14

Insights from the Application of Genetics on *Pocillopora-Symbiodinium* Associations in the Eastern Tropical Pacific

Jorge H. Pinzón C.

Abstract

As one of the most widely distributed and most studied scleractinian genera in the world, *Pocillopora* encompasses an important group of corals. In the eastern tropical Pacific, *Pocillopora* species thrive and are the major reef-building scleractinian taxon, even though conditions are considered suboptimal for coral growth and reef development. Early observations on reproduction and species distributions appear to be complicated by high phenotypic diversity and often inaccurate species identifications. New genetic-based evidence reorganizes species classifications within *Pocillopora* by delimiting boundaries to genetic recombination. Such improvements toward a natural and accurate taxonomy have further revealed important patterns in *Symbiodinium* diversity and distribution associated with *Pocillopora* in the eastern Pacific. Here, I review work on genetic connectivity and symbiosis ecology that may explain physiological, ecological and evolutionary characteristics that account for the differential success of this coral genus in the marginal eastern tropical Pacific.

Keywords

Symbiosis • Coevolution • Coral-algae interactions • Genetic connectivity • Diversity

14.1 Introduction

Corals in the genus *Pocillopora* are widely distributed throughout the Indo-Pacific region. Yet, they are sufficiently abundant to build reefs only in places where environmental factors appear to limit coral diversity and carbonate accretion, including Western Australia (Veron and Marsh 1988), the Arabian Gulf (Burchard 1979; Riegl et al. 2012), the Gulf of Oman (Glynn 1993), and the eastern Pacific (Glynn 1976; Cortés 1997; see Chap. 6, Toth et al.). Relatively cold, turbid, seasonal conditions, as well as aperiodic El Niño-Southern Oscillation events in the eastern Pacific (Veron 1995; Toth et al. 2012; see Chap. 6, Toth et al.; see Chap. 8, Glynn et al.), combined with the region's isolation from the central Indo-Pacific, severely limit scleractinian diversity (Richmond 1987a). However, shallow reef coral communities are widespread throughout the eastern tropical Pacific (ETP) and are built largely by the branching colonies of *Pocillopora* spp. that dominate these communities (Fig. 14.1) (Glynn and Ault 2000; Cortés and Jiménez 2003; Glynn 2003; Maté 2003; Reyes-Bonilla 2003; Reyes-Bonilla and Barraza 2003; Zapata and Vargas-Ángel 2003; see Chap. 6, Toth et al.). The ecological abundance and wide geographic distributional range of *Pocillopora* in the eastern Pacific have attracted the interest of many researchers, making this taxon one of the most studied scleractinian reef corals in the world (Richmond 1981, 1987a, b; Richmond and Jokiel 1984; Cortés 1997; Combosch et al. 2008; Traylor-Knowles et al. 2011; Pinzón et al. 2012; Vidal-Dupiol et al. 2013).

Research findings on eastern Pacific *Pocillopora* over the past several decades have reported old and new morphological species (Cantera et al. 1989; Glynn 1999; Reyes-Bonilla 2002; Veron 2002), extended known geographic distributions of the species (Glynn and Ault 2000), examined their associations with endosymbiotic dinoflagellates (Baker et al. 2004; LaJeunesse et al. 2008; Pettay et al. 2011; Pettay and

J.H. Pinzón C. (✉)
Department of Biology, University of Texas at Arlington,
Arlington, TX, USA
e-mail: Jorge.Pinzon@UTSouthwestern.edu

© Springer Science+Business Media Dordrecht 2017
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_14

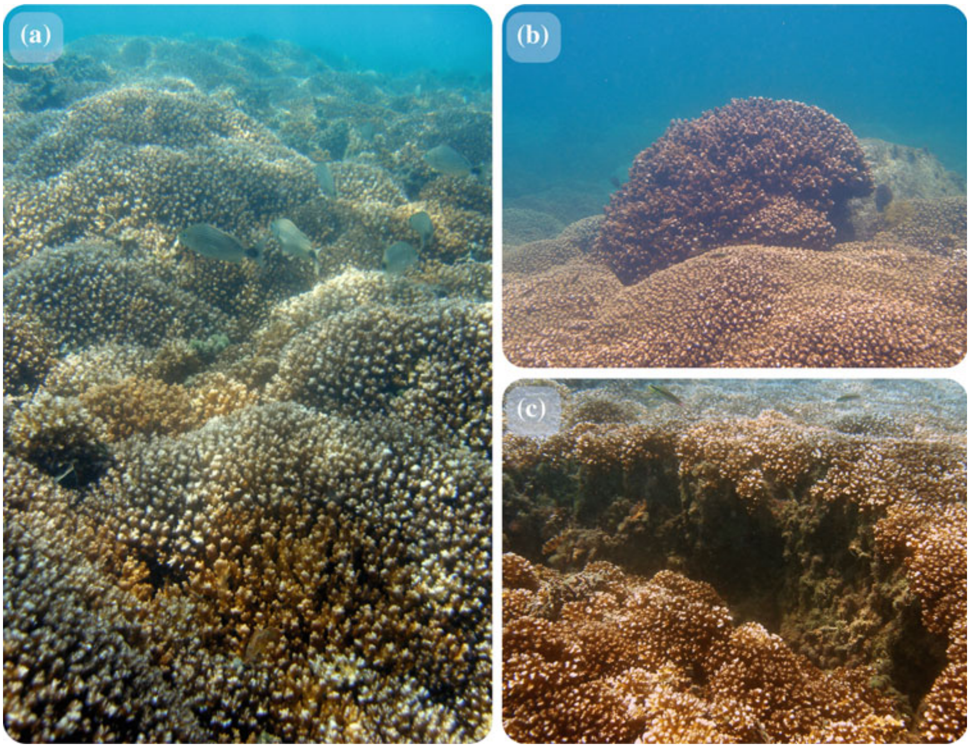


Fig. 14.1 Shallow water communities across the eastern tropical Pacific are dominated by colonies of the scleractinian genus *Pocillopora*. Communities of these corals are shown from **a** Taboga Island in the Gulf of Panama (picture taken in January 2009 at ~3 m) and **b** Punta Galeras in La Paz, Mexico (July 2009, ~3 m). **c** Skeletons of dead *Pocillopora* build much of the reef framework in this region and serve as substrate for new colonies (Gulf of Panama, January 2009 ~3 m)

LaJeunesse 2013), and measured their response to physiological stress brought on by El Niño-Southern Oscillation events (Eakin 2001; Iglesias-Prieto et al. 2003). Many of these investigations relied on assessment of visual characters to identify species by morphology, despite the complications created by phenotypic variation (Veron and Pichon 1976; Cantera et al. 1989; Cairns 1999) and transitional morphologies between several species (Schmidt-Roach et al. 2014). Recently, genetic markers applied to the analysis of seven to eight morphospecies resolved only three biological species in the ETP (Flot et al. 2008, 2010; Pinzón and LaJeunesse 2011; Pinzón et al. 2013a). In light of this new context, reinterpretations of past observations and experimental results appear to improve our understanding of the physiology and ecology of *Pocillopora* in the region (Pettay et al. 2011; Pinzón and LaJeunesse 2011; Pinzón et al. 2012, 2013a).

Many workers have speculated why *Pocillopora*, a group that is relatively susceptible to stress, is common in areas with sub-optimal conditions for coral growth and reef development (Veron 1995; Glynn and Colley 2008). While other corals also inhabit ETP reefs, *Pocillopora* species have the ability to disperse over long distances by means of larvae that can persist in the plankton for weeks or months (Richmond 1987a) and colony rafting on floating debris (Jokiel 1984), and exhibit rapid colony growth (Richmond 1987b; Guzmán and Cortés 1989) and frequent asexual propagation (Stoddart 1983; Richmond 1987b; Combosch et al. 2008; Yeoh and Dai 2010; Pinzón et al. 2012). An additional reason why eastern Pacific *Pocillopora* appear to endure environmental stressors better than in other regions (where colonies are stress-sensitive and have a lower threshold for coral bleaching—the dissociation of the coral-algal association rendering the coral colony white or bleached) is the presence of a particularly stress-tolerant symbiont. In this region, both host and symbiont are subject to selection depending on their physiological characteristics and resistance to variations in habitat conditions (LaJeunesse et al. 2009, 2010b; Pettay et al. 2011; Pettay and LaJeunesse 2013). In this chapter, I review and analyze published findings that may further explain why *Pocillopora* spp. are ecologically dominant relative to other scleractinians in the eastern Pacific. I present a brief summary of the recent failure to delimit *Pocillopora* morphospecies with genetic markers. This work has motivated a reassessment of the species diversity in the eastern tropical Pacific region and its relationship to species found in other regions. Finally, I discuss ecological and physiological attributes related to both the coral host and the associated symbionts that help explain the success of *Pocillopora* in the ETP.

