

## INVITED REVIEW

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## A biogeographic analysis and review of the far eastern Pacific coral reef region

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**Abstract** New information on the presence and relative abundances of 41 reef-building (zooxanthellate) coral species at 11 eastern Pacific and 3 central Pacific localities is examined in a biogeographic analysis and review of the eastern Pacific coral reef region. The composition and origin of the coral fauna and other reef-associated taxa are assessed in the context of dispersal and vicariance hypotheses. A minimum variance cluster analysis using coral species presence-absence classification data at the 14 localities revealed three eastern Pacific reef-coral provinces: (1) *equatorial* – mainland Ecuador to Costa Rica, including the Galápagos and Cocos Islands; (2) *northern* – mainland México and the Revillagigedo Islands; (3) *island group* – eastern Pacific Malpelo Island and Clipperton Atoll, and central Pacific Hawaiian, Johnston and Fanning Islands. Coral species richness is relatively high in the equatorial (17–26 species per locality) and northern (18–24 species) provinces, and low at two small offshore island localities (7–10 species). A high proportion (36.6%, 15 species) of eastern Pacific coral species occurs at only one or two localities; of these, three disappeared following the 1982–83 ENSO event, three occur as death assemblages at several localities, and five are endangered with known populations of ten or fewer colonies. Principal component analysis using ordinal relative density data for the 41 species at the 14 localities indicated three main species groupings, i.e., those with high, mid, and narrow spatial distributions. These groupings correlated with species population-dynamic characteristics. These results were compared with data for riverine discharges, ocean circulation patterns, shoreline habitat characteristics, and regional sea surface temperature data to help clarify the analyses as these measures of environmental variability

affect coral community composition. Local richness was highest at localities with the highest environmental variability. Recent information regarding the strong affinity between eastern and central Pacific coral faunas, abundance of teleplanic larvae in oceanic currents, high genetic similarity of numerous reef-associated species, and appearances of numerous Indo-west Pacific species in the east Pacific following ENSO activity, suggest the bridging of the east Pacific filter bridge (formerly east Pacific barrier).

**Key words** Biogeography · Eastern Pacific · Zooxanthellate corals

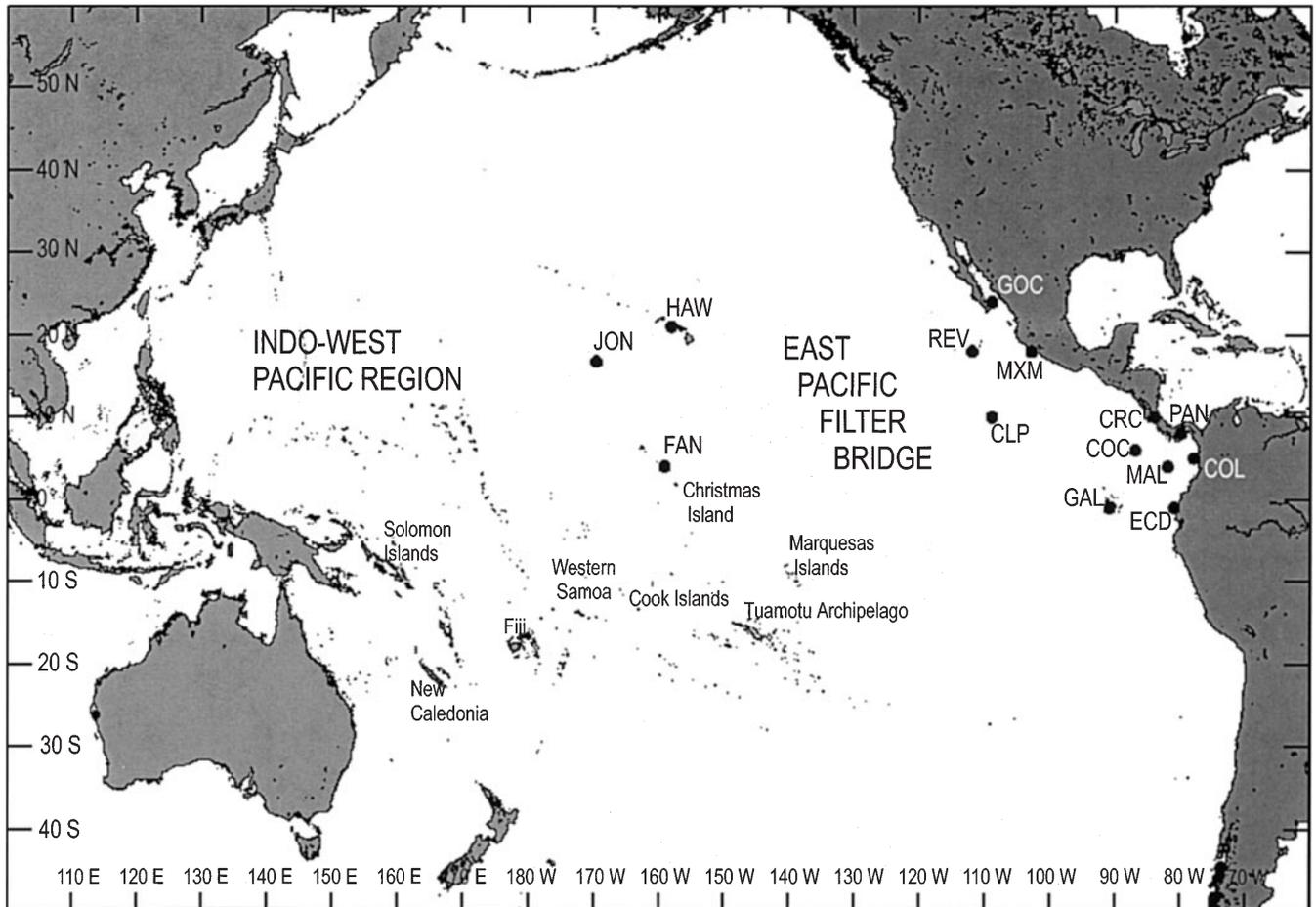
*Ecology obviously plays a crucial role and, although its effects cannot be detected in compilations of entire faunas, must be taken into account if further progress is to be made in our understanding of the history of diversity and the factors that affect speciation.* (G.J. Vermeij 1993)

### Introduction

The extreme isolation of the shallow-water, tropical biotas of the eastern Pacific region has stimulated much interest in their taxonomic composition, origin and evolution. Eastern Pacific coral reef biotas offer an advantage in interpretive biogeographic studies due to the often marginal environmental conditions affecting them. These conditions have further spurred interest in the study and documentation of local differences in biotic composition and causes of population fluctuations.

The eastern Pacific has been separated from the Caribbean Sea since the closure of the Central American portal, ca. 3.7–3 Ma (Duque-Caro 1990; Coates and Obando 1996), and is greatly distant, between 5000–8000 km across a potential migratory pathway (Dana 1975; Grigg and Hey 1992), from the Indo west Pacific biogeographic region (Fig. 1). Ekman (1953) concluded that the eastern Pacific barrier (EPB) is the world's most effective marine barrier to larval dispersal. Darwin

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**Fig. 1** Indo-west Pacific and eastern Pacific coral reef biogeographic regions. Although not shown, the entire Indian Ocean and adjacent bodies of water are also part of the Indo-West Pacific region. The 14 localities used in this study are shown with *black circles* and three-letter acronyms, which are defined in Table 1

(1880, p. 317) regarded the EPB as “impassable”. Two widely entertained hypotheses have been proposed to explain the distinctness of the eastern Pacific reef-building coral fauna: (1) long-distance dispersal, and (2) the vicariance (i.e. geographically-mediated separation) view.

In light of the taxonomic affinities of modern reef-building corals and their potential for dispersal, Dana (1975) and Glynn and Wellington (1983) proposed that the eastern Pacific region has most likely been colonized relatively recently by long distance dispersal of larvae, chiefly via the north equatorial counter current (NECC). However, McCoy and Heck (1976), and Heck and McCoy (1978) favored a vicariance explanation, namely that the eastern Pacific coral fauna was derived from pan-Tethyan, western Atlantic (Caribbean) species that historically were distributed across the shallow Central American seaway. With the closure of the Central American corridor, the vicariance hypothesis maintains that Tethyan species survived in the eastern Pacific as a relict fauna that was subsequently modified by extinc-

tions and evolution. Many of the earlier shared species became extinct in the western Atlantic as conditions deteriorated during late Pliocene and Pleistocene glaciation events (Budd 1989; Budd et al. 1994).

This essay examines both dispersal and vicariance hypotheses in light of a wealth of new evidence, including: composition of coral faunas at several localities; factors affecting the dynamics of species distributions, such as dispersal routes; length of larval life; stepping stones; rafting; El Niño-southern oscillation (ENSO) influences; and, the age and persistence of coral communities in varying eastern Pacific environmental settings. We develop and analyze a new data base on the presence and relative abundances of eastern Pacific zooxanthellate coral species to better define the spatial distribution of coral provinces and patterns of species diversity within the region. We believe that such information can offer insights regarding intraregional biotic continuity as well as potential dispersal routes across the eastern Pacific barrier. Widely distributed and rare species are examined and compared in terms of their population dynamic characteristics such as reproduction, growth, and survivorship. Only since the severe 1982–1983 ENSO event has it become recognized that sudden and marked changes in circulation routes and transport rates can greatly influence west-to-east dispersal pathways. The timing of arrival of some Indo-west Pacific

colonists following the 1982–1983 ENSO offers solid evidence of such accelerated dispersal activity. Further, it is now understood that ENSO events of this magnitude can also cause local and regional-scale extinctions, thus emphasizing the dynamic nature of the composition of eastern Pacific coral reef faunas. The data and analyses we present are framed broadly to include consideration of various biological and physical factors that can influence patterns of species distributions in tropical marine environments. Since this essay reveals many gaps in our knowledge, we conclude by outlining some critical areas where further study is needed.

### Eastern Pacific reef coral biota

Recently published contours depicting global patterns of generic and species richness show the eastern tropical Pacific (ETP) to be comprised of five genera and ten species of zooxanthellate scleractinian corals (Veron 1995). Immediately west of the EPB (including the Hawaiian and Line Islands) generic diversity doubles and then continues to increase steadily to a maximum of 70 genera in the west-central Pacific. Species richness increases in a similar manner with the 50 species contour crossing the Line Islands and increasing steadily to 450 species in the Philippine and northern Indonesian archipelagos. In contrast, on the Atlantic side of Central America, maximum taxonomic richness reaches 20 genera and 50 species in the Caribbean basin.

