from bleaching did extend into deeper zones, albeit at a reduced rate, and having high abundance at depth helped ensure some survivors for re-expansion. Among the low diversity ETP hermatypic coral faunas there are many species with wide depth ranges that may be able to benefit from depth refuges (Table 19.1).

The exact reason that some species are depth generalists while others are confined to shallower depths has not been well studied. In other systems, heterotrophic plasticity, the ability to shift from autotrophy to heterotrophy to meet colony energetic demands, has been postulated as a mechanism maintaining colony fitness at deeper depths (Lesser et al. 2010). In shallow waters less than 6 m depth in the Gulf of Panama, Palardy et al. (2005) found that the mounding corals *Pavona clavus* and *Pavona gigantea* were more adept at heterotrophic feeding on zooplankton than branching *Pocillopora damicornis* during non-upwelling conditions. The agariciids *P. clavus, P. gigantea,* and *P. varians* all have wide depth ranges across the ETP (Table 19.1) and their survival at greater depths may be facilitated by their heterotrophic food capture abilities.

Among the milleporids, *Millepora intricata* is likely a competent heterotrophic feeder (Lewis 1989) and this may facilitate its ability to occur across a variety of depths. However, under the assumption that all milleporids are efficient at heterotrophic feeding, it is not clear why the two milleporid species that went regionally extinct did not occur deeper than 15 m. They may be more dependent on phototrophy than assumed or the morphologies of *Millepora boschmai* (columnar to upright plates) and *Millepora platyphylla* (upright plates) may be maladapted to persist at low light levels and unidirectional currents of deeper water, as opposed to high light conditions and oscillatory, wave-driven currents of shallow water.

ETP coral species that occur more rarely or not at all in greater depths may have reduced fitness in deeper zones that is related to reliance on phototrophy for energy acquisition. One pattern that supports this hypothesis is that where shallow trending species do have a deep extended range it is in clear oceanic environments (Table 19.1). This includes *Porites lobata*, which may not be able to meet a majority of its energetic needs heterotrophically (Grottoli et al. 2006). This species is confined to substrates less than 20 m depth in more turbid environments, but can occur deeper at locations where the water clarity is higher. In the clear waters of the northern Galápagos Islands and Clipperton Atoll where *P. lobata* does occur below 20 m depth it is much reduced in cover relative to shallow water, unlike species in the genus *Pavona* that have a much more even distribution with depth or even increase in cover below 20 m (Glynn et al. 1996, 2015). This also suggests a greater reliance of *P. lobata* on phototrophy than *Pavona* spp.

Most of the pocilloporid species have narrow and shallow depth ranges (Table 19.1), and reveal markedly reduced fitness in deeper water. Colonies of *Pocillopora damicornis* transplanted from 10 m to 18 m in the Gulf of Chiriquí showed very low survival (6.7 %, n = 15) and negative growth (−28 %, n = 1) over 3.4 years (T. Smith, unpub. data; methods as for *Millepora intricata* in Smith et al. 2014). Reduced fitness at greater depths at the same location where *M. intricata* occurred in a refugium might indicate a decrease in colony energy with decreased photosynthesis, but this was not tested directly.

17.4.2 Vertical Connectivity of Deeper Water Refugia

Very little is known about the connectivity of deeper coral populations via pelagic larval dispersal and other areas (seeding) or among themselves (self-recruitment). While this is difficult to study, larval connectivity has extremely important ramifications for the potential contribution of deeper reef areas to the resilience of the ETP coral fauna after disturbance and its potential to serve as refugia. Deeper coral populations will go extinct if they are only sinks for shallow water larvae and shallow water corals are extirpated. Furthermore, deeper-living corals will never contribute to shallow water recovery if they are only self seeding, which might occur if deep populations are adapted to deeper-occurring habitats. In this case the deeper corals may be a refugium for the species, but not for the full genetic diversity of the species. However, if deeper corals are just part of a network of larval exchange between all habitats, then they may have an important role in coral recovery following disturbance.