14.2 Eastern Pacific *Pocillopora* Species Diversity

The genus *Pocillopora* as a group has historically challenged taxonomists (Veron and Pichon 1976). Colonies in this genus are described as branching, and only showing crustose and massive forms under extreme environmental conditions with small skeletal protuberances or verrucae, and poorly developed calices (Veron and Pichon 1976; Veron 2002). Until recently, species within *Pocillopora* were classified and identified using morphological traits, including general colony appearance, branch morphology (i.e. width, length and shape), verrucae morphology (i.e. shape, size and density), and micro-structures within calices (Veron and Pichon 1976; Glynn 1999; Veron 2000; Schmidt-Roach et al. 2014). However, there is no clear consensus among taxonomists as to which, if any, of these morphological features accurately delineate species (Budd 1990). This has resulted in uncertainty regarding the actual number of valid species (Cairns 1999; Veron 2000) and inconsistencies in the identification of individual colonies (Forsman et al. 2013).

The emergence of genetic markers in the Scleractinia has facilitated the identification of reproductively isolated groups, providing a more objective delineation of species boundaries (Stefani et al. 2008, 2011). In several cases, the integration of genetic markers with morphological studies has improved species resolutions (Forsman et al. 2005; Stefani et al. 2008; Benzoni et al. 2010; Forsman et al. 2010) and increased our understanding of the evolutionary history of Scleractinia (Fukami 2008; Budd et al. 2010). Genetic assessment of the genus *Pocillopora* appears more definitive in the identification and classification of species, as defined by the Biological Species Concept (Pinzón and LaJeunesse 2011; Pinzón et al. 2013a); and with this resolution comes a better understanding of their ecology and evolution upon which to pursue well-informed research questions.

Genetic markers used in the study of *Pocillopora* were first developed after sequencing the mitochondrial genomes of two morphospecies, *P. damicornis* and *P. eydouxi* (Flot and Tillier 2007). Comparative analyses of these mitochondrial genomes revealed a highly variable region, denoted as the Open Reading Frame (ORF). The use of this nucleotide sequence in phylogenetics has helped to distinguish genetically distinct *Pocillopora* lineages (Flot et al. 2008, 2010; Souter 2010; Pinzón and LaJeunesse 2011; Schmidt-Roach et al. 2012; Pinzón et al. 2013a). Furthermore, other mitochondrial (a control region) and nuclear (internal transcribed spacer region—ITS, the ATP synthase β—ATPSβ and the Heat Shock Protein 70—HSP70) (Flot et al. 2008, 2010; Schmidt-Roach et al. 2012, 2014) markers, including population genetic markers (microsatellites) (Pinzón and LaJeunesse 2011; Pinzón et al. 2013a) have provided similar results as those delineations obtained by means of ORF analyses. Lastly, ecological (symbiotic associations) and biogeographic data support the delineations of *Pocillopora* spp. (Pinzón and LaJeunesse 2011).

Phylogenetic patterns correspond with morphology in some geographic locales (Flot et al. 2008); but at other locations, morphology and genetics can be incongruent (Flot et al. 2010; Forsman et al. 2013; Pinzón et al. 2013a). Correspondence between genetics and morphology is restricted to locations where conditions appear "ideal" for coral development, such as Hawai'i and the Great Barrier Reef. The disparity between genetic characters and morphological features appears to be the most extreme in the ETP, especially in the Gulf of California where a single genetically-defined lineage encompassed six morphospecies (Pinzón and LaJeunesse 2011; Pinzón et al. 2012, 2013a).

Progress in coral systematics and evolution now relies on genetic-based identification and classification (Fukami et al. 2004; Fukami 2008; Huang et al. 2011; Pinzón and LaJeunesse 2011; Budd et al. 2012). A global genetic analysis recently differentiated the genus *Pocillopora* into at least nine separately evolving lineages (types 1 to 9; Fig. 14.2) based on samples obtained across the Indo-Pacific, Arabian Gulf, and Red Sea (Pinzón et al. 2013a). Only three of these lineages are known to occur in the ETP (Pinzón and LaJeunesse 2011).

Genetic boundaries between *Pocillopora* spp. are maintained among populations distributed over large geographic distances (Pinzón et al. 2013a). In the ETP, *Pocillopora* was believed to be composed of approximately seven morphologically defined species, but genetic data delineate only three distinct groups: *Pocillopora* types 1, 2 and 3 (Fig. 14.2) (Pinzón and LaJeunesse 2011). Genetic delineations were corroborated by geographic distribution analyses and the identification of a specific algal species from *Symbiodinium* clade C associated exclusively with each *Pocillopora* lineage (*Pocillopora* type 1 with C1b-c, *P.* type 2 with C1ee, and *P.* type 3 with C1d). Additional support for this conclusion was presented in an independent analysis of coral colonies from Clipperton Atoll (Flot et al. 2010).

Two studies with samples collected in the ETP disagree with the findings presented here and with those in Pinzón and LaJeunesse (2011). The first analyzed the population structure of *Pocillopora damicornis* across various locations in Panama (Combosch and Vollmer 2011). These results suggested that there were significant levels of population genetic structure with restricted gene flow among and within the surveyed regions. This might be an indication of localized differential adaptation and population differentiation, and suggests that gene flow among *P. damicornis* populations in the ETP is limited, even at scales involving 10 s of kilometers (Combosch and Vollmer 2011). This work did not include a method to phylogenetically delimit species, and based specimen identifications and subsequent data analysis on morphological features. It is possible that Combosch and Vollmer (2011) in actuality sampled colonies from different lineages and therefore their reported patterns of allele diversity and differences in relative frequency resulted from differences in the relative number of colonies from a sampling location that represents genetically distinct species.

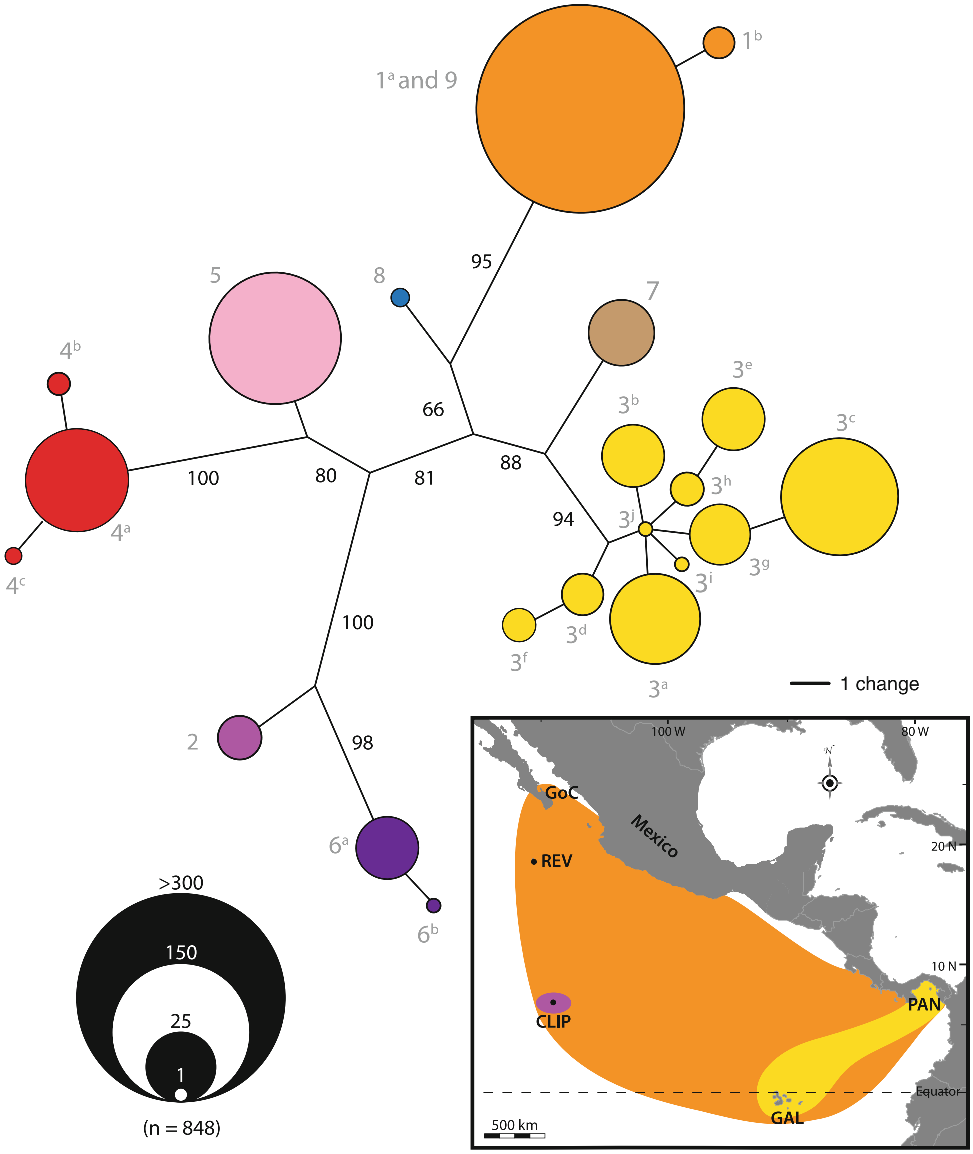


Fig. 14.2 Unrooted maximum parsimony tree showing phylogenetic relations between the genetically-delineated types of *Pocillopora* using the mitochondrial ORF region (redrawn from Pinzón et al. 2013a). Map denotes distribution of three *Pocillopora* types (1, 2 and 3) inhabiting the eastern tropical Pacific (redrawn from Pinzón and LaJenuesse 2011). Lineage designations are labeled with light grey numbers, and the size and color of each circle correspond to species-lineages and sample size. Numbers listed above branches represent bootstrap support values, on 1000 replicates, between nodes. Black and white colored circles correspond to sample size. Color shading on map matches that in tree and corresponds to known distributions of types 1, 2 and 3. (*GoC* Gulf of California, *REV* Revillagigedo Islands, *CLIP* Clipperton Atoll, *GAL* Galápagos, *PAN* Panama)