Here we examine a new data matrix denoting the presence and relative abundances of 41 species of zooxanthellate scleractinian corals and hydrocorals in the ETP region (Table 1). Eleven (1–11) of the 14 localities listed, including offshore and nearshore islands and the mainland, belong to the ETP region, and three (12–14) are located in the central Pacific, at the eastern boundary of the Indo-west Pacific region (Figs. 1 and 2). A southern dispersal route via the Marquesas Islands and Tuamotu Archipelago is not considered likely because of the present sluggish flow of the south equatorial counter-current, which is not evident east of 160° W, and the cool sea temperatures of the Peru–Chile current systems (Wyrski 1965; Fiedler 1992). We caution that these localities vary enormously in habitat space suitable for coral populations. For example, the shelf area in the Gulf of California (to 10 m depth) is 5200 km<sup>2</sup>, while Malpelo Island offers only 0.1 km<sup>2</sup> (0–20 m) of shelf habitat in the euphotic zone. Also, the coral faunas at some eastern Pacific localities are still largely unknown, e.g. in Guatemala, El Salvador, Nicaragua, and northern Peru. Further, still unknown is the proportion of shelf substrate (e.g. firm rock or stable talus versus fine grained sediments) that would support coral settlement and growth. It should also be noted that several taxonomic uncertainties exist. For example, *Pocillopora elegans* and *Pocillopora verrucosa* may be synonymous, and the presence of *Pocillopora woodjonesi* in the eastern Pacific needs further verification (Veron 1993). And

from major differences in the reproductive biology, Richmond (1985, 1987) has suggested that west/central and eastern Pacific *Pocillopora damicornis* populations may represent distinct species. Additional problematic species include the validity of *Porites sverdrupi*, and three to four species in the genus *Psammocora*. Finally, *Pocillopora* sp.A, *Porites* sp.A and *Pavona* sp.A are new species presently being described.

Our analyses were based on number of species, relative abundances and community composition. The localities of highest species richness, i.e. with 20 or more species, are the oceanic Revillagigedo Islands, mainland México, Costa Rica, Panamá, and Colombia (Fig. 3A). Lowest species richness occurs at the small offshore islands of Malpelo and Clipperton. Eleven species show a high frequency of occurrence, present at nine or more localities (≥82% occupancy, i.e. present at 9 or more of 11 ETP localities) along the eastern Pacific (Table 1, Fig. 3B). These wide-ranging species are taxonomically diverse, represented by all three eastern Pacific suborders of scleractinian corals (Archaeocoeniina, Poritiina, Fungiina) and belong to all five eastern Pacific families (Pocilloporidae, Poritidae, Siderastreaeidae, Agariciidae, Fungiidae): *Pocillopora damicornis*, *Pocillopora elegans*, *Pocillopora eydouxi*, *Pocillopora verrucosa* (Archaeocoeniina, Pocilloporidae); *Porites lobata* (Poritiina, Poritidae), *Psammocora stellata*, *Psammocora superficialis* (Fungiina, Fungiidae), *Pavona clavus*, *Pavona gigantea*, *Pavona varians* (Fungiina, Agariciidae), and *Cycloseris curvata* (Fungiina, Fungiidae). The range of colony morphologies are equally diverse: *Pocillopora* spp. have large branching colonies, *P. lobata*, *P. clavus* and *P. gigantea* have massive colonies, *P. stellata* has a small, stubby, branching colony, *P. varians* is laminar (platy) to spherical, and *Cycloseris* is solitary and discoid.

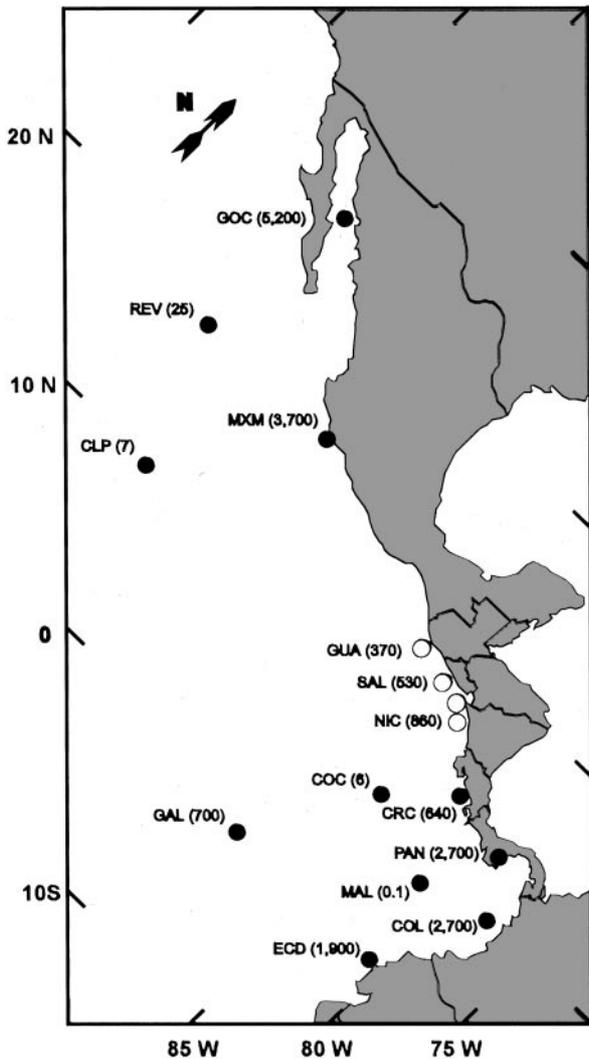
A high proportion (36.6%, 15 species) of all ETP zooxanthellate corals are found at only one or two eastern Pacific localities (Fig. 3B). Fourteen of these narrowly distributed or rare species occur at high diversity (with 20 or more species) localities (México, Revillagigedo Islands, Costa Rica, Panamá) and three at localities (Gulf of California, Clipperton Island, Cocos Island) with less diverse (≤19 species) coral faunas. Two scleractinians (*Acropora valida*, *Porites rus*) and a hydrocoral (*Millepora platyphylla*) disappeared following the 1982–83 ENSO warming event (Glynn and Weerdt 1991; Glynn 1997). Only dead colonies of three species (*Leptoseris papyracea*, *Cycloseris curvata*, *Dia-seris distorta*) have been found at several localities, and five species (*Pocillopora woodjonesi*, *Siderastrea glynni*, *Pavona frondifera*, *Pavona xarifae*, *Millepora boschmai*) are considered endangered, i.e. with known populations of ten or fewer colonies.

Veron's (1995) biogeographic analysis of the eastern Pacific zooxanthellate coral fauna recognized three provinces: Gulf of California, Far East (mainland Central America, from southern México to Peru) and the Galápagos Islands. These coral provinces are very sim-

**Table 1** Eastern Pacific zooxanthellate coral occurrences and relative abundance estimates at 14 localities, 11 in east Pacific and 3 in central Pacific regions. For the relative abundance of corals in given habitat areas, the density measure used (colonies per unit area) makes differences between sites with large and small shelf areas comparable. Species denoted by *E* are now presumed to be locally extinct. Species locality records and abundances were compiled from the published literature and the observations of various investigators as follows: Gulf of California (Reyes Bonilla 1992, 1993; Reyes Bonilla et al. 1997); Mexican mainland (Reyes Bonilla 1993; Carriquiry and Reyes Bonilla 1997; Glynn and Leyte Morales 1997; Revillagigedo Islands (Glynn et al. 1996a; Ketchum and Reyes Bonilla 1997; Veron JEN pers. comm.); Clipperton Atoll (Glynn et al. 1996a; Maté JL pers. comm.); Cocos Island and Costa Rican mainland (Cortés and Guzmán 1998; Cortés J, Guzmán HM, Jiménez CE, pers. comm.); Panamá (Holst and Guzmán 1993; Glynn 1997; Maté JL, Guzmán HM, pers. comm.); Colombian mainland and Malpelo Island (Birkeland et al. 1975; Glynn et al. 1982; Prah and Erhardt 1985; Vargas Angel 1996; Vargas Angel B pers. comm.); Galápagos Islands and Ecuadorian mainland (Glynn 1997, Feingold JS pers. comm.). *A* abundant, *C* common, *U* uncommon, *R* rare, *E* locally extinct, – unrecorded

Species	Eastern Pacific region														Central Pacific region				Sites present	% of sites
	GOC	MXM	REV	CLP	CRC	COC	PAN	COL	MAL	ECD	GAL	HAW	JON	FAN	FAN					
Code	1	2	3	4	5	6	7	8	9	10	11	12	13	14	14					
1 <i>Pocillopora capitata</i> Verrill	PCAP	C	U	U	–	R	R	C	U	–	U	–	–	–	–	9	64.3%			
2 <i>Pocillopora damicornis</i> (Linnaeus)	PDAM	C	U	U	–	U	R	A	–	U	U	A	U	–	–	11	78.6%			
3 <i>Pocillopora elegans</i> Dana	PELE	C	A	C	–	R	R	A	U	C	C	–	–	–	–	10	71.4%			
4 <i>Pocillopora eydouxi</i> Milne Edwards	PEYD	R	U	U	–	R	R	U	C	–	R	U	U	U	U	12	85.7%			
5 <i>Pocillopora inflata</i> Glynn	PINF	R	R	–	–	R	–	U	–	–	U	–	–	–	–	5	35.7%			
6 <i>Pocillopora meandrina</i> Dana	PMEA	C	U	R	–	R	C	U	–	–	R	A	A	A	A	10	71.4%			
7 <i>Pocillopora</i> sp. A	PSPE	R	–	U	A	–	–	–	–	–	–	–	–	–	–	3	21.4%			
8 <i>Pocillopora verrucosa</i> (Ellis and Solander)	PVER	A	C	A	–	U	R	A	C	U	–	–	–	–	–	9	64.3%			
9 <i>Pocillopora woodjonesi</i> Vaughan	PWOO	–	–	R	–	–	–	–	–	–	–	–	–	–	–	1	7.1%			
10 <i>Acropora valida</i> Dana	AVAL	–	–	–	–	–	–	E	–	–	–	–	U	–	–	2	14.3%			
11 <i>Porites australiensis</i> Vaughan	PAUS	–	R	U	–	–	–	–	–	–	–	–	–	–	–	2	14.3%			
12 <i>Porites baueri</i> Squires	PBAU	–	U	–	–	–	–	–	–	–	–	–	–	–	–	1	7.1%			
13 <i>Porites lichen</i> Dana	PLIC	–	R	C	–	–	–	–	–	–	–	C	–	–	3	21.4%				
14 <i>Porites lobata</i> Dana	PLOB	–	U	C	A	U	C	A	C	R	C	C	A	U	13	92.9%				
15 <i>Porites lutea</i> Milne Edwards and Haime	PLUT	–	–	U	–	–	–	–	–	–	–	–	U	–	2	14.3%				
16 <i>Porites panamensis</i> Verrill	PPAN	A	C	U	–	U	–	C	U	–	R	–	–	–	7	50.0%				
17 <i>Porites</i> rus Forskål	PRUS	–	–	–	–	E	–	–	–	–	–	–	–	–	1	7.1%				
18 <i>Porites sverdrupi</i> Durham	PSVE	U	–	–	–	–	–	–	–	–	–	–	–	–	1	7.1%				
19 <i>Porites</i> sp. A	PSPA	–	–	R	A	–	–	–	–	–	–	–	–	–	2	14.3%				
20 <i>Psammocora brighami</i> (Vaughan)	PBRI	U	U	–	–	–	–	–	–	–	R	–	–	–	4	28.6%				
21 <i>Psammocora obtusangula</i> (Lamarck)	POBT	–	–	–	–	R	–	U	–	–	–	–	–	–	3	21.4%				
22 <i>Psammocora stellata</i> (Verrill)	PSTE	C	U	U	R	R	C	C	–	R	U	C	C	–	12	85.7%				
23 <i>Psammocora superficialis</i> Gardiner	PSUP	U	U	R	–	R	U	R	–	R	U	–	–	–	9	64.3%				