In the only demonstrated example of a deep refugium—*Millepora intricata* in the Gulf of Chiriquí—larval contribution from deep to shallow was inferred, suggesting the ability for deep populations to increase resilience (Smith et al. 2014). The inference was made possible because shallow water populations were likely to have been extirpated across most of the range, whereas deeper populations were extant. When shallow water populations reappeared at study sites a few years after a severe El Niño thermal disturbance it seemed likely they recruited from abundant deeper populations within a hundred meters distance, rather than from distant shallow water survivors, if present but not observed. In other species where shallow water populations are not entirely decimated by El Niño disturbances, demonstrating connectivity and its importance for population recovery will require genetic methodologies. This presents its own challenges, such as the development of genetic markers for different species, lack of population structure, and the need for many samples to be compared from each of the habitats. A full evaluation of the hypothesis that deeper areas are refugia from thermal stress events will require these sorts of studies.

17.5 Regional Refugia (Scales of 1000 km and Greater)

Regional refugia occur when large-scale physical oceanographic conditions increase the probability of survival for a large proportion of reef organisms over a large-scale disturbance. The best, and perhaps only, possible example of regional refuges occur in large scale upwelling centers where cooler conditions may act to lower thermal stress during ENSO associated warming events. A regional refugium may also exist, however, as a meta-refuge due to interacting networks of refuges at smaller scales. Thus, there are two types of regional refuges that might occur: (1) an overarching regional refugium where conditions provide avoidance for some of the corals in a region, and (2) a meta-refugium, where regional conditions favour the formation of multiple refuges that combine to increase the potential of a region to maintain biodiversity. We will address overarching and meta-refugia separately.

17.5.1 Overarching Regional Refugia

The most cited overarching regional refugia for corals includes areas where relatively cooler water is present during large-scale high thermal stress events. Conditions for shallow water regional refugia are largely favoured by upwelling of cool water into surface layers (Glynn 1996; West and Salm 2003). Distinct seasonal upwelling occurs at three areas along the Central American coastline (Gulf of Tehuantepec, Gulf of Papagayo, and the Gulf of Panama). Seasonal upwelling in the Gulf of Panama provided a thermal refuge for corals during ENSO related sea warming over the 1997–98 El Niño event (Glynn et al. 2001). In addition, non-seasonal upwelling has been suggested as lowering the incidence of bleaching during the 1997–98 El Niño event in the Gulf of California relative to lower-latitude areas of the ETP (Reyes-Bonilla 2001). More continuous upwelling occurs in the western Galápagos, due to the shoaling of the equatorial undercurrent (Cromwell current), and along the South American mainland coast (Colombia, Ecuador, Peru) from Ekman coastal upwelling.

Scaling upwelling refuges to long-term refugia is compromised if upwelling and thermal stress timing are not coincident (Chollett et al. 2010), or if upwelling prevents acclimation to anomalously warm conditions (D’Croz and Maté 2004). Since high thermal stress created by El Niño conditions can occur throughout the year there is not always synchrony between heat stress and the seasonal upwelling in the Gulf of Panama (Glynn et al. 2001; Chollett et al. 2010). Furthermore, ENSO results in a general deepening of the thermocline (Enfield 2001; Fiedler and Talley 2006) and therefore upwelled waters may still be anomalously warm, even if cooler than the mean temperatures of adjacent areas. Since coral bleaching thresholds are specific to the background climatology (Coles et al. 1976) and corals from the Gulf of Panama have been shown to be more sensitive to thermal stress (D’Croz et al. 2001; D’Croz and Maté 2004), a long-term refugium caused by the Gulf of Panama upwelling may be compromised. The same general principles apply for the upwelling Gulf of Papagayo, whereby there is potentially some benefit from upwelling, but positive thermal anomalies associated with El Niño events do occur and result in moderate coral mortality (Jiménez et al. 2001, 2010). Upwelling as a mechanism creating a thermal refugium has been examined less extensively for coastal upwelling in the Gulf of Tehuantepec.

Positive El Niño-Southern Oscillation anomalies are most pronounced at the equator (+0.5–1.0 °C) and this negates the potential for an upwelling refugium in the Galápagos Archipelago. The corals and coral reefs of the equatorial upwelling Galápagos Archipelago were shown to be very sensitive to thermal stress in the 1982–83 and 1997–98 El Niño events (Glynn 1994; Glynn et al. 2001). Here, heterogeneous thermal zones across the region were uniformly warm, causing anomalies as high as 1–2 °C (Glynn 1990; Wellington et al. 2001). The entire equatorial region is highly susceptible to positive temperature anomalies (+1–2 °C) during El Niño events because the mixed layer depth remains relatively constant, whereas the thermocline is depressed below the mixed layer and cool water is not brought to the surface (Fiedler and Talley 2006).