In the second study, the disagreement is more on the methodology than with the identity of the *Pocillopora* species. This study argues that the use of *Symbiodinium* identity, namely the presence or absence of a stress tolerant taxon, to delineate species of *Pocillopora* is not accurate (Cunning et al. 2013), as it found both *Symbiodinium* clades C and D in the two analyzed host species. The disagreement is based on the method used to identify the symbiont species. On one hand, the method (actin targeted quantitative PCR—qPCR) used in Cunning et al. (2013) differentiates clade diversity, while the methods (Denature Gradient Gel Electrophoresis of the ITS2 rDNA region and sequencing of the non-coding region of the psbA minicircle—$psbA^{ncr}$) used by Pinzón and LaJeunesse (2011) each resolves within clade diversity, that is *Symbiodinium* types. The latter approach clearly provides better definition and accuracy when it comes to identify *Symbiodinium* species. In fact, Pinzón and LaJeunesse (2011) found that each *Pocillopora* lineage harbors a particular species of *Symbiodinium* clade C (*Pocillopora* type 1 with C1b-c, *P.* type 2 with C1ee, and *P.* type 3 with C1d). The thermally tolerant type (*Symbiodinium glynni*—D1) was not used to delineate host species as it was common in *Pocillopora* type 1, but was also found in the other two *Pocillopora* lineages (Pinzón and LaJeunesse 2011). Regardless of the different approaches and the argument concerning the symbiont's identity, the delineation of *Pocillopora* in Panama, from both studies (Pinzón and LaJeunesse 2011; Cunning et al. 2013) suggests the presence of only two host lineages at this locality (*Pocillopora* type 1 and type 3).

Pocillopora type 1 is the most widely-distributed and abundant species in the ETP. Colonies of this lineage are found from the Gulf of California to Panama and at several offshore islands along this broad latitudinal gradient (Fig. 14.2). Type 2 appeared to be endemic to Clipperton Atoll, but also may occur at Malpelo and Cocos Islands, and possibly in some reef communities from the Central Pacific (Pinzón and LaJeunesse 2011; Pinzón et al. 2013a). Finally, *Pocillopora* type 3 is found in the southern ETP (Panama and the Galápagos Islands). This type also occurs worldwide with genetically interconnected populations (Pinzón et al. 2013a). More extensive sampling across the eastern Pacific region may eventually find it at other localities as well (Fig. 14.2).

A recent attempt to review the taxonomy of the "*Pocillopora* complex" (Schmidt-Roach et al. 2014) partially disagrees with the findings presented here and with Pinzón et al. (2013a). In Schmidt-Roach et al. (2014), an assessment of the diversity of *Pocillopora* from Australia is presented. The main conclusion of this work is that the use of morphological features, in combination with genetic analyses, resolves species in the genus. However, this work is geographically restricted and appears to have several contradictions; for example, the main result is the description of eight species, but these are grouped into five randomly-defined genetic clades (Schmidt-Roach et al. 2014). This contradiction is explained by the fact that there are morphological "transitions" between all species in the genus, leading to taxonomic confusion. In fact, the study presents a reassignment analysis from which one of the proposed morphospecies has been removed because it possesses many morphological features that overlap with other morphospecies (Schmidt-Roach et al. 2014). Despite this clear disconnection between morphology and genetics, the species descriptions presented are largely based on morphological characters and continue to force traditional morphology-based names of the species (Schmidt-Roach et al. 2014). The exception was *Pocillopora bairdi*, a putatively newly described species delineated mainly by genetics, and whose ORF sequence appeared central to all other "clade 2" (i.e. type 3 in Pinzón et al. 2013a) sequences. Thus, *P. bairdi* appears to be a variant of the pocilloporid "clade" that exhibits high levels of genetic and morphological variation (Pinzón et al. 2013a; Schmidt-Roach et al. 2014).

This latest attempt to combine morphology and genetics in *Pocillopora* species' delimitations highlights the confusion created by forcing morphologically based nomenclature on a group whose genetics is not concordant with traditional binomial nomenclature. In the future, such a situation could be avoided by utilizing binomial names that do not reflect previous, and misleading, conceptions caused by morphology having been a poor proxy for species differentiations in *Pocillopora*. Genetic tools have been shown to delineate species accurately in the genus, and the type-based nomenclature used by Flot et al. (2010), Pinzón and LaJeunesse (2011) and Pinzón et al. (2013a) is less confusing while generating the most parsimonious conclusions about the ecology and evolution of *Pocillopora* (see below). Additionally, molecular tools are now part of the day-to-day endeavors in many research laboratories since it has become less expensive to sequence genes from several samples than, for example, acquiring an electron microscope for micro-skeletal measurements. In addition to direct sequencing, other genetic methods have been explored to identify *Pocillopora* types in the eastern Pacific (Cunning et al. 2013) and Australia (Torda et al. 2013), and these might work on a larger geographic scale. More reliable and inexpensive genetic approaches provide better resolution of species diversity than traditional morphological identifications, at least among *Pocillopora*.

14.3 Assessing Symbiont Species Diversity

Symbiosis is a common type of interaction among marine organisms, with most associations formed between invertebrates and various taxa of microorganisms (Bucher et al. 2016). Such relationships are important for the survival of individuals, and in some cases the productivity of ecosystems (Muscatine 1990; Friedrich et al. 1999; see Chap. 9, Enochs and Glynn). The key factor in the structure of coral reefs is the mutualism between scleractinian corals and the dinoflagellate algae in the genus *Symbiodinium*. In this relationship, the coral host provides an ideal environment and inorganic nutrients for the algae, which provide energy for the coral (Muscatine 1967; Pearse and Muscatine 1971; Muscatine and Porter 1977; Trench 1979; Sutton and Hoegh-Guldberg 1990; Swanson and Hoegh-Guldberg 1998; Stat et al. 2006).

The genus *Symbiodinium* comprises numerous evolutionarily divergent lineages or clades, with some of these containing tens and potentially 100s of diverging sub-lineages distinguished ecologically by differences in host species association, depth, and geographic range, and differences in physiology (Berkelmans and van Oppen 2006; Rodriguez-Lanetty et al. 2006; Sampayo et al. 2008; Hannes et al. 2009). The ETP is populated with a diverse array of coral-*Symbiodinium* associations (see Chap. 13, Baker et al.), among them the *Pocillopora*–*Symbiodinium* symbioses represent the most common and chief reef-building associations in the region; therefore, study of these symbioses is imperative for understanding the dynamics of ETP coral reef ecosystems.

Pocilloporids are among the corals that transfer their endosymbiotic dinoflagellates from the maternal parent to developing ova (Hirose et al. 2008). This explains, in part, the relatively high specificity these corals display for certain symbiont species (LaJeunesse et al. 2003, 2004; Sampayo et al. 2007). While most *Pocillopora* symbionts currently lack formal taxonomic binomial names, they do represent distinct genetic and ecological entities. At coarse levels of genetic resolution, two clades of *Symbiodinium*, Clade C and Clade D, predominate at varying frequencies among *Pocillopora* populations across the eastern Pacific, relating to regional temperatures, water turbidity, and bleaching-mortality history (Glynn et al. 2001; Baker et al. 2004; LaJeunesse et al. 2007, 2008, 2010b; Cunning et al. 2013).

ETP *Pocillopora*-*Symbiodinium* combinations involve a broadly occurring representative of Clade D (LaJeunesse et al. 2010a; Pinzón and LaJeunesse 2011; Cunning et al. 2013). Genetic markers, as well as host specific ecology, distinguish this *Symbiodinium* species from other members of clade D that occur elsewhere in the world (LaJeunesse et al. 2014). Given this finding, it has tentatively been designated *Symbiodinium "glynni"* (*nomen nudum*, pending formal description). While *S. "glynni"* may exist at low abundance background populations in other eastern Pacific corals (LaJeunesse et al. 2007), it is known only to occur in a stable state and at high abundances in *Pocillopora* type 1, and at a lesser prevalence among *Pocillopora* type 3 colonies (Cunning et al. 2013). The presence of this symbiont clearly affects the physiology of the symbiosis in response to stress created by natural temperature anomalies lasting several weeks or more (Glynn et al. 2001; LaJeunesse et al. 2007, 2010b) and during experimental exposures to high temperatures (McGinley et al. 2012). The presence or absence of *S. "glynni"* ultimately influences differential survival of colonies in a population (Sampayo et al. 2008; LaJeunesse et al. 2010b), and may explain why colonies with this symbiont are abundant in areas where seasonal temperatures are variable and water conditions more turbid (LaJeunesse et al. 2010a; Cunning et al. 2013).