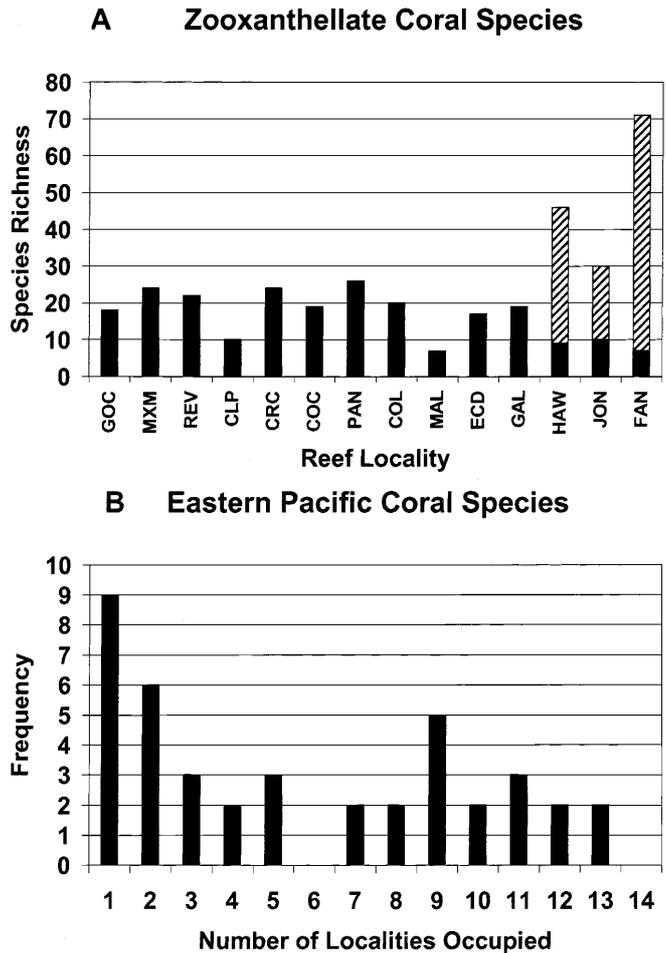




**Fig. 2** Eastern Pacific coral reef localities and respective shelf areas (km<sup>2</sup>) potentially supporting coral growth. Locality codes and maximum shelf depths where coral communities and/or reefs have been observed follow: *GOC* Gulf of California, including all islands, 10 m; *MXM* Mexican mainland south of Mazatlán, 10 m; *REV* Revillagigedo Islands, 20 m; *CLP* Clipperton Atoll, 70 m; *CRC* Costa Rican mainland, 10 m; *COC* Cocos Island, 20 m; *PAN* Panamanian mainland, 10 m; *COL* Colombian mainland, 10 m; *MAL* Malpelo Island, 20 m; *ECD* Ecuadorian mainland, 10 m; *GAL* Galápagos Islands, 20 m. The coral fauna is unknown at the following four localities: *GUA* Guatemala, 10 m; *SAL* El Salvador, 10 m; *NIC* Nicaragua, 10 m. Estuarine coastal stretches were excluded from the shelf areas. *Black circles* indicate data available for locality and *open circles* indicate no data available

ilar to the classic biogeographic model derived from the distributional analysis of several taxa, mainly mollusks, crustaceans and fishes (Briggs 1974; Brusca and Wallerstein 1979). The only difference is that Veron's (1995) Far East province is subdivided by most workers into a subtropical Mexican province and a tropical Panamá province.

Our analysis of the structure of the multidimensional coral species-locality distribution data matrix (Table 1) was undertaken with the sole objective of simplifying the



**Fig. 3** **A** Species richness of zooxanthellate corals at 14 eastern Pacific localities (11 eastern Pacific and 3 east-central Pacific). *Black* histogram segments denote coral species occurring in the eastern Pacific, and *cross-hatched* histogram segments denote coral species occurring in the central Pacific. Species richness for Hawaii from Maragos (1995), for Johnston Atoll from Maragos and Jokiel (1986), and for Fanning Atoll from Maragos (1974). **B** Number of localities occupied by each of 41 eastern Pacific coral species

ecological interpretation of the phenomenon being quantified, and separating the data into groups (i.e., clusters of locales) whose identities were not known in advance. The analyses were conducted to produce an empirically useful stratification of the data, and to potentially suggest a biophysical basis for the observed structure in the data (Johnson and Wichern 1992). Several clustering methods were explored, but Ward's minimum variance method was deemed most robust, particularly to outliers. Central to the idea of clustering of data points is the idea of distance. In the Ward's minimum variance method, the distance between two clusters is the ANOVA sum of squares between the two clusters added up over all the variables.

Broadly, the results of the cluster analyses show three main types of site affinities with respect to coral species distributions. A strong affinity among far eastern equatorial localities is revealed (from Ecuador through

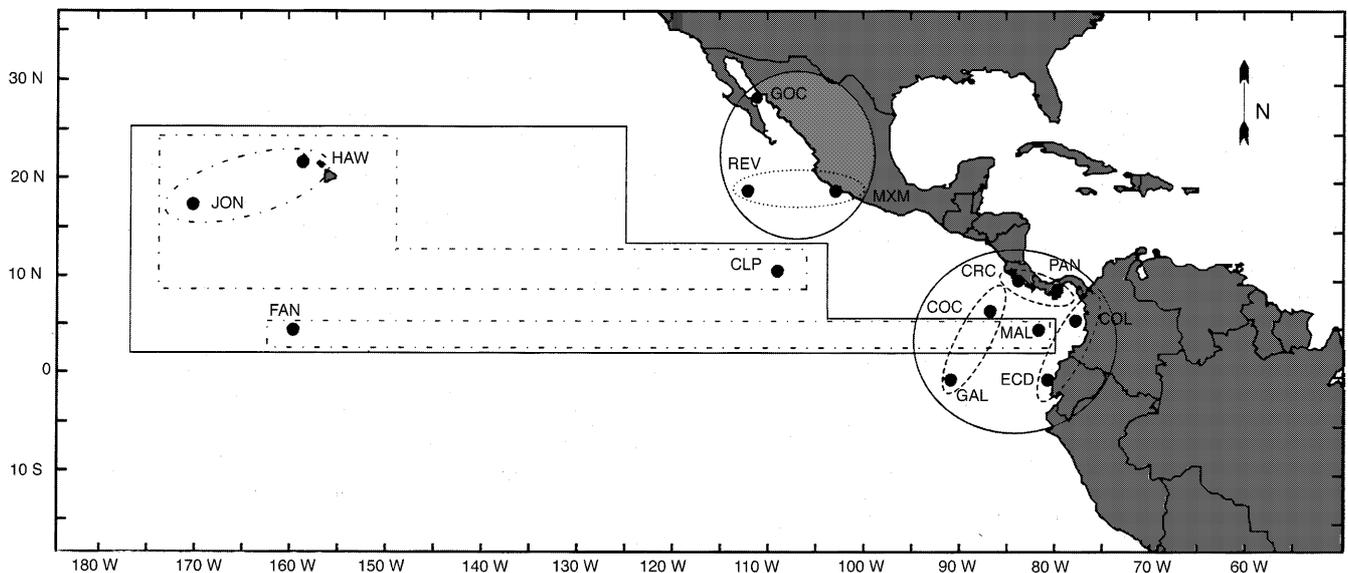
mainland Costa Rica), but the Galápagos Islands and Cocos Island coral faunas are also closely aligned with the mainland (Fig. 4). Within this main cluster, the coral communities of Ecuador and Colombia are similar to each other as are those of Panamá and Costa Rica, but these two subclusters are different. Endemism, the criterion for distinguishing a unique Galápagos Province [e.g., ranging from 18% endemics for shallow-living mollusks, Kay (1991), Finet (1991), and 36% endemics for algae, Silva (1966)] is not represented by a single zooxanthellate coral (Durham 1966; Glynn and Wellington 1983). It is cautioned that this result is based on morphological characters and it is possible that molecular genetic studies may disclose the presence of sibling species (Knowlton 1993). The Cocos Island coral fauna, grouping closely with the Galápagos, has a single Indo-Pacific coral species (*Pavona xarifae*) found nowhere else in the ETP region (Cortés 1996–1997). The Revillagigedo Islands, Gulf of California and Mexican mainland also show a close relationship, and can be regarded as a northern coral province. Both the equatorial and northern eastern Pacific coral provinces demonstrate relatively high species richness with 17–26 and 18–24 species per locality respectively. A third group, including small isolated Malpelo and Clipperton Islands, and three island localities in the central Pacific (Hawaiian Islands, Fanning and Johnston Islands), are also closely aligned. The two eastern Pacific islands are impoverished with ten or fewer zooxanthellate corals. The central Pacific islands also contain ten or fewer eastern Pacific corals, but with the addition of several Indo-west Pacific species exceed the species richness of any ETP locality. Stehli and Wells' (1971) analysis of zooxanthellate coral genera also revealed a discrete cluster relating the east Pacific mainland fauna with several central Pacific island localities, e.g. Easter, Marquesas, Johnston, Hawaii and Midway.

At the ecosystem scale, ETP coral reefs are small, patchy and discontinuous in distribution, often confined

to shallow depths at mainland sites that support reef frameworks dominated by one or a few species (Glynn et al. 1972; Porter 1972; Glynn and Wellington 1983; Colgan 1990; Guzmán and Cortés 1993; Cortés 1997). Unlike coral communities in other biogeographic regions, associated invertebrate taxa, such as sponges, alcyonarians, soft corals, anemones, zoanthids, polychaete worms, bryozoans, mollusks, echinoderms and tunicates, contribute relatively little to the epibenthos of ETP coral reefs (Glynn 1982; Wulff 1997). Also, while ETP reef fishes are abundant, they support relatively low species diversity with roughly three-quarters to one-third respectively of the species present on central (Polynesia, Society Islands) and western Pacific (Australia, GBR) reefs (Robertson 1998). Notwithstanding the impoverished coral fauna, coral skeletal growth rates and framework accumulation rates are comparable to those in other coral reef regions (Glynn 1977; Glynn and Macintyre 1977; Macintyre et al. 1992; Cortés et al. 1994).