Other over-arching regional refugia may be found in coastal areas. There is some evidence that neritic regions near the Central American coast may be less sensitive to coral bleaching than offshore regions. There may have been an offshore-to-onshore decline in coral mortality during El Niño events in Ecuador and Panama due to lower SSTs and reduced light penetration and irradiance stress (Glynn et al. 2001). However, it is also possible to expect the same offshore-to-inshore differences due to a reduction in the penetration of Kelvin waves associated with El Niño events by geomorphological and orographic effects in neritic habitats. If true, this may provide additional support for Macintyre’s hypothesis (Macintyre et al. 1992) that sheltering from El Niño warming events and cool upwelling conditions could facilitate the accumulation of large coral reef frameworks in some near-shore eastern Pacific areas via avoidance.

17.5.2 Meta-Refugia

Refugia operate on scales of time and space that necessitate protection from multiple disturbances. Different types of refuges across diverse habitats may be protective (e.g., prevent extirpation) in any given disturbance, but perhaps not in subsequent disturbances. In this case no particular refuge may be a refugium because of vulnerability at some point in time and space. However, within a spatial network of habitat patches connected by larval exchange and the possibility of recolonization, different refuges acting in concert could act as a meta-refugium that reduces the risk of regional extinctions. Under this scenario a network of ephemeral refuges permits expansion under classical meta-population dynamics (Hanski 1998). While metapopulation theory is well established, the suggestion of meta-refugia is here used to illustrate the idea that having resistant populations in a diversity of refuges, even if no one refuge can scale to a refugium, may limit the chance of extinction across all interconnected habitat patches and together these multiple patches (refuges) may scale to a refugium.

The prospect of meta-refugia is hypothetical, but some areas of the ETP may be less resistant to long-term changes in ENSO frequency and intensity because of a lack of refuge networks. For example, upwelling areas have low habitat diversity because upwelling limits depth refuges and restricts most coral growth to protected areas in the lee of persistent upwelling streams. Therefore, upwelling areas may be less resistant and resilient in the context of meta-refugia, since all biota may respond equally to large-scale disturbances, such as El Niño seawater warming. Conversely, neritic, non-upwelling areas north of the equator in Costa Rica and Panama may have an increased possibility for meta-refuges since they have the potential for depth refuges, possess a high degree of habitat heterogeneity (turbidity gradients, island and coastal areas, oceanographic variability), and could be well connected. They also have a high abundance of corals, which could be evidence that refugia are present and have been protective in the past, or that refugia are present because of the high abundance of corals. While this may seem circular, large populations increase the number of habitats, including refuges, that are occupied (Hanski 1998), and occupation of more refuge habitats may increase the resilience of metapopulations. Empirically, from the marine fossil record, being widespread and having greater habitat breadth, albeit at a coarser scale than we are examining here, has been shown to decrease the probability of extinction (Harnick et al. 2012).

17.6 Conclusion

Refugia as a means for corals to avoid extinction or to rapidly recolonize susceptible habitats after disturbance seem to be an important mechanism for coral and coral reef persistence in the marginal eastern tropical Pacific Ocean. However, it seems that certain types of refuges may be more likely to scale to a refugium. In particular, conditions that favour partial colony mortality, such as intra-colony environmental heterogeneity, may favour refugia for shallow-water species susceptible to seawater warming, such as *Pocillopora* spp. and *Gardineroseris planulata*. Intra-reef and inter-reef thermal refugia may occur where temperatures are normally elevated, such as lagoons, reef flats, or on reefs that are relatively warm relative to local open ocean conditions. These areas may increase local tolerance through acclimation or adaptation. Avoidance of thermal stress at intra- and inter-reef scales may be comparatively rare, however, since cooling processes are often not reliable during warm anomalies, and corals in cooler environments are susceptible to any change from the highest normal mean thermal conditions. A depth refugium was confirmed for at least one zooxanthellate species, the hydrocoral *Millepora intricata*, and a refuge was shown for a fungiid scleractinian species at one site over the 1997–98 El Niño event. Other depth generalist species, such as *Pavona* spp. may benefit from increased resilience after disturbance because of reduced or no mortality in depth refuges; however, demonstrating depth refugia for other species still needs empirical data through El Niño disturbances. At the scale of regions, seasonal upwelling has been shown to be a refuge over specific events, but whether this scales to a long-term refugium depends critically on whether cooling from upwelling is always timed to avoid periods of thermal stress. Other large-scale upwelling areas, such as the western and southern Galápagos and the South American coast appear vulnerable to the cessation of cooling upwelling during El Niño events. In these areas reduced cooling due to a deepened equatorial thermocline during El Niño and a coral fauna that may be more susceptible to elevated temperatures because of normally cooler temperatures, may compromise regional refuges and refugia. Hypothetically, the existence of meta-refugia may ensure the long-term persistence of coral species and coral reefs in the ETP by supporting corals in diverse types of refuges that together scale to a refugium.