In the ETP, high-resolution genetic markers identified distinct lineages of Clade C *Symbiodinium* that associate specifically with each of the three *Pocillopora* types. Sequences of the non-coding region of the psbA minicircle (*psbA^{ncr}*), which can evolve at rates 10 to 20 times faster than ITS rDNA, resolve Clade C lineages that have been evolutionarily distinct for several millions of years and more (LaJeunesse and Thornhill 2011; Thornhill et al. 2014). The phylogenetic comparison among closely related Clade C *Symbiodinium* from other scleractinians in the ETP reveals that *Pocillopora*-specific lineages are monophyletic (Fig. 14.3), and that many of the other ETP scleractinian genera associate with distinct *Symbiodinium* C lineages as well (LaJeunesse et al. 2008). The host-specific distributions of these *Symbiodinium* suggest that they are distinct species that may exhibit differences in physiology, and whether they respond differently to thermal stress requires further experimental research. Pinzón and LaJeunesse (2011) suggested that the ecological dominance of *Pocillopora* type 1 was explained by its propensity to harbor *S. "glynni"* (Clade D), but the clade C symbiont (C1b-c) may also impart a level of thermal tolerance that is greater than the symbionts associated with *Pocillopora* types 2 and 3 (C1ee and C1b, respectively).

Clade C symbionts of eastern Pacific *Pocillopora* spp. also associate with these corals in the central and western Pacific. The increased phylogenetic resolution provided by *psbA^{ncr}* indicates that type *C1b-c* in the eastern Pacific is simply a genetic variant of type *C1c* present in western and central Pacific regions. Together, these populations comprise a distinct and undescribed species of *Symbiodinium* (Thornhill et al. 2014) that occurs with *Pocillopora* type 1 across the Pacific.

Changes in host-symbiont combinations that occur over large geographic scales may be influenced by either environmental gradients or genetic drift in isolation. For example, *Pocillopora* type 3 on O'ahu, Hawai'i, is synonymous with *P. molokensis*, and harbors a distinct symbiont type *C34* (Pinzón et al. 2013a). The number of colonies examined, however, were few and collected at considerable depth (>20 m; LaJeunesse et al. 2004). Likewise, *Pocillopora* type 5 (the canonical *P. damicornis*), which is not known to occur in the eastern Pacific (LaJeunesse et al. 2004; Pinzón and LaJeunesse 2011; Cunning et al. 2013), harbored *C1d* at sites around O'ahu, Hawai'i (LaJeunesse et al. 2004; Pinzón and LaJeunesse 2011: unpub. observ.). This indicates that while *C1d* is *Pocillopora* specific, it can associate with more than one species, depending on geographical and historical factors. Phylogeographic partitions based on *psbA^{ncr}* haplotypes discerned Hawai'i *C1d* populations from those in the eastern Pacific. However, genotypes from Palau also occurred in each grouping. The lack of clear genetic divergence among *psbA^{ncr}* haplotypes within each *Symbiodinium* sp. further suggests that populations of *Pocillopora* are genetically connected across the Pacific basin, which likely engenders greater connectivity among populations of their symbionts (Pettay and LaJeunesse 2013).

The developmental biology of *Pocillopora*, which involves translocation of symbionts to the developing ovum, may considerably enhance the dispersal capability of their associated *Symbiodinium*. Population genetic markers applied to the analyses of both host and symbiont indicate successful co-dispersal across large expanses of the eastern Pacific (Pettay and LaJeunesse 2013). The only location where strong genetic structure exists for *S. "glynni"* (but not for populations of the host) is at the boundary between the Gulf of California and populations along the central Mexican coast. The Gulf of California represents the northern most range of *Pocillopora*, where seasonal environmental conditions (e.g., light and temperature) are extreme relative to southern locations (Pettay and LaJeunesse 2013). Based on available evidence, it is reasonable to propose that environmental selection has created this population genetic break and those populations of *Pocillopora* type 1 associated with locally adapted genotypes of *Symbiodinium "glynni"*.

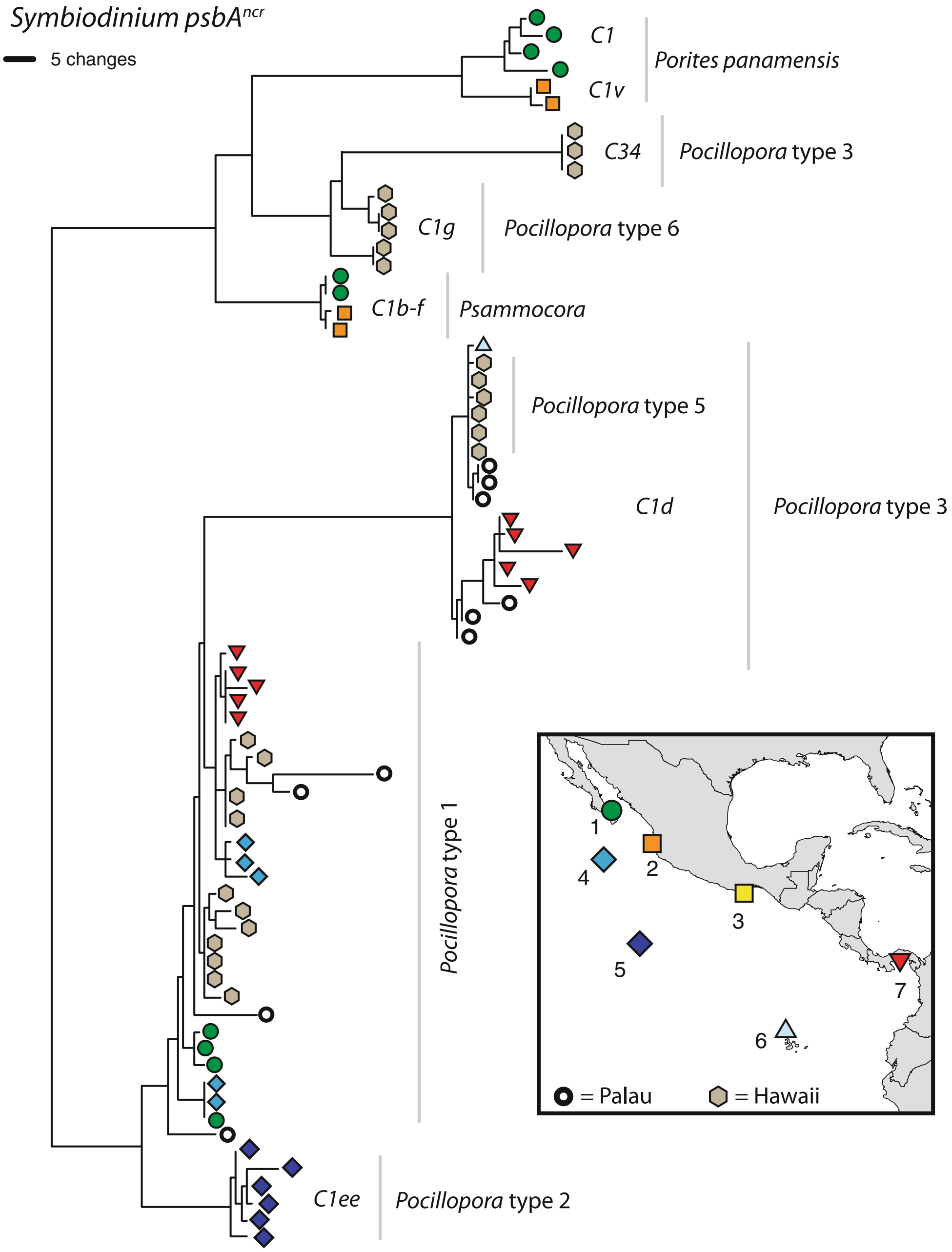


Fig. 14.3 Maximum parsimony phylogenetic reconstruction of Clade C *Symbiodinium* associated with eastern Pacific Scleractinia based on *psbA*^{ncr} haplotype sequences. Geographic origin of each sample is indicated by symbols that correspond to its location on the map (inset; *1* Gulf of California, *2* Banderas Bay, *3* Oaxaca, *4* Revillagigedo Islands, *5* Clipperton Atoll, *6* Galápagos, *7* Panama). The ITS2-DGGE fingerprint type is indicated to the right of each lineage indicating that nuclear and chloroplast DNA loci are concordant. The sequence similarity break evident between lineages suggests that most corals represent distinct species (data provided by Todd C. LaJeunesse. Alignment in nexus format can be found at the University of Texas Research Commons Library—https://uta-ir.tdl.org/uta-ir/handle/10106/24302)

14.4 Factors Driving *Pocillopora's* Success in the Eastern Tropical Pacific

14.4.1 *Pocillopora* Shows High Connectivity Within the Eastern Pacific and Across the Indo-Pacific

Gene flow is a homogenizing force of evolution (Slatkin 1987), and varying rates can influence the local adaptation of populations to different environments that may exist across a species' geographic range (Bridle et al. 2010). For species with broad distributions, the influence of gene flow and selection pressure impact the adaptation of populations across environmental clines. In some cases, there is sufficient genetic variation among individuals that all populations are adapted to the full range of environmental conditions found throughout the species' distribution. In other examples, geographically discreet populations contain individuals adapted to local environmental conditions (Kirkpatrick and Barton 1997; Bridle et al. 2010).