The initiation of Holocene reef growth in the eastern Pacific seems somewhat delayed compared with the Caribbean. Core drilling and radiocarbon dating indi-

**Fig. 4** Eastern Pacific zooxanthellate coral provinces and similarity to central Pacific localities. The coral biogeography data consist of  $s$  rows (i.e.,  $s = 1, \dots, 41$  species) and  $\ell$  columns (i.e.,  $\ell = 1, \dots, 14$  localities; Table 1). The  $(i, j)$ -th element of the matrix represents the presence or absence and relative abundance of the species ( $i = 1, \dots, s$ ) at a particular locale ( $j = 1, \dots, \ell$ ) in the eastern Pacific region. From these data we developed similarity coefficients for the binary presence-absence coral species data at localities to measure the association of the coral community between localities. The similarity coefficient we explored was Jaccard's coefficient of community  $S_j$ , that is a measure of resemblance that gives equal weight to all the terms, placing twice the weight of the other terms to double presences since one may consider the presence of a species as more informative than its absence. The similarity matrix formed the basis of the data matrix for a range of clustering models we explored. We used the statistical analysis package SAS (SAS Institute 1990) to convert similarity measures to dissimilarities (i.e.,  $1 - S_j$ ) before clustering



cate that the oldest known Pacific reefs are 4000 years old in Costa Rica (Macintyre et al. 1992; Cortés et al. 1994) and 5600 years old in Panamá (Glynn and Macintyre 1977). Reef building in the Caribbean started about 10000 years BP, was interrupted briefly in many areas by shelf flooding during the Holocene transgression, and then resumed about 7000 years BP to the present (Neumann and Macintyre 1985; Macintyre 1988). Further, elevated and drowned Quaternary reefs are numerous and widespread throughout the Caribbean (Lighty et al. 1982; Edwards et al. 1986/1987; Edwards et al. 1987; Fairbanks 1989; Chen et al. 1991; Blanchon and Shaw 1995), whereas only a few minor fossil reef formations and coral communities are known in the eastern Pacific (Palmer 1928; Durham 1947, 1950; Squires 1959; Walker 1991; Cortés 1993). Cortés (1993) advanced the following observations to explain the poor preservation of coral reefs in the east Pacific compared with the Caribbean: (1) the structural integrity of reef frameworks is less, (2) submarine cementation is rare, (3) crustose coralline algal pavements are poorly developed, and (4) bioerosion proceeds at high rates.

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### Biogeographic hypotheses and supporting evidence

The major hypotheses advanced to explain the origin of the ETP reef coral fauna involve dispersion or vicariance processes (Veron 1995). Dana's (1975) dispersal hypothesis assumes that modern eastern Pacific (EP) corals are recent immigrants that have colonized western American shores from the central Pacific via the NECC. The Line Islands chain is regarded as the central Pacific source area, which moved by sea floor spreading toward the northwest, into the path of the east-flowing NECC beginning during the Pliocene. This hypothesis also presupposes the extinction of all EP corals (including Indo-west Pacific as well as Caribbean relicts) during extreme low Pleistocene sea temperature and sea level fluctuations. Indirect evidence supporting this hypothesis has been advanced by Glynn and Wellington (1983), Glynn et al. (1983), Cortés (1986), Grigg and Hey (1992), and Ketchum and Bonilla (1997) for corals, by Emerson (1978, 1991, 1993, 1994), Emerson and Chaney (1995), and Vermeij (1978) for mollusks, and by additional workers for other coral-associated taxa (Rosenblatt et al. 1972; Garth 1974; Lessios et al. 1996; Robertson and Allen 1996; Allen and Robertson 1997). Richmond's (1990) extension of the long distance dispersal hypothesis invokes accelerated west to east dispersal during ENSO events. Several studies have offered evidence of increased arrivals of Indo-Pacific mollusks (Emerson 1991; Emerson and Chaney 1995; Finet 1991; Kay 1991), echinoids (Lessios et al. 1996, 1998) and fishes (Groves 1984, 1989; Robertson and Allen 1996) during the very strong 1982–83 ENSO event. Molecular studies of allozyme differences between eastern Pacific and central-west Pacific conspe-

cific populations of several taxa have demonstrated little if any genetic divergence, suggesting reproductive connectivity across the entire EP ocean basin. This has been shown for crab symbionts inhabiting corals (Huber 1985), shore fish species (Rosenblatt and Waples 1986), the crown-of-thorns sea star *Acanthaster* (Nishida and Lucas 1988), and sea urchins (Lessios et al. 1996, 1998), the last study supporting recent gene flow across the eastern Pacific, perhaps related to the 1982–83 ENSO event. It is not known if the high affinity of these taxa is a result of reciprocal gene flow across the eastern Pacific or one-way interchange from west to east or east to west. While allozyme differences between conspecific zooxanthellate coral populations have been detected in several studies (e.g., Stoddart 1984; Weil 1993; Benzie et al. 1995), the affinities of disjunct populations have not yet been reported.

A second dispersion hypothesis is the 'vortex model' proposed by Jokiel and Martinelli (1992). This hypothesis postulates a predominantly east to west dispersal of propagules, following prevailing ocean current flows, with species accumulations in the west and faunal attenuation along eastern boundary basins. Supporting evidence for this model is the predominant movement of currents from east to west at tropical latitudes and the documentation of rafting coral propagules along the same course (Jokiel 1984, 1990a, b).

The vicariance hypothesis (McCoy and Heck 1976; Heck and McCoy 1978) maintains that eastern Pacific reef-building corals (and seagrasses and mangroves) are descended from a widespread Neogene Caribbean biota. Thus, eastern Pacific corals represent a modern relict fauna that became separated ca 3.7–3 Ma from the Caribbean basin following closure of the marine corridors across Central America (Duque-Caro 1990; Coates and Obando 1996). Since isolation, the ETP biota has been modified largely by tectonic events, speciation and extinctions. From an analysis of American Neogene fossil distributions and morphometrics, Budd (1989) concluded that some modern eastern Pacific corals could be descended from a southern eastern Pacific relict fauna that experienced widespread extinctions in the Caribbean during Pleistocene environmental upheaval. Eight of the ten Modern EP scleractinian coral genera were present in the Caribbean during Pliocene and Pleistocene times (Budd 1989 and in press). *Psammocora* disappeared from the Caribbean during the Pliocene and *Gardineroseris*, *Pavona* and *Pocillopora* during the Pleistocene. *Acropora* (extinct since 1983), *Leptoseris*, *Porites* and *Siderastraea* are shared between the ETP and Caribbean in the Modern faunas. *Cycloseris* and *Diaseris* are the only Pacific genera that have not been found in the Caribbean fossil record. Several species of the hydrocoral *Millepora* also are members of Modern transisthmian zooxanthellate coral faunas. It is possible that species in these genera evolved in the central/west Pacific and invaded the eastern Pacific after closure of the Central American seaway. Thus, these distributional records leave open the possibility that some ETP corals

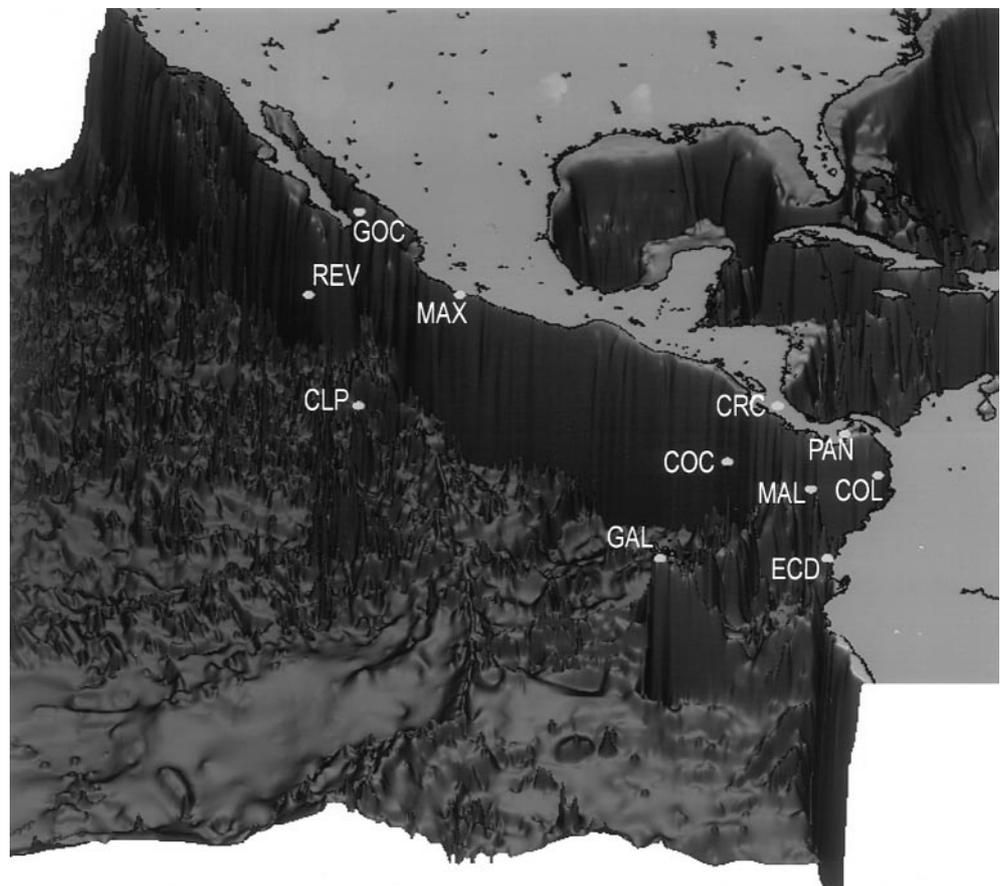
may represent descendents of vicariant species. Although Veron (1995) has discredited this vicariance explanation, chiefly on the basis of numerous factual errors in the distributions of fossil and modern coral taxa, dismissal of this hypothesis seems unwarranted at this time.