There remains a great deal of work to be done if we are to understand how refugia support corals and other sessile marine species in a warming ocean. Future research in the ETP should target the thermal responses of species in more marginal hermatypic coral habitats, such as deep areas below the thermocline, and corals growing on rock outcrops and unconsolidated substrates. This will help us understand the full demographic ramifications of refugia in maintaining coral populations. In addition, the impacts of chronic stress, such as low aragonite saturation states or low oxygen concentrations, in limiting the extent of coral development and growth are important considerations for understanding the limits to the scale of refugia. Because the ETP has a substantial record of coral ecological research, is prone to repeated thermal disturbances, has a wide diversity of oceanographic conditions, and supports a number of coral species at various stages of rarity and vulnerability to regional extinction, it is an ideal region to continue the study of refugia in the modern ocean.

Acknowledgements We thank Jorge Cortés, Peter Glynn, Katherine Mejía, Carlos Muñoz, Héctor Reyes Bonilla, Bernardo Vargas-Ángel, and Fernando Zapata for personal observations and unpublished data. These workers kindly shared their vast knowledge of corals in the eastern Pacific and helped to make this a more complete chapter. Peter Glynn provided a helpful review of an earlier draft and was particularly important for forming our earlier ideas of reef refugia. Likewise we also thank Iliana Chollet and Aaron O'Dea who provided excellent reviews and provided many helpful comments that are reflected in this chapter. We also thank the editors for their patience and guidance in producing this superb collection of papers on corals and coral reefs of the eastern tropical Pacific Ocean.

References

Baker AC, Glynn PW, Riegl B (2008) Climate change and coral reef bleaching: an ecological assessment of long-term impacts, recovery trends and future outlook. Estuar Coast Shelf S 80:435–471

Baker AC, Starger CJ, McClanahan TR, Glynn PW (2004) Coral reefs: corals' adaptive response to climate change. Nature 430:741

Bakus GJ (1975) Marine zonation and ecology of Cocos Island, off Central America. Atoll Res Bull 179:1–9

Banks S, Vera M, Chiriboga Á (2009) Establishing reference points to assess long-term change in zooxanthellate coral communities of the northern Galápagos coral reefs. Galápagos Res 66:43–64

Barshis DJ, Ladner JT, Oliver TA, Seneca FO, Traylor-Knowles N, Palumbi SR (2013) Genomic basis for coral resilience to climate change. Proc Natl Acad Sci USA 110:1387–1392

Baums IB, Boulay JN, Polato NR, Hellberg ME (2012) No gene flow across the Eastern Pacific Barrier in the reef-building coral *Porites lobata*. Mol Ecol 21:5418–5433

Bellantuono AJ, Hoegh-Guldberg O, Rodriguez-Lanetty M (2011) Resistance to thermal stress in corals without changes in symbiont composition. Proc R Soc B: Biol Sci 279:1100–1107

Bender EA, Case TJ, Gilpin ME (1984) Perturbation experiments in community ecology: theory and practice. Ecology 65:1–13

Birkeland C, Meyer DL, Stames JP, Buford CL (1975) Subtidal communities of Malpelo Island. In: JB Graham (ed) The biological investigation of Malpelo Island, Colombia. Smith Contrib Zool 176:55–68

Bongaerts P, Ridgway T, Sampayo E, Hoegh-Guldberg O (2010) Assessing the 'deep reef refugia' hypothesis: focus on Caribbean reefs. Coral Reefs 29:309–327

Brown BE (1997) Coral bleaching: causes and consequences. Coral Reefs 16:S129–S138