A wide expanse of deep water between the central and eastern Pacific (~5000 km), known as the eastern Pacific Barrier, poses a significant challenge for the dispersal of most marine species (Grigg and Hey 1992; Lessios and Robertson

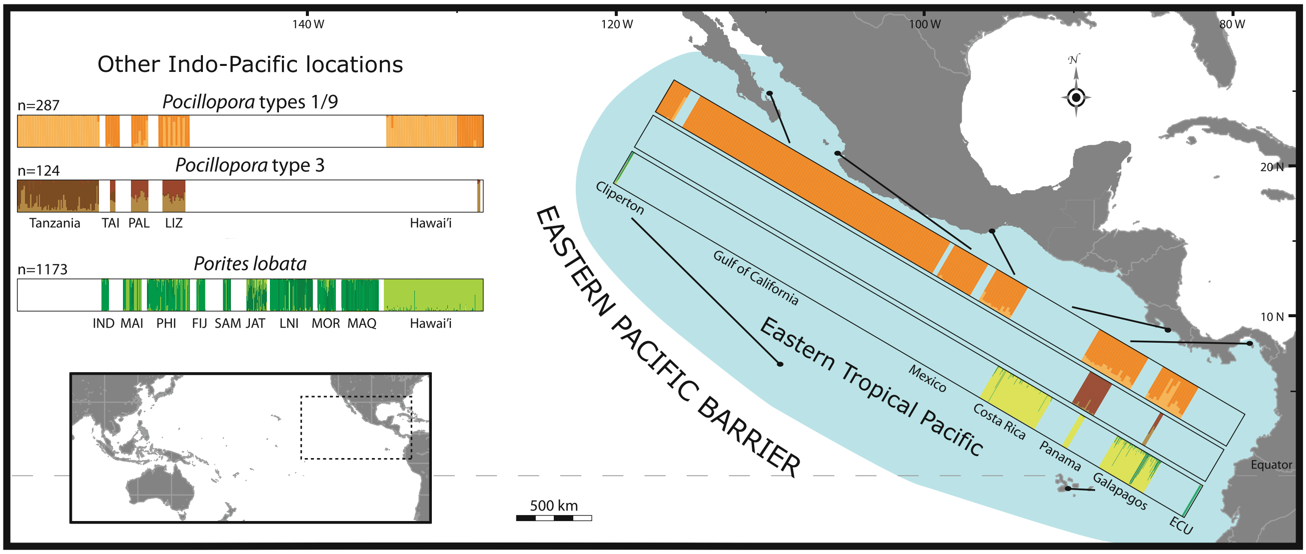


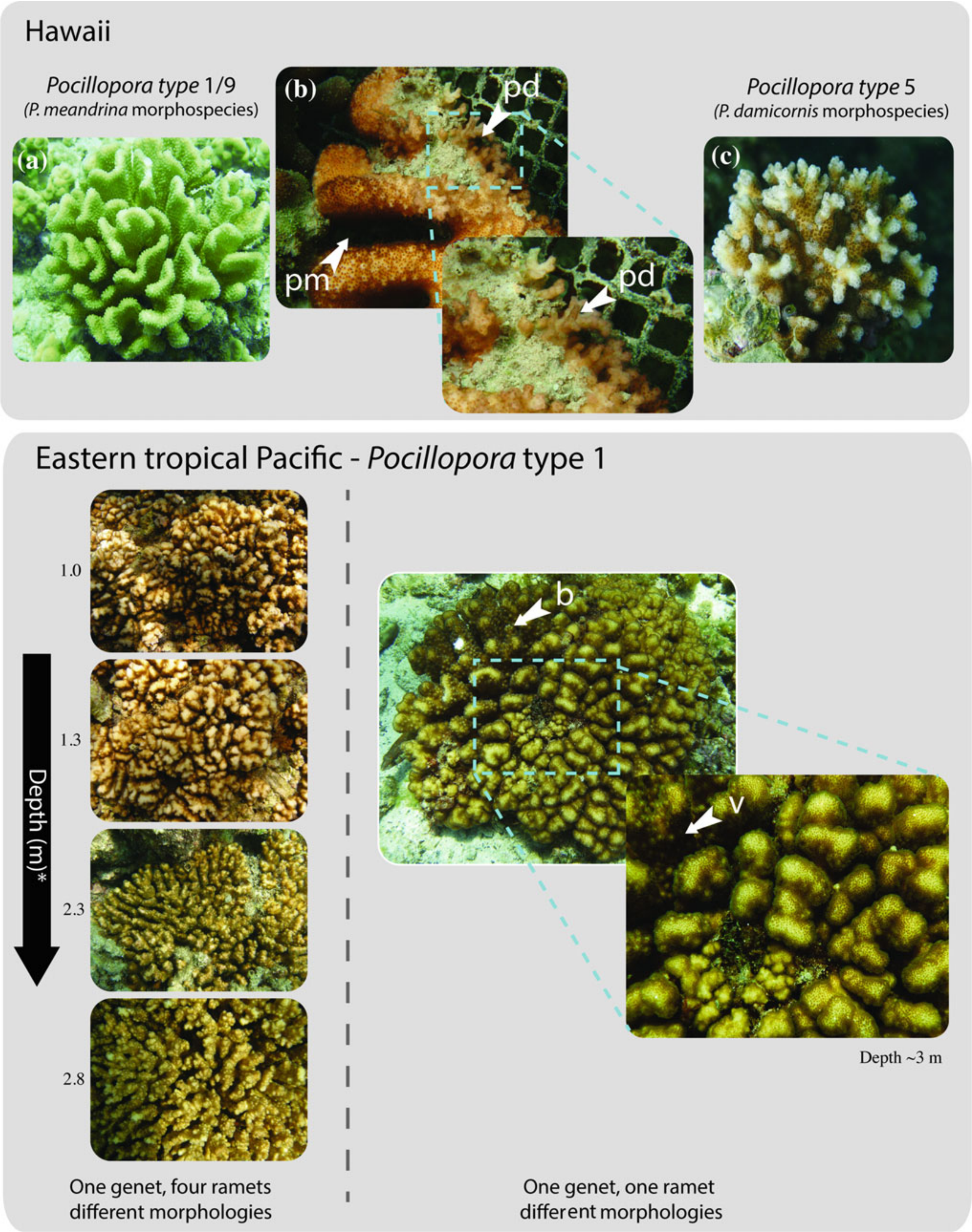
Fig. 14.4 Map of the eastern tropical Pacific and a portion of the Central Pacific showing the population structure of *Pocillopora* and *Porites* species. Clustering was determined on Structure (version 3.2) using 7 microsatellite loci for *Pocillopora* types 1/9 (*orange tones*) and *Pocillopora* type 3 (*brown tones*), and 12 for *Porites lobata* (*yellow* and *green tones*). These scleractinian corals showed no population differentiation within the ETP, having single, region-wide, well-connected populations. On a larger scale, however, the *Pocillopora* species, contrary to *P. lobata*, remain genetically connected to populations from other locations in the central Pacific and elsewhere in the Indo-Pacific region. (*TAI* Thailand, *PAL* Palau, *LIZ* Lizard Island, *IND* Indonesia, *MAI* Marshall Islands, *PHI* Phoenix Islands, *FIJ* Fiji, *SAM* Samoa, *JAT* Johnston Atoll, *LAI* Line Islands, *MOR* Moorea, *MAQ* Marquesas Islands, *ECU* Ecuador). *Pocillopora* (Pinzón and Lajeunesse 2010; Pinzón et al. 2013a, b) and *Porites* (Baums et al. 2012a, b) data downloaded from Dryad Digital Repository

2006; see Chap. 16, Lessios and Baums). This barrier consequently generates various levels of isolation across different species and is an ideal region to study genetic connectivity, or the lack thereof, in marine species. Population genetic studies of the corals *Porites lobata* (Baums et al. 2012a), *Pocillopora* type 1, and *Pocillopora* type 3 (Pinzón and LaJeunesse 2011; Pinzón et al. 2013a), show contrasting patterns in genetic structure and relative isolation across the same Indo-Pacific region. *Porites lobata* and *Pocillopora* type 1 are distributed widely throughout the Indo-Pacific and co-occur in the ETP from the equatorial Galápagos Islands to the high northern latitude of Banderas Bay, Mexico (Pinzón and LaJeunesse 2011; Baums et al. 2012a). Data from both species in the ETP suggest high gene flow at regional scales (Pinzón and LaJeunesse 2011; Baums et al. 2012a; Pinzón et al. 2013a) (Fig. 14.4). Other aspects (such as migration from the Central Pacific) could generate similar patterns, however this appears unlikely, at least for *Porites lobata* (Baums et al. 2012a). Over larger scales, encompassing the thousands of kilometers separating the central Pacific (Hawai'i) from the eastern Pacific, *Pocillopora* type 1 populations appear well connected and show no perceptible differentiation between these two regions (Pinzón et al. 2013a). In contrast, populations of *Porites lobata* are genetically isolated (Baums et al. 2012a) (Fig. 14.4). Wide interconnected populations appear to be common among *Pocillopora* species with geographically wide distributions. *Pocillopora* type 3, for example, is less abundant than *Pocillopora* type 1 and *Porites lobata* in the ETP (Pinzón and LaJeunesse 2011; Baums et al. 2012a; Pinzón et al. 2013a), but is also widely distributed and shows intermediate levels of genetic connectivity throughout the Indo-Pacific region (Pinzón et al. 2013a).