Another hypothesis, which serves more to explain the impoverished nature of the ETP coral fauna, is based on the unstable composition of faunas in remote marginal regions (Veron 1995). Due mainly to physical perturbations, species already living near their tolerance limits become locally extinct and are not soon replenished after disturbances because of their relative isolation from source populations. Besides the ETP, other impoverished marginal coral faunas include Henderson Island, southeast Polynesia (Paulay and Spencer 1988), the Hawaiian Islands (Grigg 1981, 1988; Jokiel 1987), northern Japan (Veron 1992), and Lord Howe Island off eastern Australia (Harriott 1992). Evidence of changing faunal composition from both long-term (e.g. sea level fluctuations and associated conditions) and short-term (e.g. periods of cool water intrusions) disturbances is reflected in fossil-to-recent species turnover and in marked variations in species population abundances respectively. Further discussion of variants of the above and other coral biogeographic hypotheses can be found in Rosen (1988).

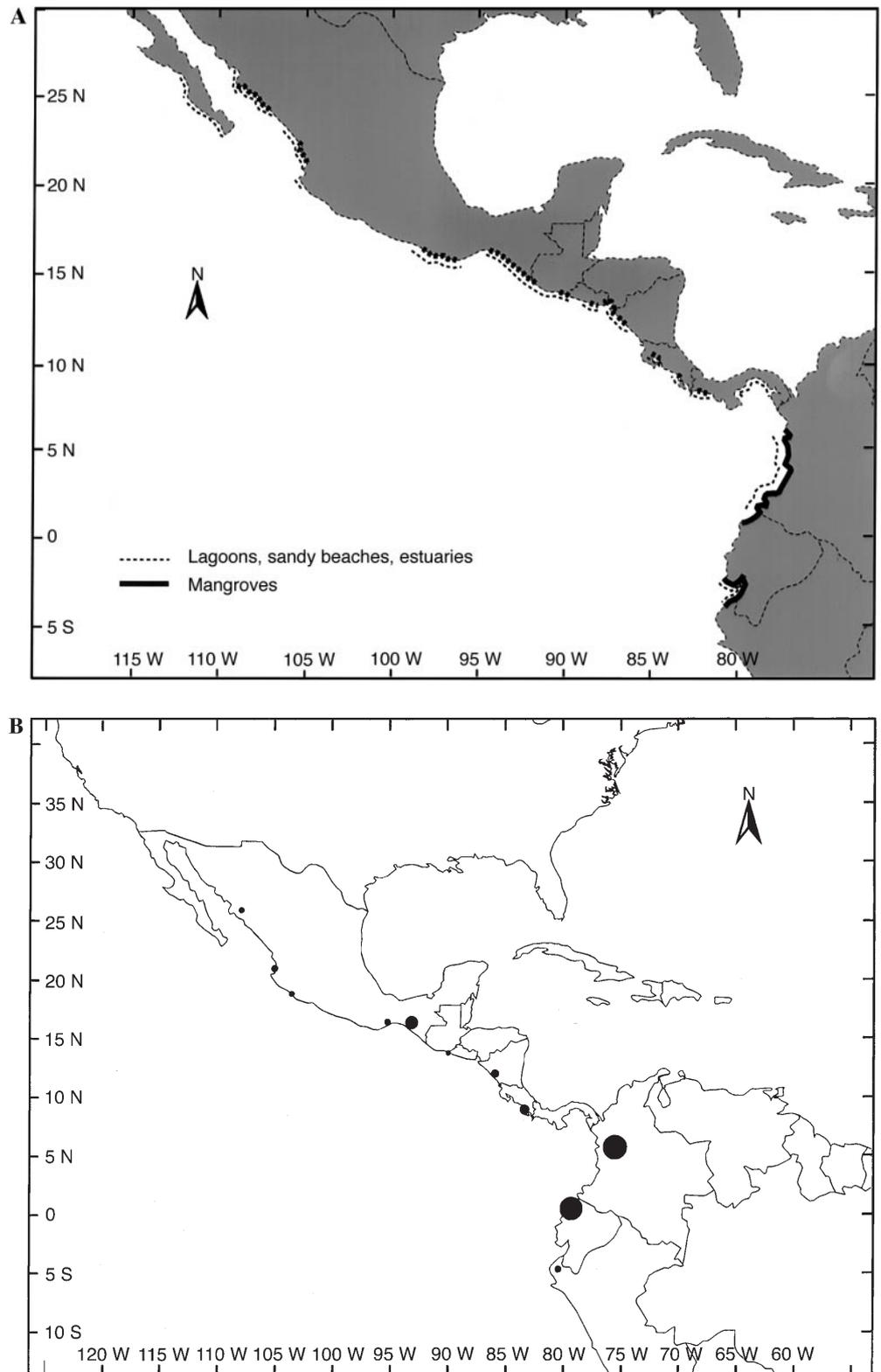
### Physical environmental setting

With the Middle American Trench and Colombian Trench closely bordering the ETP mainland, the continental shelf areas are narrow and offer relatively little shallow habitat for coral reef development (Fig. 5). The largest areas of potential reef habitat are the Gulf of California (GOC), Mexican mainland (MXM), Panamá (PAN), Colombia (COL), and Ecuador (ECD) with a combined area of 16200 km<sup>2</sup> (Figs. 2, 6A). Aside from two young volcanic island groups [i.e., Revillagigedo (REV) and Galápagos (GAL) Islands], only three small isolated islands [Clipperton (CLP), Cocos (COC) and Malpelo (MAL)] make up the remainder of ETP oceanic island environments, with a total shelf area of 738 km<sup>2</sup>. The Galápagos Islands contribute nearly 95% to this total area. Spatially, the potentially habitable coral reef zone is peninsular or track-like, thus constraining biotic migrations along a predominantly southeast to northwest course. Some coastal margins are bordered by long stretches of freshwater lagoons, estuaries, sandy beaches and mangrove forests (Briggs 1974; Carriquiry and Reyes Bonilla 1997), thus fragmenting potential reef habitats. A close correspondence between these types of ecosystems and high freshwater discharge is noted (Fig. 6A, B). One such area, between southern México

**Fig. 5** Three-dimensional depiction of eastern tropical Pacific bathymetry showing the near-absence of shallow continental shelves. (Data from National Ocean Service, 15 s grided bathymetry for the Global Ocean)



**Fig. 6A, B** Distribution of non-coral reef ecosystems and freshwater runoff in the east Pacific region. **A** Mangrove shores (solid black lines), and coastal lagoons, sandy beaches and estuaries (dashed lines); mangroves from Spalding et al. (1997), other coastal ecosystems from hydrographic charts. **B** Freshwater discharge rates are scaled as proportions of maximum rate of  $17650 \text{ m}^3 \text{ s}^{-1}$  off Colombia. From R-Hydro-net v1.0, a regional hydrometeorological data network for Central and South America sponsored by CATALAC, ROSTLAC, US Committee on Scientific Hydrology, University of New Hampshire at <http://www.r-hydronet.sr.unh.edu>. We compiled monthly time series and climatologies, point, hydrometeorological from the level 1.0 data sets on Central and South American discharge and meteorological time series data. The discharge data were then summarized into 17 areas constituting  $5^\circ$  by  $5^\circ$  tiles of the east Pacific Ocean coastal regime running from Baja California and northern México ( $30^\circ \text{ N}$ ,  $110^\circ \text{ W}$ ) to northern Peru ( $4.65^\circ \text{ S}$ ,  $80.49^\circ \text{ W}$ )



(Tangola Tangola Bay, Huatulco) and the Gulf of Fonseca, Nicaragua, spanning a distance of nearly 1000 km of coastline, is known as the “Pacific Central American faunal gap” because of the absence of rocky shore fish records (Springer 1958). Actually, with the

reporting of reef coral communities and associated fishes at Los Cóbano, El Salvador (Orellana Amador 1985), and the presence of breakwaters and other marine structures along the coast (Roberts and Roberts 1995), stepping stone habitats are now available that could

facilitate an interchange of coral species from southern México to Nicaragua.

Because of the importance of ocean currents as vehicles of marine larval dispersal (e.g. Ekman 1953; Scheltema 1968, 1988; Grigg 1981; Jokiel 1990a, b; Briggs 1995; Clarke 1995), we describe briefly the main hydrodynamic current systems in the ETP. The latitudinally skewed position of the ETP, from about the equator to the tropic of Cancer, is due to the concentration of continents in the northern hemisphere and the oceanic influence of the California and Peru surface currents (Fig. 7). These major eastern boundary currents gradually turn westward, becoming the north equatorial (NEC) and south equatorial (SEC) currents respectively. The eastward flowing NECC, located between 3° and 10° N, moves by the Line Islands at 160°W and generally enters the ETP near 80°W at Colombia, Panamá and Costa Rica. Occasionally it also skirts Clipperton Atoll at 10°N, 109°W. During ENSO activity the NECC increases in velocity, volume transport and duration

(Firing and Lukas 1983; Wyrтки 1985; Kessler and Taft 1987; Hansen and Herman 1989; Glynn et al. 1996a). Accelerated NECC flow can reduce the transit time between the Line Islands and east Pacific by half or more, to 50–80 days instead of 160 days (Richmond 1990; Grigg and Hay 1992). A second eastward flowing current, originating near the Line Islands, is the equatorial undercurrent (EUC), which moves between 50–300 m depth and surfaces on the west side of the Galápagos Islands (Wyrтки 1967). The chief ETP currents are the Costa Rican coastal current (CRCC), the Panamá Bight gyre (PBG), and the Panamá current (PC). The CRCC is best developed from June to August, when it penetrates as far north as the Gulf of California. A southwest-flowing current also develops seasonally (January–April), the Panamá current, which advects Panamá Bight surface water toward the Galápagos Islands.

The equatorward flow of the relatively cool California and Peru currents, coupled with coastal upwelling, restrict the northern and southern latitudinal limits, respectively, of coral distribution in the ETP. Three well defined, local areas of wind-induced upwelling also occur within the ETP region, namely in the Gulfs of Tehuantepec, Papagayo and Panamá. During periods of strong upwelling, low sea water temperature, eutrophication, algal overgrowth, and bioerosion, acting alone or together, can reduce live coral cover and perhaps even cause local extinctions. Evidence suggestive of a climatic cooling event during the Little Ice Age (mid 15th to 19th Centuries) was advanced by Glynn et al. (1983) to explain the death of a 100 km coral reef tract in the Gulf of Papagayo, Costa Rica. In 1985, massive dinoflagellate blooms in nonupwelling areas of Costa Rica and Panamá led to a high mortality of corals that survived the 1982–83 bleaching event (Guzmán et al. 1990). Areas outside the three main upwelling centers that also experience periodic upwellings are located off the southeast coast of Baja California Sur and at Banderas Bay and farther south (Jalisco, central mainland México). The mortality of *Pocillopora* corals reported off Baja California Sur during the winter-spring of 1988 (Wilson 1990) was attributed to cool water stress by Reyes Bonilla (in press), and the absence of reef development at Banderas Bay and farther south is believed due in part to upwelling (Carriquiry and Reyes Bonilla 1997).