Brown BE, Dunne RP, Goodson MS, Douglas AE (2002) Experience shapes the susceptibility of a reef coral to bleaching. Coral Reefs 21:119–126

Carriquiry JD, Reyes Bonilla H (1997) Community structure and geographic distribution of the coral reefs of Nayarit, Mexican Pacific. Cienc Mar 23:227–248

Castillo KD, Ries JB, Weiss JM, Lima FP (2012) Decline of forereef corals in response to recent warming linked to history of thermal exposure. Nature Clim Change 2:756–760

Chollett I, Mumby P, Cortés J (2010) Upwelling areas do not guarantee refuge for coral reefs in a warming ocean. Mar Ecol Prog Ser 416:47–56

Coles SL, Jokiel PL, Lewis CR (1976) Thermal tolerance in tropical versus subtropical reef corals. Pac Sci 30:159–166

Cortés J, Jiménez C (2003) Corals and coral reefs of the Pacific of Costa Rica: history, research and status. In: Cortés J (ed) Latin American coral reefs. Elsevier, Amsterdam, pp 361–385

D'Croz L, Maté JL (2004) Experimental responses to elevated water temperature in genotypes of the reef coral *Pocillopora damicornis* from upwelling and non-upwelling environments in Panama. Coral Reefs 23:473–483

D'Croz L, O'Dea A (2007) Variability in upwelling along the Pacific shelf of Panama and implications for the distribution of nutrients and chlorophyll. Estuar Coast Shelf S 73:325–340

D'Croz L, Maté J, Oke J (2001) Responses to elevated sea water temperature and UV radiation in the coral *Porites lobata* from upwelling and non-upwelling environments on the Pacific coast of Panama. Bull Mar Sci 69:203–214

Darling ES, Alvarez-Filip L, Oliver TA, McClanahan TR, Côté IM (2012) Evaluating life-history strategies of reef corals from species traits. Ecol Lett 15:1378–1386

Davis KA, Lentz SJ, Pineda J, Farrar JT, Starczak VR, Churchill JH (2011) Observations of the thermal environment on Red Sea platform reefs: a heat budget analysis. Coral Reefs 30:25–36

de Boyer Montégut C, Madec G, Fisher AS, Lazar A, Iudicone D (2004) Mixed layer depth over the global ocean: an examination of profile data and a profile-based climatology. J Geophys Res 109: C12003

Enfield DB (2001) Evolution and historical perspective of the 1997–1998 El Niño-Southern Oscillation event. Bull Mar Sci 69:7–25

Feingold J (2001) Response of three coral communities to the 1997–98 El Niño-Southern Oscillation: Galápagos Islands, Ecuador. Bull Mar Sci 69:61–77

Fiedler P (1992) Seasonal climatologies and variability of eastern tropical Pacific surface waters. NOAA Tech Rept NMFS [NOAA TECH. REP. NMFS], vol 109

Fiedler PC, Talley LD (2006) Hydrography of the eastern tropical Pacific: a review. Prog Oceanogr 69:143–180

Giraldo A, Rodríguez-Rubio E, Zapata FA (2008) Condiciones oceanográficas en Isla Gorgona, Pacífico oriental tropical de Colombia. Lat Am J Aquat Res 36:121–128

Glynn PW (1976) Some physical and biological determinants of coral community structure in the eastern Pacific. Ecol Monogr 46:431–456

Glynn PW (1990) Coral mortality and disturbances to coral reefs in the tropical eastern Pacific. In: Glynn PW (ed) Global ecological consequences of the 1982-83 El Niño-Southern Oscillation. Elsevier Sci Pub BV, Amsterdam, pp 55–126

Glynn PW (1994) State of coral reefs in the Galápagos Islands: natural vs anthropogenic impacts. Mar Poll Bull 29:131–140

Glynn PW (1996) Coral reef bleaching: facts, hypotheses and implications. Glob Change Biol 2:495–509

Glynn PW (2000) Eastern Pacific coral reef ecosystems. In: Seeliger U, Kjerfve B (eds) Coastal marine ecosystems of Latin America. Ecol Stud, vol 144, Springer-Verlag, Berlin pp 281–305

Glynn PW (2003) Coral communities and coral reefs of Ecuador. In: Cortés J (ed) Latin American coral reefs. Elsevier Science BV, Amsterdam, pp 449–472