Gene flow and genetic variation affect the adaptive potential of all animals, including corals. In the ETP, *Porites lobata* has relatively lower abundances with populations apparently more isolated (Baums et al. 2012a; see Chap. 16, Lessios and Baums); in contrast, *Pocillopora* types 1 and 3 have larger population sizes and greater gene flow between populations based on previously analyzed data (Pinzón and LaJeunesse 2011; Pinzón et al. 2013a). Individuals of *Pocillopora* spp. are exposed to diverse conditions across their distributional range, affecting growth rates and morphology, and local distributions among reefs. Population connectivity, combined with biological and ecological adaptations, suggests that these species are well adapted to each location, while preserving a single widely distributed genetically connected population.

14.4.2 Is Phenotypic Variation Enhanced by Inter- or Intraspecific Competition?

Among the many factors that can influence diversification, competition plays an important role (Pfennig and Pfennig 2012; Robinson and Pfennig 2013). Natural selection favors


Hawaii
Pocillopora type 1/9
(P. meandrina morphospecies)
(a)
(b)
pd
pm
pd
Pocillopora type 5
(P. damicornis morphospecies)
(c)
Eastern tropical Pacific - Pocillopora type 1
Depth (m)*
1.0
1.3
2.3
2.8
b
v
Depth ~3 m
One genet, four ramets
different morphologies
One genet, one ramet
different morphologies

◀ **Fig. 14.5** High levels of phenotypic plasticity in *Pocillopora* spp. are common across different locations. In Hawai'i (*upper panel*), where morphology and genetics have shown some agreement in the delineation of species, **a**, **b** colonies of *P. meandrina* (=*Pocillopora* type 1/9) develop morphological features characteristic of **c** *P. damicornis* (= *P.* type 5) after being exposed to environmental conditions of deeper habitats (i.e., less water movement and lower light levels—Forsman, unpub. data). In the ETP (lower panel) due to high levels of plasticity, colony morphology is less informative for the identity of species than in Hawai'i. **d** Ramets of the same genet of *Pocillopora* type 1 from the Gulf of California show different colony morphologies, across relatively short distances (less than 90 m), as a response to deep, and possibly wave action, differences. **e** Additionally, different areas of a single *Pocillopora* type 1 colony developed morphologies characteristic of different *Pocillopora* morphospecies; notice spacing between branches (b) and presence of verrucae (v) on left side of colony. All five colonies depicted in the lower panel were identified using mitochondrial ORF and genotyped with 7 microsatellite loci. (pm = *Pocillopora meandrina*, pd = *Pocillopora damicornis*, * = depth not to scale)

individuals with phenotypes that utilize resources unexploited by competing species (Darwin 1859; Robinson and Pfennig 2013), and/or individuals or populations within the same species (Dayan and Simberloff 2005; Rueffler et al. 2006; Johansson and Richter-Boix 2013). In areas where competition is weak, specialized phenotypes are less likely to be eliminated and capable of utilizing all available resources. In that context, the reduced scleractinian diversity in the ETP is ideally suited to offer an environment of reduced competition where dominant organisms, such as *Pocillopora* species, exploit resources otherwise utilized by competitors. Niche expansion may have resulted in character release, an evolutionary phenomenon suggested to have occurred within the genus *Montastraea* (=*Orbicella*) in the Caribbean (Pandolfi et al. 2002).

High phenotypic plasticity among *Pocillopora* spp. affects morphologically-based species' delineations, but this could be a key feature of their success in the ETP. In Hawai'i, colonies of *Pocillopora* type 9 (*P. meandrina*) develop branches similar to the genetically distinct *Pocillopora* type 5 (*P. damicornis*) after being transplanted to other than usual environments (Forsman unpub; Fig. 14.5 upper panel). Coral species diversity in Hawai'i may increase competition while limiting phenotypic divergence between and within species. In other words, phenotypic variation might be constrained by competition between different species. However, intermediate morphologies among distinct species are common, suggesting that species of *Pocillopora* may contain substantial genetic variation that can account for broad phenotypic variation in some populations/locations. In the ETP, the lack of species diversity suggests that competition for space and other resources is relaxed. Inter- and intraspecific competition in *Pocillopora* allows individuals with different phenotypes to broaden the range of resources. Colonies and ramets from the same genet are known to develop distinctive morphologies that may be related to environmental conditions, such as a constant rate of water flow, wave energy, and depth (Fig. 14.5, lower panel).

14.5 Conclusions

Species of *Pocillopora* in general display high phenotypic plasticity, increased reproductive rates, long-distance dispersal, and high fragmentation rates across several locations. Populations in the ETP show particular *Pocillopora-Symbiodinium* associations, high levels of gene flow, and high genetic variation. The success of *Pocillopora* in the ETP is likely a result of the combination and synergy between the general aspects of the species in the genus coupled with the particular characteristics of the populations inhabiting the region.

Studies of natural populations distributed through heterogeneous environments can help discern the ecological and/or genetic factors that promote or hinder evolutionary adaptation. Likewise, similarities and differences among genetic lineages can provide insight on the history of a "species" as well as its potential survival in the future (Dionne et al. 2008). Thus, further research is needed to assess how variable environments and lack of competition affect morphological variation and plasticity among *Pocillopora* populations in the ETP, as these traits may influence the success of corals across the Indo-Pacific region in generations to come. Ultimately the survival of any organism depends on its interactions with the surrounding physical environment and other organisms, as well as its capacity for coping with stressful conditions. Therefore physiological and ecological studies on populations that appear more resilient to environmental stress, such as *Pocillopora* in the ETP, may offer important insights towards understanding how corals respond to adverse environmental change.

Acknowledgements I would like to express my gratitude to Todd C. LaJeunesse for the *Symbiodinium* data provided and help with the manuscript. Scott Santos and Dan Thornhill provided comments during the review process. Zac Forsman provided the photographs of *Pocillopora* from Hawai'i. Finally, Peter Glynn, Waleska Castro and Whitney Mann offered helpful comments on early versions of this chapter.

References

Baker AC, Starger CJ, McClanahan T, Glynn PW (2004) Corals' adaptive response to climate change. Nature 430:410

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

Baums IB, Boulay JN, Polato NR, Hellberg ME (2012b) Data from: No gene flow across the Eastern Pacific Barrier in the reef-building coral *Porites lobata*. doi:10.5061/dryad.7gp1f

Benzoni F, Stefani F, Pichon M, Galli P (2010) The name game: morpho-molecular species boundaries in the genus *Psammocora* (Cnidaria, Scleractinia). Zool J Linn Soc 160:421–456

Berkelmans R, van Oppen MJ (2006) The role of zooxanthellae in the thermal tolerance of corals: a 'nugget of hope' for coral reefs in an era of climate change. Proc R Soc Lond, Ser B: Biol Sci 273:2305–2312

Bridle JR, Polechová J, Kawata M, Butlin RK (2010) Why is adaptation prevented at ecological margins? New insights from individual-based simulations. Ecol Lett 13:485–494

Bucher M, Wolfowicz I, Voss PA, Hambleton EA, Guse A (2016) Development and symbiosis establishment in the cnidarian endosymbiosis model *Aiptasia* sp. Sci Rep 6:19867. doi:10.1038/srep19867

Budd AF (1990) Longterm patterns of morphological variation within and among species of reef-corals and their relationship to sexual reproduction. Syst Biol 15:150–165

Budd AF, Romano S, Smith N, Barbeitos M (2010) Rethinking the phylogeny of scleractinian corals: a review of morphological and molecular data. Integr Comp Biol 50:411–427

Budd AF, Fukami H, Smith ND, Knowlton N (2012) Taxonomic classification of the reef coral family Mussidae (Cnidaria: Anthozoa: Scleractinia). Mol Ecol Resour 166:465–529

Burchard JE (1979) Coral fauna of the western Arabian Gulf. Arabian American Oil Company, Dhahran, Saudi Arabia, p 129

Cairns SD (1999) Species richness of recent Scleractinia. Atoll Res Bull 459:1–45