Briggs (1995) points out that CLIMAP (1981) sea surface temperature (SST) reconstructions, based on oxygen isotope records of planktonic Foraminifera, reveal no temperatures low enough to cause coral extinctions in the ETP during the last glacial maximum (LGM), ca. 18–20 kyears ago. Accordingly, he suggested that elevated nutrients that would promote phytoplankton and benthic algal growth could be an important factor limiting corals rather than low temperatures per se. Eutrophication causing increased competition with filamentous and fleshy algae (Glynn and Stewart 1973; Birkeland 1977), and elevated bioerosion (Highsmith 1980) can limit reef building, and if prolonged, could result in the disappearance of coral reef buildups

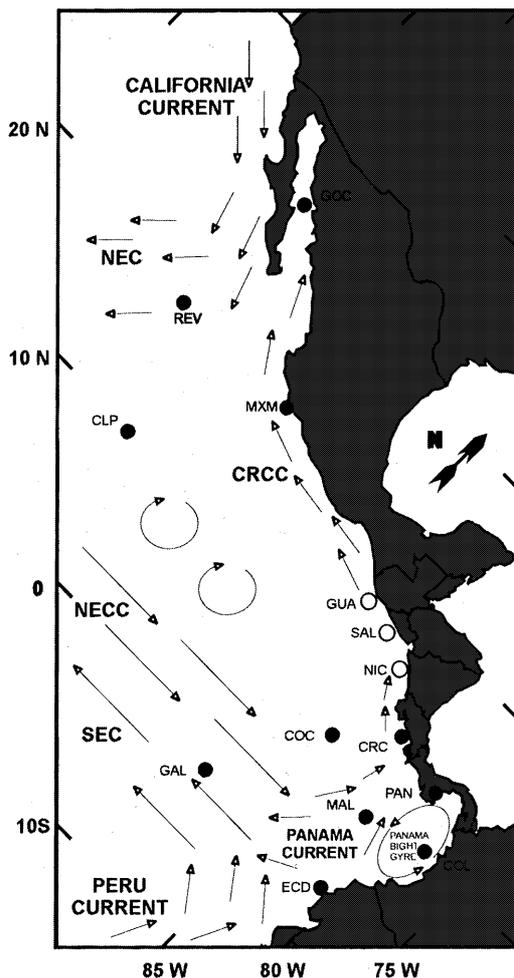


Fig. 7 General sea surface circulation in the ETP (after Wyrтки 1967 and Fiedler 1992). The NECC is best developed from June through November; the CRCC from June to August, when it reaches the Gulf of California; and the Panamá Current from December to April

(Hallock and Schlager 1986; Hallock 1988; Hallock et al. 1988). Recent evidence from high temporal resolution coral isotope thermometry and other studies indicates that tropical SSTs were probably significantly lower during the LGM than the  $-1$  to  $-2$  °C reported by the CLIMAP (1981) findings. Results from west equatorial Atlantic (Guilderson et al. 1994) and southwest Pacific (McCulloch et al. 1996; Beck et al. 1997) sites show that late LGM to early Holocene SSTs were 4–6°C lower than today. If these results are substantiated it is likely that low temperature stress and correlated conditions (noted above) have been adversely affecting ETP coral reef growth during Pleistocene and early Holocene times. Upwelling centers would probably be most severely affected.

ENSO disturbances to coral reefs during 1982–83, and more recently (1997–98), have demonstrated that prolonged sea warming can also have devastating effects in the ETP region. For example, the 1982–83 ENSO caused mean coral mortality of 97% in the Galápagos Islands (Glynn 1990a), and with the failure of reef recovery and continued intense bioerosion, coral reef structures have been virtually eliminated from this area (Glynn 1994; Reaka-Kudla et al. 1996). In light of such catastrophic events, it is important to know how long these kinds of perturbations have occurred in the ETP and the localities affected. With the closure of the Central American seaway ca. 3.7–3 Ma, the modern equatorial Pacific surface circulation developed with the onset of ENSO events. Colgan (1990) noted the thermal extremes set in motion that would affect ETP reef growth during the Quaternary: (1) lowered sea level and cool water conditions during glacial periods and (2) high sea level and unpredictable sea water warming events during interglacial periods. Between 18 to 65 ENSO events of the 1982–83 magnitude may have disrupted reef growth during the latest high sea level stand. A composite plot of positive SST anomalies observed during five recent well documented ENSO events indicates that Colombia, Panamá and Costa Rica, including Cocos and Malpelo Islands, are located within a region of frequent impact (Fig. 8A). Anti-El Niño (La Niña) events occur frequently in the same region, but are also shifted more toward the northwest, as far as El Salvador and Clipperton Atoll (Fig. 8B).

Since reef building corals require high levels of visible light to sustain their endosymbiotic algal flora, conditions which increase turbidity, such as plankton blooms or suspended sediment loading, would tend to depress calcification rates and decrease reef building potential at greater depths. The maximum depth distributions of zooxanthellate corals in oceanic environments with high light penetration, 30–70 m respectively in the Galápagos Islands (Glynn and Wellington 1983) and at Clipperton Atoll (Glynn et al. 1996a), compared with 10–15 m at relatively turbid continental sites (Dana 1975; Glynn 1976; Guzmán and Cortés 1989a), tend to support this trend. High seasonal turbidity, due chiefly to elevated plankton abundance, occurs at

mainland upwelling centers (Gulfs of Tehuantepec, Papagayo, Panamá) and on the west sides of Fernandina and Isabela Islands, Galápagos Islands where the equatorial undercurrent surfaces. High turbidity due to seasonal freshwater discharge and sporadic flooding is notable at several localities, e.g. in the Gulf of Fonseca (Honduras), Gulfs of Nicoya and Dulce (Costa Rica), Gulf of Chiriquí (Panamá), along the Darien (Chocó) coast (Colombia) and in the Gulf of Guayaquil (Ecuador). River flows along the east coast of the Panamá Bight, where mean annual rainfall exceeds 7.5 m along the coastal mountain range (Forsbergh 1969), are the highest in the ETP region (Fig. 6B). On coral reefs in Costa Rica and Panamá, it is not uncommon for underwater visibility to be reduced to 0.5 m or less during heavy runoff of sediment laden waters (Dana 1975; Cortés 1990).

Although the number of hurricanes generated in the ETP is relatively high, these usually form offshore and move in a west to northwest direction, thus avoiding landfall (Scoffin 1993; Glynn and Maté 1997). However, during ENSO events, storm tracts can be diverted to more northerly courses, resulting in damage to coral communities and coral reefs along the mainland coast of México and the Gulf of California (Glynn et al. 1998). Nonetheless, while hurricanes in some regions – e.g. the Caribbean and western Pacific – may cause high local coral mortality and have significant effects on reef geomorphology, the elimination of a coral species from any given fauna is unknown.

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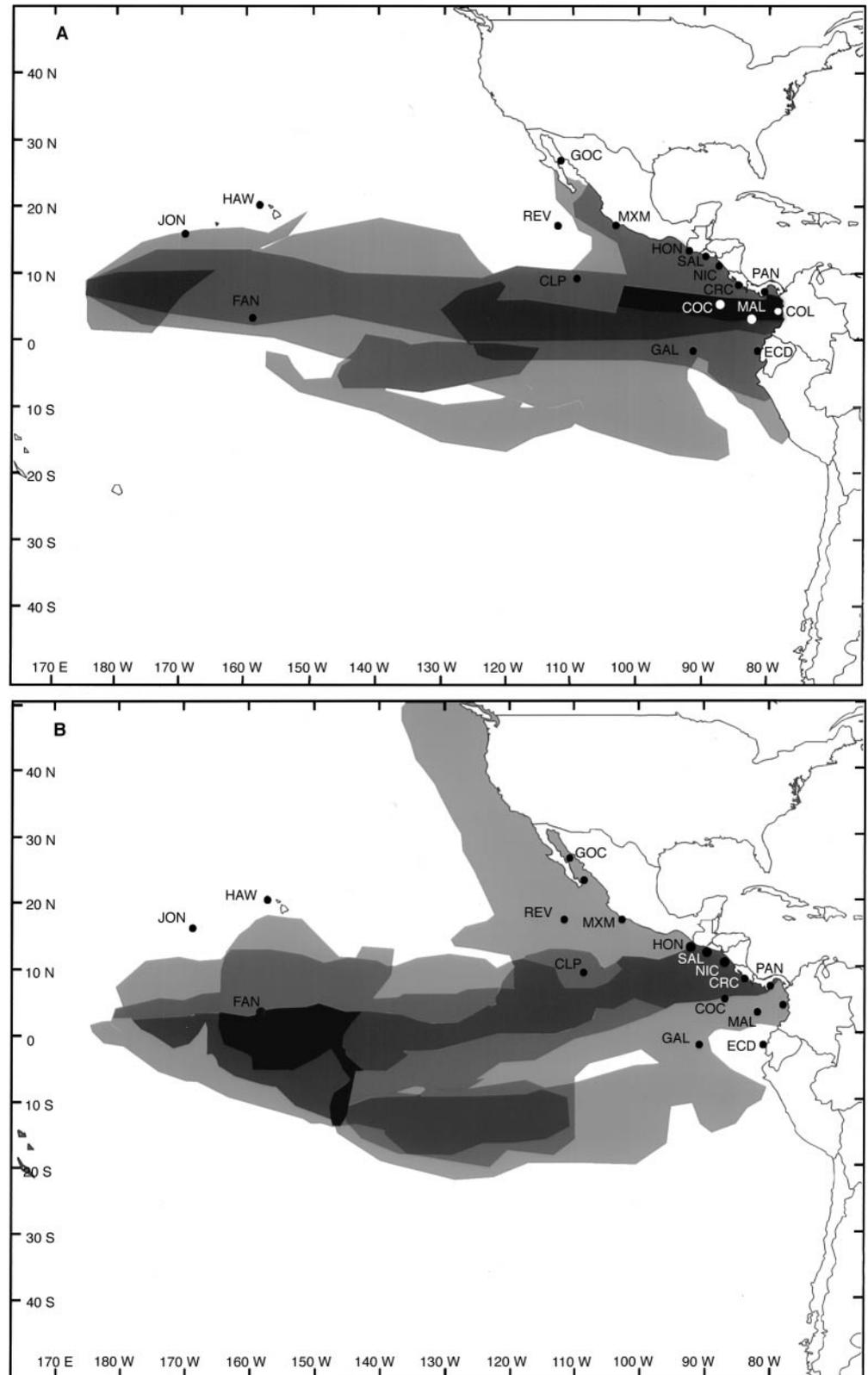
### Ecological factors

Species distributions are also to a large extent controlled by population dynamics, i.e., reproductive traits, population growth characteristics, and survivorship. Here we examine some biotic and environmental factors that may influence the dispersal potential of corals and their persistence once colonizing new areas. Traits of widely and narrowly distributed species are contrasted to help identify ecological factors related to these varying patterns of abundance (Table 2). While this discussion will focus on available knowledge of ETP coral biology and ecology, occasional reference will be made to central/western Pacific conspecific populations when relevant information on EP species is lacking. Known traits of reproduction are examined first, followed by growth, which may affect critically such population dynamic processes as predation, competitive potential, population resilience and community persistence.