Glynn PW (2011) In tandem reef coral and cryptic metazoan declines and extinctions. Bull Mar Sci 87:767–794

Glynn PW, Ault JS (2000) A biogeographic analysis and review of the far eastern Pacific coral reef region. Coral Reefs 19:1–23

Glynn PW, Colley SB (2008) Survival of brooding and broadcasting reef corals following large scale disturbances: is there any hope for broadcasting species during global warming? In: Proceedings of 11th International Coral Reef Symposium, Ft Lauderdale, pp 361–365

Glynn PW, Fong P (2006) Patterns of reef coral recovery by the regrowth of surviving tissues following the 1997-98 El Niño warming and 2000, 2001 upwelling cool events in Panamá, eastern Pacific. In: Proceedings of 10th International Coral Reef Symposium, vol 1, Okinawa, pp 624–630

Glynn PW, Leyte-Morales GE (1997) Coral reefs of Huatulco, west México: reef development in upwelling Gulf of Tehuantepec. Rev Biol Trop 45:1033–1047

Glynn PW, Maté JL (1997) Field guide to the coral reefs of Panamá. Proceedings of 8th International Coral Reef Symposium, vol 1, Panama, pp 145–166

Glynn PW, Stewart RH (1973) Distribution of coral reefs in the Pearl Islands (Gulf of Panama) in relation to thermal conditions. Limnol Oceanogr 18:367–379

Glynn PW, Wellington GM (1983) Corals and coral reefs of the Galápagos Islands. Univ California Press, Berkeley, p 330

Glynn PW, Veron JEN, Wellington GM (1996) Clipperton Atoll (eastern Pacific): oceanography, geomorphology, reef-building coral ecology and biogeography. Coral Reefs 15:71–99

Glynn PW, Maté JL, Baker AC, Calderón MO (2001) Coral bleaching and mortality in Panama and Ecuador during the 1997-1998 El Niño-Southern Oscillation event: spatial/temporal patterns and comparisons with the 1982-1983 event. Bull Mar Sci 69:79–109

Glynn PW, Wellington GM, Wieters EA, Navarrete SA (2003) Reef-building coral communities of Easter Island (Rapa Nui), Chile. In: Cortés J (ed) Latin American coral reefs. Elsevier Science, Amsterdam, pp 473–494

Glynn PW, Riegl B, Correa AMS, Baums IB (2009) Rapid recovery of a coral reef at Darwin Island, Galapagos Islands. Galapagos Res 66:6–13

Glynn PW, Riegl B, Purkis S, Kerr J, Smith TB (2015) Coral reef recovery at Darwin, the northern-most of the Galápagos Islands. Coral Reefs 34:421–436

Gorospe KD, Karl SA (2011) Small-scale spatial analysis of *in situ* sea temperature throughout a single coral patch reef. J Mar Biol art ID 719580

Grottoli AG, Rodrigues LJ, Palardy JE (2006) Heterotrophic plasticity and resilience in bleached corals. Nature 440:1186–1189

Guest JR, Baird AH, Maynard JA, Muttaqin E, Edwards AJ, Campbell SJ, Yewdall K, Affendi YA, Chou LM (2012) Contrasting patterns of coral bleaching susceptibility in 2010 suggest an adaptive response to thermal stress. PLoS ONE 7:e33353

Guzmán HM, Cortés J (1989) Coral reef community structure at Caño Island, Pacific Costa Rica. PSZNI: Mar Ecol 10:23–41

Guzmán HM, Cortés J (1992) Cocos Island (Pacific of Costa Rica) coral reefs after the 1982-1983 El Niño disturbance. Rev Biol Trop 40:309–324

Guzmán HM, Cortés J (2007) Reef recovery 20 years after the 1982–1983 El Niño massive mortality. Mar Biol 151:401–411

Guzmán HM, Guevara CA, Breedy O (2004) Distribution, diversity, and conservation of coral reefs and coral communities in the largest marine protected area of Pacific Panama (Coiba Island). Environ Conserv 31:111–121

Hanksi I (1998) Metapopulation dynamics. Nature 396:41–49

Harnik PG, Lotze HK, Anderson SC, Finkel ZV, Finnegan S, Lindberg DR, Liow LH, Lockwood R, McClain CR, McGuire JL, O'Dea A, Pandolfi JM, Simpson C, Tittensor DP (2012) Extinctions in ancient and modern seas. Trends Ecol Evol 27:608–617