Cantera JR, von Prahl H, Escobar JC, Peña E (1989) Sistemática de los corales del género *Pocillopora* del pacífico colombiano utilizando taxonomía numérica. Rev Biol Trop 37:23–28

Combosch DJ, Vollmer SV (2011) Population genetics of an ecosystem-defining reef coral *Pocillopora damicornis* in the tropical eastern Pacific. PLoS ONE 6:e21200

Combosch DJ, Guzmán HM, Schuhmacher H, Vollmer SV (2008) Interspecific hybridization and restricted trans-Pacific gene flow in the tropical eastern Pacific *Pocillopora*. Mol Ecol 17:1304–1312

Cortés J (1997) Biology and geology of eastern Pacific coral reefs. Coral Reefs 16:S39–S46

Cortés J, Jiménez C (2003) Corals and coral reefs of the Pacific of Costa Rica: history, research and status. In: Cortes J (ed) Latin American coral reefs. Elsevier Science, Amsterdam, pp 361–386

Cunning R, Glynn PW, Baker AC (2013) Flexible associations between *Pocillopora* corals and *Symbiodinium* limit utility of symbiosis ecology in defining species. Coral Reefs 1–7

Darwin C (1859) On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London

Dayan T, Simberloff D (2005) Ecological and community-wide character displacement: the next generation. Ecol Lett 8:875–894

Dionne M, Caron F, Dodson JJ, Bernatchez L (2008) Landscape genetics and hierarchical genetic structure in Atlantic salmon: the interaction of gene flow and local adaptation. Mol Ecol 17:2382–2396

Eakin CM (2001) A tale of two ENSO events: carbonate budgets and the influence of two warming disturbances and intervening variability, Uva Island, Panama. Bull Mar Sci 69:171–186

Flot J-F, Tillier S (2007) The mitochondrial genome of *Pocillopora* (Cnidaria: Scleractinia) contains two variable regions: the putative D-loop and a novel ORF of unknown function. Gene 401:80–87

Flot J-F, Magalon H, Cruaud C, Couloux A, Tillier S (2008) Patterns of genetic structure among Hawaiian corals of the genus *Pocillopora* yield clusters of individuals that are compatible with morphology. C R Biol 331:239–247

Flot J-F, Couloux A, Tillier S (2010) Haplowebs as a graphical tool for delimiting species: a revival of Doyle's "field for recombination" approach and its application to the coral genus *Pocillopora* in Clipperton. BMC Evol Biol 10:372. doi:10.1186/1471-2148-10-372

Forsman ZH, Guzmán HM, Chen CA, Fox GE, Wellington GM (2005) An ITS region phylogeny of *Siderastrea* (Cnidaria: Anthozoa): is *S. glynni* endangered or introduced? Coral Reefs 24:343–347

Forsman ZH, Martinez JA, Maragos JE, Toonen RJ (2010) Resurrection of *Porites hawaiiensis* Vaughan, 1907; a Hawaiian coral obscured by small size, cryptic habitat, and confused taxonomy. Zootaxa 2624:67–68

Forsman ZH, Johnston E, Brooks A, Adam TC, Toonen RJ (2013) Genetic evidence for regional isolation of *Pocillopora* corals from Moorea. Oceanography 26:153–155

Friedrich A, Merkert H, Fendert T, Hacker J, Proksch P, Hentschel U (1999) Microbial diversity in the marine sponge *Aplysina cavernicola* (formerly *Verongia cavernicola*) analyzed by fluorescence in situ hybridization (FISH). Mar Biol 134:461–470

Fukami H (2008) Short review: molecular phylogenetics analyses of reef corals. Galaxea 10:47–55

Fukami H, Budd AF, Paulay G, Sole-Cava A, Chen CA, Iwao K, Knowlton N (2004) Conventional taxonomy obscures deep divergence between Pacific and Atlantic corals. Nature 427:832–835

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

Glynn PW (1993) Monsoonal upwelling and episodic *Acanthaster* predation as probable controls of coral reef distribution and community structure in Oman, Indian Ocean. Atoll Res Bull 379:1–86

Glynn PW (1999) *Pocillopora inflata*, a new species of scleractinian coral (Cnidaria:Anthozoa) from the eastern Pacific. Pac Sci 53:168–180

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

Glynn PW, Ault J (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, vol 1, Ft Lauderdale, pp 361–365

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

Grigg RW, Hey R (1992) Paleoceanography of the Tropical Eastern Pacific Ocean. Science 255:172–178

Guzmán HM, Cortés J (1989) Growth rates of eight species of scleractinian corals in the eastern Pacific (Costa Rica). Bull Mar Sci 44:1186–1194

Hannes AR, Barbeitos M, Coffroth MA (2009) Stability of symbiotic dinoflagellate type in the octocoral *Briareum asbestinum*. Mar Ecol Prog Ser 391:65–72

Hirose M, Reimer JD, Hidaka M, Suda S (2008) Phylogenetic analyses of potentially free-living *Symbiodinium* spp. isolated from coral reef sand in Okinawa. Japan. Mar Biol 155:105–112

Huang D, Licuanan WY, Baird AH, Fukami H (2011) Cleaning up the "Bigmessidae": molecular phylogeny of scleractinian corals from

Faviidae, Merulinidae Pectiniidae and Trachyphylliidae. BMC Evol Biol 11:37

Iglesias-Prieto R, Reyes-Bonilla H, Riosmena Rodríguez R (2003) Effects of 1997–1998 ENSO on coral reef communities in the Gulf of California, Mexico. Geofis Int 42:467–472

Johansson F, Richter-Boix A (2013) Within-population developmental and morphological plasticity is mirrored in between-population differences: linking plasticity and diversity. Evol Biol 1–10

Jokiel PL (1984) Long distance dispersal of reef corals by rafting. Coral Reefs 3:113–116

Kirkpatrick M, Barton NH (1997) Evolution of a species' range. The Amer Nat 150:1–23

LaJeunesse TC, Thornhill DJ (2011) Improved resolution of reef-coral endosymbiont (*Symbiodinium*) species diversity, ecology, and evolution through psbA non-coding region genotyping. PLoS ONE 6:e29013

LaJeunesse TC, Loh W, van Woesik R, Hoegh-Guldberg O, Schmidt GW, Fitt WK (2003) Low symbiont diversity in southern Great Barrier Reef corals, relative to those of the Caribbean. Limnol Oceanogr 48:2046–2054

LaJeunesse TC, Bhagooli R, Hidaka M, de Vantier L, Done T, Schmidt GW, Fitt WK, Hoegh-Guldberg O (2004) Closely related *Symbiodinium* spp. differ in relative dominance in coral reef host communities across environmental, latitudinal and biogeographic gradients. Mar Ecol Prog Ser 284:147–161

LaJeunesse TC, Reyes-Bonilla H, Warner ME (2007) Spring "bleaching" among *Pocillopora* in the Sea of Cortez. Eastern Pacific. Coral Reefs 26:265

LaJeunesse TC, Reyes-Bonilla H, Warner ME, Wills M, Schmidt GW, Fitt WK (2008) Specificity and stability in high latitude eastern Pacific coral–algal symbioses. Limnol Oceanogr 53:719–727

LaJeunesse TC, Loh W, Trench RK (2009) Do introduced endosymbiotic dinoflagellates 'take' to new hosts? Biol Invasions 11:995–1003

LaJeunesse TC, Pettay D, Sampayo EM (2010a) Long-standing environmental conditions, geographic isolation and host–symbiont specificity influence the relative ecological dominance and genetic diversification of coral endosymbionts in the genus *Symbiodinium*. J Biogeogr 37:785–800

LaJeunesse TC, Smith R, Pinzón JH, Pettay DT, McGinley M, Medina-Rosas P, Cupul-Magaña AL, Pérez A, Reyes-Bonilla H, Warner ME (2010b) Host-symbiont recombination vs. natural selection in the response of coral-dinoflagellate symbioses to environmental disturbance. Proc R Soc Lond, Ser B: Biol Sci 277:2925–2934

LaJeunesse T, Wham D, Pettay D, Parkinson J, Keshavmurthy S, Chen C (2014) Ecologically differentiated, stress tolerant endosymbionts in the dinoflagellate genus *Symbiodinium* Clade D are different species. Phycologia 53:305–319

Lessios H, Robertson D (2006) Crossing the impassable: genetic connections in 20 reef fishes across the eastern Pacific barrier. Proc R Soc Lond, Ser B: Biol Sci 273:2201–2208

Maté JL (2003) Corals and coral reefs of the Pacific coast of Panamá. In: Cortes J (ed) Latin American coral reefs. Elsevier Science, Amsterdam, pp 387–418

McGinley MP, Aschaffenburg MD, Pettay DT, Smith RT, LaJeunesse TC, Warner ME (2012) *Symbiodinium* spp. in colonies of eastern Pacific *Pocillopora* spp. are highly stable despite the prevalence of low-abundance background populations. Mar Ecol Prog Ser 462:1–7

Muscatine L (1967) Glycerol excretion by symbiotic algae from corals and *Tridacna* and its control by the host. Science 156:516–519