#### Life history and population dynamic characteristics

Corals exhibit two basic modes of development, namely (1) brooding, with internal fertilization and the retention of larvae that are subsequently released, and (2)

**Fig. 8A, B** Spatial extent and overlapping occurrence of five major El Niño and La Niña events inclusive over a 35 year period (1953–1989). **A** El Niño positive SST anomalies ( $\geq 1^\circ\text{C}$ ) for 1953, 1958, 1969, 1983, and 1987. **B** La Niña negative SST anomalies ( $\leq 1^\circ\text{C}$ ) for 1956, 1967, 1971, 1975, and 1989. Darker shades of grey denote areas of highest overlap from a maximum of five to two events. For identification of extreme events, we used the multivariate ENSO index provided by the NOAA-CIRES Climate Diagnostics Center, University of Colorado, Boulder (<http://www.cdc.noaa.gov/~kew/MEI/>). ENSO spatial coverage after Allan et al. (1996)



spawning, involving the shedding of gametes with external fertilization producing free-swimming planula larvae (Fadlallah 1983; Harrison and Wallace 1990; Richmond and Hunter 1990). While brooded larvae

have the potential to remain in the water column for prolonged periods – due to their large size, high lipid content and the presence of zooxanthellae (Richmond 1981) – they generally tend to settle near the parent

**Table 2** Reproductive (1–7), growth (8–10) and survivorship (11–15) characteristics of widely and narrowly distributed eastern Pacific corals. Widely and narrowly distributed species are defined as those occurring at 11 or more and 1–2 localities respectively. Species attributes are for eastern Pacific populations unless otherwise noted. Refer to Table 1 for coral species code names. Symbols: ? preceding an entry indicates the need for verification; – indicates unknown; L low; M moderate; H high; the meaning of other symbols in the explanatory notes at the bottom of the table

Attribute	Widely distributed species						Narrowly distributed species					
	PDAM	PLOB	PSTE	PCLA	PVAR	PGIG	MBOS	MINT	MLPA	AVAL	PAUS	PLUT
1 Developmental mode	S <sup>a</sup>	S <sup>a</sup>	S <sup>a</sup>	S <sup>a</sup>	S <sup>a</sup>	S <sup>a</sup>	M	M <sup>b</sup>	M <sup>c</sup>	S <sup>d</sup>	S <sup>e</sup>	S <sup>e</sup>
2 Zooxanthellae presence	Y <sup>a</sup>	Y <sup>a</sup>	N <sup>a</sup>	N <sup>a</sup>	N <sup>a</sup>	N <sup>a</sup>	?N <sup>a</sup>	Y <sup>b</sup>	?N <sup>a</sup>	?N <sup>c</sup>	N <sup>d</sup>	N <sup>d</sup>
3 Reproductive period	YR <sup>a</sup>	YR <sup>a</sup>	YR <sup>a</sup>	WS <sup>b</sup>	YR <sup>a</sup>	WS <sup>a</sup>	?YR	SM <sup>c</sup>	SP <sup>d</sup>	SM <sup>c</sup>	SM <sup>f</sup>	SM <sup>f</sup>
4 Min. reprod. age (yrs)	1–2 <sup>a</sup>	10–15 <sup>b</sup>	–	L/H <sup>c</sup>	5 <sup>c</sup>	11 <sup>d</sup>	–	?3–4 <sup>c</sup>	–	3–4 <sup>f</sup>	4 <sup>g</sup>	4 <sup>g</sup>
5 Fecundity (sexual)	?H	L/H <sup>a</sup>	M/H <sup>b</sup>	L	H	H	–	?M <sup>d</sup>	?M <sup>d</sup>	L <sup>e</sup>	M <sup>f</sup>	M <sup>f</sup>
6 Asexual fragmentation	H <sup>a</sup>	H <sup>a</sup>	L	L	L	L	L <sup>b</sup>	H <sup>b</sup>	L <sup>b</sup>	L <sup>c</sup>	H <sup>d</sup>	H <sup>d</sup>
7 Rafting	Y <sup>a</sup>	Y <sup>b</sup>	N	N	N	N	Y <sup>c</sup>	Y <sup>c</sup>	Y <sup>c</sup>	Y <sup>d</sup>	Y <sup>b</sup>	Y <sup>b</sup>
8 Recruitment success	L <sup>a</sup>	L <sup>b</sup>	M <sup>b</sup>	L <sup>b</sup>	M <sup>b</sup>	M <sup>b</sup>	?L <sup>c</sup>	H <sup>c</sup>	L <sup>c</sup>	H <sup>d</sup>	–	–
9 Colony growth form	R	M	N	M	E	M	P	R	P/B	R	M	M
10 Growth rate	H	M	L	M	L/M	M	M	H <sup>a</sup>	M	H <sup>b</sup>	M	M
11 Frame building potential	H	H	L	H	L	M	L	H <sup>a</sup>	H	H <sup>b</sup>	H	H
12 Relative abundance	A	A	A	C	A	A	R	R/A <sup>a</sup>	R/E <sup>b</sup>	R/E <sup>c</sup>	R/C <sup>d</sup>	R/C <sup>d</sup>
13 Predation prone	H <sup>a</sup>	L	M <sup>b</sup>	M <sup>b</sup>	M <sup>b</sup>	L	L <sup>c</sup>	H <sup>c</sup>	L <sup>c</sup>	H <sup>d</sup>	?L <sup>e</sup>	?L <sup>e</sup>
14 Competitive ability	H	M	M	M	M	H	M	H	M/H	?M	?M	?M
15 Resilience	M	H	H	H	?M	H	L	H	L	L <sup>a</sup>	?M	?M
16 Community persistence	H	H	H	?H	H	H	L	L	L	L <sup>a</sup>	?H <sup>b</sup>	?H <sup>b</sup>

Explanatory notes:

1 S = broadcast spawner, spawns gametes; M = release gonochoric medusae that subsequently release gametes

<sup>a</sup> Glynn et al. (1991, 1994, 1996b, unpub. data)

<sup>b</sup> Observed releasing medusae at Okinawa, Yamaguchi M (pers. comm.)

<sup>c</sup> Taiwan (Soong and Cho 1998)

<sup>d</sup> Great Barrier Reef (GBR), Central Pacific (Richmond and Hunter 1990)

<sup>e</sup> GBR (Harriott 1983)

2 <sup>a</sup> Y = yes, N = no, zooxanthellae present in mature eggs (Glynn et al. 1991, 1994, 1996b, unpub. data); ?N, absence of zooxanthellae from eggs uncertain

<sup>b</sup> Zooxanthellae observed in mature eggs in histological preparations (unpub. observ.)

<sup>c</sup> Acquisition of zooxanthellae probably occurs between 5 and 10 days after settlement in *Acropora millepora* on the Great Barrier Reef (Babcock 1985)

<sup>d</sup> Harriott (1983)

3 YR = year round, WS = wet season, SM = summer, SP = spring

<sup>a</sup> Sexually active year round in thermally stable, high temperature environments; active in warm season in seasonally varying environments

<sup>b</sup> Most active during early wet season (unpub. observ.)

<sup>c</sup> Early summer, Okinawa, Yamaguchi M (pers. comm.)

<sup>d</sup> Taiwan (Soong and Cho 1998)

<sup>e</sup> Early summer (Wallace 1985)

<sup>f</sup> Harriott (1983)

4 <sup>a</sup> Harrison and Wallace (1990)

<sup>b</sup> Calculated from Glynn et al. (1994)

<sup>c</sup> From unpub. observs

<sup>d</sup> From Glynn et al. (1996b)

<sup>e</sup> Ampullae abundant on 3–4-year-old colonies in Panamá

<sup>f</sup> Wallace (1985).

<sup>g</sup> 8-cm-diameter colonies (Harriott 1983) assuming 1 cm/year growth rate

- 5 H = high, M = moderate, L = low fecundity  
 a Low in seasonally varying environments, high in thermally stable high temperature environments  
 b Moderate to high at thermally stable Caño and Uva Islands, high in warm season in Gulf of Panamá and Galápagos Islands  
 c Low in Costa Rica and Panamá, high in the Galápagos Islands  
 d Numerous medusae released in Okinawa (Yamaguchi M, pers. comm.) and Taiwan (Soong and Cho 1998)  
 e Wallace (1985)  
 f Harrison and Wallace (1990)  
 6 H = high, L = low fragmentation  
 a *Pocillopora* spp. propagate more by mechanical breakage and *Porites lobata* by incidental ballistid predation on lithophagine bivalves (Guzmán 1988)  
 b Not observed in *M. boschmai* or *M. platyphylla*, frequent in *M. intricata*, Panamá  
 c Wallace (1985)  
 d Harriott (1983)  
 7 Y = yes, N = not reported  
 a *P. danicornis* observed on a sunken tree trunk in Panamá (Glynn pers. obs.); *Pocillopora* sp. observed rafting in Colombia (Prah 1988) and at several localities in central-west Pacific (Jokiel 1984, 1990, 1992)  
 b *Porites* sp. observed in West Pacific (Jokiel 1990, 1992)  
 c *Millepora* sp. observed rafting in West Atlantic (Bertelsen and Ussing 1936); *M. exaesa* found on floating coconut at Ifaluk Atoll, Caroline Islands (F.M. Bayer, USNM collections)  
 d *Acropora* sp., West Pacific (Jokiel 1990)  
 8 L = low, M = moderate larval recruitment  
 a Low sexual recruitment (Glynn et al. 1991; Birkeland 1977), high recruitment by fragmentation (Highsmith 1982)  
 b From monitored study plots in Costa Rica, Panamá and Galápagos Islands (unpub. data) and Birkeland (1977), Glynn et al. (1994, 1996b)  
 c No recruits of *M. boschmai* or *M. platyphylla* observed, *M. intricata* recruits abundant after 1985 (Glynn and Weerd 1991)  
 d High on reef flat (Wallace 1985)  
 9 E = encrusting, M = massive, N = nodular, P = contorted plates and lobes, P/B = thick plates, box-like, R = ramose or branching  
 10 H = high, M = moderate, L = low. Mean growth defined as follows: high, 25–40 mm/year; moderate, 8–15 mm/year; low,  $\leq 8$  mm/year (see Guzmán and Cortés 1989b)  
 a About 55 mm/year (Glynn and Weerd 1991)  
 b Chave et al. (1972), Glynn et al. (1993)  
 11 H = high, M = moderate, L = low capacity to build reef frameworks  
 12 A = abundant, C = common, R = rare, E = extinct. Relative abundance arbitrarily defined as: abundant,  $\geq 10^3$  colonies at five or more localities; common,  $10^2$  colonies present at seven or more localities  
 a Low following 1982–83 ENSO bleaching event, moderate from 1995 to 1997 (Glynn 1997)  
 b Rare in Panamá before 1982–83 ENSO, now presumably extinct in east Pacific (Glynn and Weerd 1991)  
 c Rare in 1983, now extinct (Prah and Mejia 1985; Glynn et al. 1993; Guzmán, pers. comm.)  
 d Rare in eastern Pacific, common in central/western Pacific  
 13 <sup>a</sup> Usually resulting in partial mortality  
 b *Acanthaster planci* has a feeding preference for this species (Glynn 1974)  
 c No corallivores ever observed feeding on *M. boschmai* or *M. platyphylla*, *Acanthaster* feeds preferentially on *M. intricata* (see Glynn 1976)  
 d High in areas with *Acanthaster*, no *Acanthaster* reported at Gorgona Island  
 e Avoided by *Acanthaster* at American Samoa (see Glynn 1990b, Fig. 13.8)  
 14 H = high, M = moderate ability to compete with other benthic species  
 15 H = high, M = moderate ability to recover from ENSO warming events (Glynn 1997)  
 a Low, based on disappearance at Gorgona Island (see Guzmán pers. comm. in Glynn et al. 1993)  
 16 H = high, corals 10<sup>3</sup>–10<sup>6</sup> years old based on core drilling studies and fossil deposits. From Glynn and Wellington (1983, Table 24), Cortés et al. (1994), Macintyre et al. (1992), Squires (1959), Durham (1947), Glynn and Macintyre (1977)  
 a Based on disappearance at Gorgona Island after 1983 (see Guzmán, pers. comm. in Glynn et al. 1993)  
 b Colonies reach large size (Potts et al. 1985)