Hinderstein L, Marr J, Martinez F, Dowgiallo M, Puglise K, Pyle R, Zawada D, Appeldoorn R (2010) Theme section on mesophotic coral ecosystems: characterization, ecology, and management. Coral Reefs 29:247–251

Holling CS (1973) Resilience and the stability of ecological systems. Annu Rev Ecol Syst 4:1–23

Hubbard DK, Garcia M (2003) The corals and coral reefs of Easter Island—a preliminary look. In: Loret J, Tanacredi JT (eds) Easter Island: scientific exploration into the world's environmental problems in microcosm. Kluwer Academic/Plenum Pub, New York, pp 53–79

Hughes TP, Bellwood DR, Connolly SR, Cornell HV, Karlson RH (2014) Double jeopardy and global extinction risk in corals and reef fishes. Curr Biol 24:2946–2951

Jiménez C (2001) Seawater temperature measured at the surface and at two depths (7 and 12 m) in one coral reef at Culebra Bay, Gulf of Papagayo, Costa Rica. Rev Biol Trop 49(Suppl 2):153–161

Jiménez C, Cortés J, León A, Ruíz E (2001) Coral bleaching and mortality associated with the 1997-98 El Niño in an upwelling environment in the Eastern Pacific (Gulf of Papagayo, Costa Rica). Bull Mar Sci 69:151–169

Jiménez C, Bassey G, Segura Á, Cortés J (2010) Characterization of the coral communities and reefs of two previously undescribed locations in the upwelling region of Gulf of Papagayo (Costa Rica). Rev Cienc Mar Cost 2:95–108

Keppel G, Van Niel KP, Wardell-Johnson GW, Yates CJ, Byrne M, Mucina L, Schut AGT, Hopper SD, Franklin SE (2012) Refugia: identifying and understanding safe havens for biodiversity under climate change. Global Ecol Biogeogr 21:393–404

Leichter JJ, Genovese SJ (2006) Intermittent upwelling and subsidized growth of the scleractinian coral *Madracis mirabilis* on the deep fore-reef of Discovery Bay, Jamaica. Mar Ecol Prog Ser 316:95–103

Lesser MP (1997) Oxidative stress causes coral bleaching during exposure to elevated temperatures. Coral Reefs 16:187–192

Lesser MP, Slattery M, Stat M, Ojimi M, Gates RD, Grottoli A (2010) Photoacclimatization by the coral *Montastraea cavernosa* in the mesophotic zone: light, food, and genetics. Ecology 91:990–1003

Lewis JB (1989) The ecology of *Millepora*. Coral Reefs 8:99–107

Loreau M (2010) Linking biodiversity and ecosystems: towards a unifying ecological theory. Philos T Roy Soc B: Biol Sci 365:49–60

Loya Y, Sakai K, Yamazato K, Nakano Y, Sambali H, van Woesik R (2001) Coral bleaching: the winners and the losers. Ecol Lett 4:122–131

Macintyre IG, Glynn PW, Cortés J (1992) Holocene reef history in the eastern Pacific: mainland Costa Rica, Caño Island, Cocos Island, and Galápagos Islands. In: Proceedings of 7th International Coral Reef Symposium, vol 2, Guam, pp 1174–1184

Manzello DP (2010) Ocean acidification hotspots: spatiotemporal dynamics of the seawater CO_2 system of eastern Pacific coral reefs. Limnol Oceanogr 55:239–248

Maté JL (2003) Corals and coral reefs of the Pacific coast of Panamá. In: Cortés J (ed) Latin American coral reefs. Elsevier, Amsterdam, pp 387–417

McCann KS (2000) The diversity-stability debate. Nature 405:228–233

McClanahan TR, Ateweberhan M, Muhando CA, Maina J, Mohammed MS (2007) Effects of climate and seawater temperature variation on coral bleaching and mortality. Ecol Monogr 77:503–525

McKinney ML (1997) Extinction vulnerability and selectivity: combining ecological and paleontological views. Annu Rev Ecol Syst 28:495–516

Mumby PJ, Chisholm JRM, Edwards AJ, Andrefouet S, Jaubert J (2002) Cloudy weather may have saved Society Island reef corals during the 1998 ENSO event. Mar Ecol Prog Ser 222:209–216