Muscatine L (1990) The role of symbiotic algae in carbon and energy flux in reef corals. In: Dubinsky Z (ed) Ecosystems of the World 25. Elsevier, Amsterdam, pp 75–87

Muscatine L, Porter J (1977) Reef corals: mutualistic symbioses adapted to nutrient-poor environments. Bioscience 27:454–460

Pandolfi JM, Lovelock CE, Budd AF (2002) Character release following extinction in a Caribbean reef coral species complex. Evolution 56:479–501

Pearse VB, Muscatine L (1971) Role of symbiotic algae (zooxanthellae) in coral calcification. Biol Bull (Woods Hole) 141:350–363

Pettay DT, LaJeunesse T (2013) Long-range dispersal and high-latitude environments influence the population structure of a "stress-tolerant" dinoflagellate endosymbiont. PLoS ONE. doi:10.1371/journal.pone.0079208

Pettay DT, Wham D, Pinzón JH, LaJeunesse TC (2011) Genotypic diversity and spatial-temporal distribution of *Symbiodinium* clones in an abundant reef coral. Mol Ecol 20:5197–5212

Pfennig DW, Pfennig KS (2012) Development and evolution of character displacement. Ann N Y Acad Sci 1256:89–107

Pinzón JH, Lajeunesse TC (2010) Data from: species delimitation of common reef corals in the genus *Pocillopora* using nucleotide sequence phylogenies, population genetics, and symbiosis ecology. doi:10.5061/dryad.7908

Pinzón JH, LaJeunesse TC (2011) Species delimitation of common reef corals in the genus *Pocillopora* using nucleotide sequence phylogenies, population genetics and symbiosis ecology. Mol Ecol 20:311–325

Pinzón JH, Reyes-Bonilla H, Baums I, LaJeunesse T (2012) Contrasting clonal structure of a single population of *Pocillopora* (Scleractinia) at two nearby sites in the Gulf of California. Coral Reefs 31:765–777

Pinzón JH, Sampayo EM, Cox EF, Chauka LJ, Chen CA, Voolstra CR, LaJeunesse TC (2013a) Blind to morphology: genetics identifies several widespread ecologically common species and few endemics among Indo-Pacific cauliflower corals (*Pocillopora*, Scleractinia). J Biogeogr 40:1595–1608

Pinzón JH, Sampayo EM, Cox EF, Chauka LJ, Chen CA, Voolstra CR, LaJeunesse TC (2013b) Data from: Blind to morphology: genetics identifies several widespread ecologically common species and few endemics among Indo-Pacific cauliflower corals (*Pocillopora*, Scleractinia). Dryad digital repository. doi:10.5061/dryad.jd512

Reyes-Bonilla H (2002) Checklist of valid names and synonyms of stony corals (Anthozoa: Scleractinia) from the eastern Pacific. J Nat Hist 36:1–13

Reyes-Bonilla H (2003) Coral reefs of the Pacific coast of Mexico. In: Cortés J (ed) Latin American coral reefs. Elsevier Science, pp 331–349

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

Richmond RH (1981) Energetic considerations in the dispersal of *Pocillopora damicornis* (Linnaeus) planulae. In: Proceedings of 4th International Coral Reef Symposium, vol 1, Manila, pp 153–156

Richmond RH (1987a) Energetics, competency, and long-distance dispersal of planula larvae of the coral *Pocillopora damicornis*. Mar Biol 93:527–533

Richmond RH (1987b) Energetic relationships and biogeographical differences among fecundity, growth and reproduction in the reef coral *Pocillopora damicornis*. Bull Mar Sci 41:594–604

Richmond RH, Jokiel PL (1984) Lunar periodicity in larva release in the reef coral *Pocillopora damicornis* at Enewetak and Hawaii. Bull Mar Sci 34:280–287

Riegl BM, Purkis SJ eds (2012) Coral reefs of the Gulf: adaptation to climate extremes. Coral reefs of the world 3, Springer p 379

Robinson BW, Pfennig DW (2013) Inducible competitors and adaptive diversification. Curr Zool 59:537–552

Rodriguez-Lanetty M, Wood-Charlson E, Hollingsworth L, Krupp D, Weis V (2006) Temporal and spatial infection dynamics indicate recognition events in the early hours of a dinoflagellate/coral symbiosis. Mar Biol 149:713–719

Rueffler C, Van Dooren TJM, Leimar O, Abrams PA (2006) Disruptive selection and then what? Trends Ecol Evol 21:238–245

Sampayo EM, Franceschinis L, Hoegh-Guldberg O, Dove S (2007) Niche partitioning of closely related symbiotic dinoflagellates. Mol Ecol 16:3721–3733

Sampayo EM, Ridgway T, Bongaerts P, Hoegh-Guldberg O (2008) Bleaching susceptibility and mortality of corals are determined by fine-scale differences in symbiont type. Proc Natl Acad Sci USA 105:10,444–10,449

Schmidt-Roach S, Lundgren P, Miller KJ, Gerlach G, Noreen AME, Andreakis N (2012) Assessing hidden species diversity in the coral *Pocillopora damicornis* from eastern Australia. Coral Reefs 1–12

Schmidt-Roach S, Miller KJ, Lundgren P, Andreakis N (2014) With eyes wide open: a revision of species within and closely related to the *Pocillopora damicornis* species complex (Scleractinia; Pocilloporidae) using morphology and genetics. Zool J Linn Soc 170:1–33

Slatkin M (1987) Gene flow and the geographic structure of natural populations. Science 236:787–792

Souter P (2010) Hidden genetic diversity in a key model species of coral. Mar Biol. doi:10.1007/s00227-009-1370-3

Stat M, Carter D, Hoegh-Guldberg O (2006) The evolutionary history of *Symbiodinium* and scleractinian hosts—Symbiosis, diversity, and the effect of climate change. Perspect Plant Ecol Evol Syst 8:23–43

Stefani F, Benzoni F, Pichon M, Cancelliere C, Galli P (2008) A multidisciplinary approach to the definition of species boundaries in branching species of the coral genus *Psammocora* (Cnidaria, Scleractinia). Zool Scr 37:71–91

Stefani F, Benzoni F, Yang SY, Pichon M, Galli P, Chen C (2011) Comparison of morphological and genetic analyses reveals cryptic divergence and morphological plasticity in *Stylophora* (Cnidaria, Scleractinia). Coral Reefs 30:1033–1049

Stoddart JA (1983) Asexual production of planulae in the coral *Pocillopora damicornis*. Mar Biol 76:279–284

Sutton D, Hoegh-Guldberg O (1990) Host-zooxanthella interactions in four temperate marine invertebrate symbioses: assessment of effect of host extracts on symbionts. Biol Bull (Woods Hole) 178:175–186

Swanson R, Hoegh-Guldberg O (1998) Amino acid synthesis in the symbiotic sea anemone *Aiptasia pulchella*. Mar Biol 131:83–93

Thornhill DJ, Lewis AM, Wham DC, LaJeunesse TC (2014) Host-specialist lineages dominate the adaptive radiation of reef coral endosymbionts. Evolution 68:352–367

Torda G, Schmidt-Roach S, Peplow L, Lundgren P, van Oppen MJH (2013) A rapid genetic assay for the identification of the most common *Pocillopora damicornis* genetic lineages on the Great Barrier Reef. PLoS ONE. doi:10.1371/journal.pone.0058447

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

Traylor-Knowles N, Granger BR, Lubinski TJ, Parikh JR, Garamszegi S, Xia Y, Marto JA, Kaufman L, Finnerty JR (2011) Production of a reference transcriptome and transcriptomic database (PocilloporaBase) for the cauliflower coral *Pocillopora damicornis*. BMC Genomics 12:585

Trench RK (1979) The cell biology of plant-animal symbiosis. Annu Rev Plant Physiol 30:485–531

Veron JEN (1995) Corals in space and time. The biogeography and evolution of the Scleractinia. Comstock/Cornell, Ithaca and London, p 321

Veron JE (2000) Corals of the world, 3 vols. Australian Institute of Marine Science, Townsville, pp 429, 463, 490

Veron JE (2002) New species described in corals of the world. Australian Institute of Marine Science, Townsville, Australia

Veron JEN, Marsh LM (1988) Hermatypic corals of Western Australia: records and annotated species list. Rec West Aust Mus 29:1–136

Veron JE, Pichon M (1976) Scleractinia of eastern Australia. Part I. Families Thamnasteriidae, Astrocoeniidae, Pocilloporidae. Australian Institute of Marine Science, Monograph Series, vol 1, p 86

Vidal-Dupiol J, Zoccola D, Tambutté E, Grunau C, Cosseau C, Smith KM, Freitag M, Dheilly NM, Allemand D, Tambutte S (2013) Genes related to ion-transport and energy production are upregulated in response to CO_2-driven pH decrease in corals: New insights from transcriptome analysis. PLoS ONE 8:e58652. doi:10.1371/journal.pone.0058652

Yeoh S-R, Dai C-F (2010) The production of sexual and asexual larvae within single broods of the scleractinian coral, *Pocillopora damicornis*. Mar Biol 157:351–359

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, Amsterdam, pp 419–448