Nakamura T, van Woesik R (2001) Water-flow rates and passive diffusion partially explain differential survival of corals during the 1998 bleaching event. Mar Ecol Prog Ser 212:301–304

Oliver TA, Palumbi SR (2011) Do fluctuating temperature environments elevate coral thermal tolerance? Coral Reefs 30:429–440

Palardy JE, Grottoli AG, Matthews KA (2005) Effects of upwelling, depth, morphology and polyp size on feeding in three species of Panamanian corals. Mar Ecol Prog Ser 300:79–89

Palumbi SR, Barshis DJ, Traylor-Knowles N, Bay RA (2014) Mechanisms of reef coral resistance to future climate change. Science 344:895–898

Pineda J, Starczak VR, Tarrant A, Blythe J, Davis K, Farrar J, Berumen M, da Silva JCB (2013) Two spatial scales in a bleaching event: corals from the mildest and the most extreme thermal environments escape mortality. Limnol Oceanogr 58:1531–1545

Reyes Bonilla H (2001) Effects of the 1997-1998 El Niño-Southern Oscillation on coral communities of the Gulf of California, Mexico. Bull Mar Sci 69:251–266

Reyes Bonilla H (2003) Corals and coral reefs of the Pacific coast of México. In: Cortés J (ed) Latin American coral reefs. Elsevier, Amsterdam, pp 331–350

Reyes Bonilla H, Barraza JE (2003) Corals and associated marine communities from El Salvador. In: Cortés J (ed) Latin American coral reefs. Elsevier, Amsterdam, pp 351–360

Riegl B, Piller WE (2003) Possible refugia for reefs in times of environmental stress. Int J Earth Sci 92:520–531

Rowan R, Knowlton N, Baker A, Jara J (1997) Landscape ecology of algal symbiont communities explains variation in episodes of coral bleaching. Nature 388:265–269

Sebens KP, Grace SP, Helmuth B, Maney EJ Jr, Miles JS (1998) Water flow and prey capture by three scleractinian corals, *Madracis mirabilis*, *Montastrea cavernosa* and *Porites porites*, in a field enclosure. Mar Biol 131:347–360

Smith TB, Glynn PW, Maté JL, Toth LT, Gyory J (2014) A depth refuge from catastrophic coral bleaching mortality twice prevented regional extinction. Ecology 95:1663–1673

Smith TB, Brandt ME, Calnan JM, Nemeth RS, Blondeau J, Kadison E, Taylor M, Rothenberger JP (2013) Convergent mortality responses of Caribbean coral species to seawater warming. Ecosphere 4:art87. http://dx.doi.org/10.1890/ES13-00107.1

Springer VG (1958) Systematics and zoogeography of the clinid fishes of the subtribe Labrisomini Hubbs. Pubs Inst Mar Sci Univ Texas 5:417–492

Toth LT, Aronson RB, Vollmer SV, Hobbs JW, Urrego DH, Cheng H, Enochs IC, Combosch DJ, van Woesik R, Macintyre IG (2012) ENSO drove 2500-year collapse of eastern Pacific coral reefs. Science 337:81–84

van Woesik R, Sakai K, Ganase A, Loya Y (2011) Revisiting the winners and the losers a decade after coral bleaching. Mar Ecol Prog Ser 434:67–76

van Woesik R, Franklin EC, O'Leary J, McClanahan TR, Klaus JS, Budd AF (2012a) Hosts of the Plio-Pleistocene past reflect modern-day coral vulnerability. Proc R Soc B: Biol Sci 279:2448–2456

van Woesik R, Houk P, Isechal AL, Idechong JW, Victor S, Golbuu Y (2012b) Climate-change refugia in the sheltered bays of Palau: analogs of future reefs. Ecol Evol 2:2474–2484

Wellington GM, Strong AE, Merlen G (2001) Sea surface temperature variation in the Galápagos Archipelago: a comparision between AVHRR nighttime satellite data and in situ instrumentation (1982-1998). Bull Mar Sci 69:27–42

West JM, Salm RV (2003) Resistance and resilience to coral bleaching: implications for coral reef conservation and management. Conserv Biol 17:956–967

Zapata FA, Vargas-Ángel B (2003) Corals and coral reefs of the Pacific coast of Colombia. In: Cortés J (ed) Latin American coral reefs. Elsevier Science BV, Amsterdam, pp 419–448