colony. An exception is the brooder *Pocillopora damicornis*, which produces larvae that may remain competent for 100 days or longer (Harrigan 1972; Richmond 1989). Interestingly, central and west Pacific populations of *P. damicornis* are brooders whereas east Pacific populations are spawners (Richmond and Hunter 1990; Glynn et al. 1991). The six scleractinian species with wide distributions are spawners, as are the three narrowly distributed species with Indo-Pacific affinities (Table 2). Until recently it was assumed that the small size and low energy reserves in the eggs of spawning corals dictated a brief period in the plankton. However, some observations show that larvae developing from spawning corals can have long settlement competency periods. The maximum competency periods of two *Acropora* species are 20 (Richmond 1989) and 91 days (Harrison et al. 1984; two species also demonstrated longevities of only 5 to 7 days in the laboratory), and range from 26 to 78 days for three subtropical/tropical coral genera (Wilson and Harrison 1998). Of the ten EP zooxanthellate species thus far studied, only *Porites panamensis* broods its larvae and settles within a few meters of the parent colonies (Smith 1991; Glynn et al. 1994). Perhaps reflecting a limited capacity for dispersal, this species is absent from four of five offshore EP island localities (Table 1). Moreover, populations separated by about 250 km along the Pacific coast of Panamá demonstrate significant genetic divergence (Weil 1993).

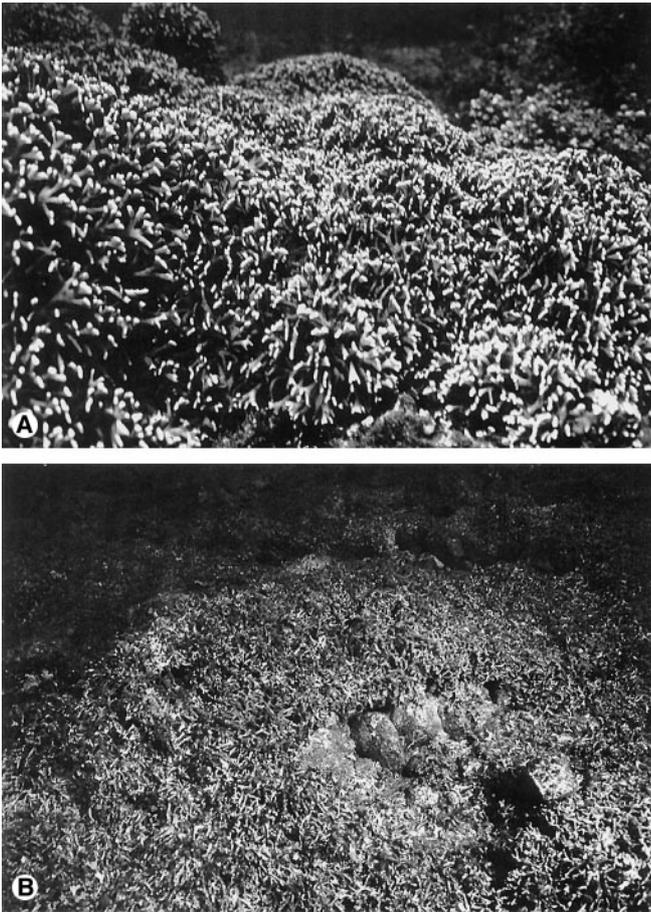
Zooxanthellae occur in the eggs of *Pocillopora damicornis*, *Porites lobata* and *Millepora intricata*, but not in the eggs of four other wide-ranging (ubiquitous) species, nor in the gametes or larvae of five narrowly distributed (restricted) species. Reproductive activity is more prolonged in ubiquitous than restricted species, perhaps allowing the former a greater opportunity for dispersal during periods of favorable current advection (Abbott 1966). Except for *P. damicornis*, the information available for ubiquitous species indicates that they require a longer period to reach reproductive maturity than restricted species. However, every ubiquitous species has some populations with high fecundity in contrast to low-moderate fecundity in restricted species. Of the remaining reproductive traits, no clear trend in asexual fragmentation or recruitment success is evident. Preceding recruitment, larvae must undergo settlement and metamorphosis, which may require specific substrata, chemical cues or both (Morse 1990; Pawlik and Hadfield 1990). Therefore, coral larvae that have crossed the east Pacific filter bridge may still face a critical period that determines successful recruitment. Crustose coralline red algae, a preferred substrate for the settlement of some coral larvae (Morse et al. 1994), are not as abundant on east Pacific reefs as elsewhere in the Pacific Ocean (Glynn and Macintyre 1977; Cortés 1993). Unfortunately, no information on this aspect of east Pacific coral larval ecology is available. Unexpectedly, rafting has been observed in the genera of all restricted species, but only in two of the four genera of ubiquitous species.

## Coral growth and frame-building potential

Growth traits possibly related to species distributional ranges are colony growth form, growth rate and frame-building potential. Many ramose corals, particularly species of *Pocillopora*, *Millepora* and *Acropora*, reproduce asexually by fragmentation, a process that could enhance the spread and persistence of populations locally (Tunncliffe 1981; Bothwell 1982; Highsmith 1982; Wallace 1985). Also, the colony surface of *Porites lobata*, a massive species, bears protuberances that are incidentally bitten off by balistids but often survive, thus expanding local populations. The breakage and dispersal of coral fragments by fishes has long been recognized as an important means of asexual propagation in the east Pacific (Glynn et al. 1972; Highsmith 1982; Guzmán 1988; Guzmán and Robertson 1989). High skeletal growth rates are also associated with ramose colonies, but these traits are not consistently related to east Pacific species abundances. Since east Pacific reefs are constructed of one or a few species, and are hundreds to a few thousands of years old (Glynn and Wellington 1983; Cortés 1993), it is reasonable to assume that species forming reef frameworks would persist for long periods. Such a relationship is not evident.

## Interspecific interactions

Survivorship capacity of widely and narrowly distributed species was examined with reference to relative abundance, susceptibility to predation, competitive ability (both intra- and interphyletic), resilience and persistence. Nearly all ubiquitous species were abundant with local populations consisting of approximately  $10^4$  colonies. All restricted species populations were small, consisting of usually ten or fewer colonies. Two species (*Millepora platyphylla*, *Acropora valida*) are now presumably extinct in the east Pacific, and two others (*Millepora boschmai*, *Millepora intricata*) have precariously small populations (Fig. 9). Four of the six restricted species with small populations declined markedly during the 1982–83 ENSO disturbance, and all of the declines in *Millepora* spp. could be attributed to prolonged sea warming (Glynn and Weerdt 1991; Glynn 1997). Differences in the ability to avoid predation or compete for space with other epibenthos may be influenced by colony growth form and the spatial arrangement of colonies growing in juxtaposition. High coral densities in the east Pacific often result in: (1) the stabilization of colonies, (2) the protection of centrally located colonies from predatory sea stars (*Acanthaster*), and (3) rapid vertical growth, all attributes that promote survival and persistence (Porter 1974; Glynn 1985; Richmond 1985). However, differences in the ability to avoid predation or compete for space with other epibenthic taxa do not seem critical in comparing the two groups. Resilience, the capacity to recover from disturbances, and persistence, the long-term presence of spe-



**Fig. 9A, B** Massive mortality of *Millepora intricata* at Uva Island, Panamá (Gulf of Chiriquí) during the 1997–98 ENSO event (7 m depth). **A** Live, normally pigmented colonies before initiation of sea warming (29 January 1997). **B** Dead, algal covered and partially eroded colonies following sea warming (18 March 1998)

cies at particular localities, were more commonly observed in ubiquitous than restricted species.

### Multivariate biogeographic analysis

Principal component analysis (PCA), following Preisendorfer (1988), was used to determine the spatial relationships of biological-physical fields relating to the population dynamics of 41 coral species at 14 localities in the east and central Pacific Ocean. The matrix of coral species  $s$  relative abundance  $x$  in the localities  $l$  (Table 1) was converted to a numerical abundance  $x_{sl}$  where abundant was 10000, common was 1000, uncommon was 100, rare was 10, locally extinct was 1, and unrecorded was 0. Individual species abundance observations  $x$  were then transformed to natural-logarithm scale, i.e.,  $\ln(x_{sl} + 1)$ , to approximate a normal distribution for subsequent ordinal analyses. A coral population was considered to be a member of the east Pacific fauna if it has been cited recently or in the recent past at a particular locality. The ‘new’ matrix of relative abun-

dance in numerical terms was then analyzed using PCA multivariate statistical methods to assess the biogeographic ‘connectiveness’ between subpopulations of adult corals separated by hundreds to thousands of kilometers in space distributed over the east Pacific. By centering the reference frame of the data on mean locale abundance and rotating  $\theta$  radians counterclockwise about the joint column means, PCA enhances the ability to distinguish differences in spatial distribution between species while preserving the total variance of the data that is invariant under rotation of coordinates to the principal frame.

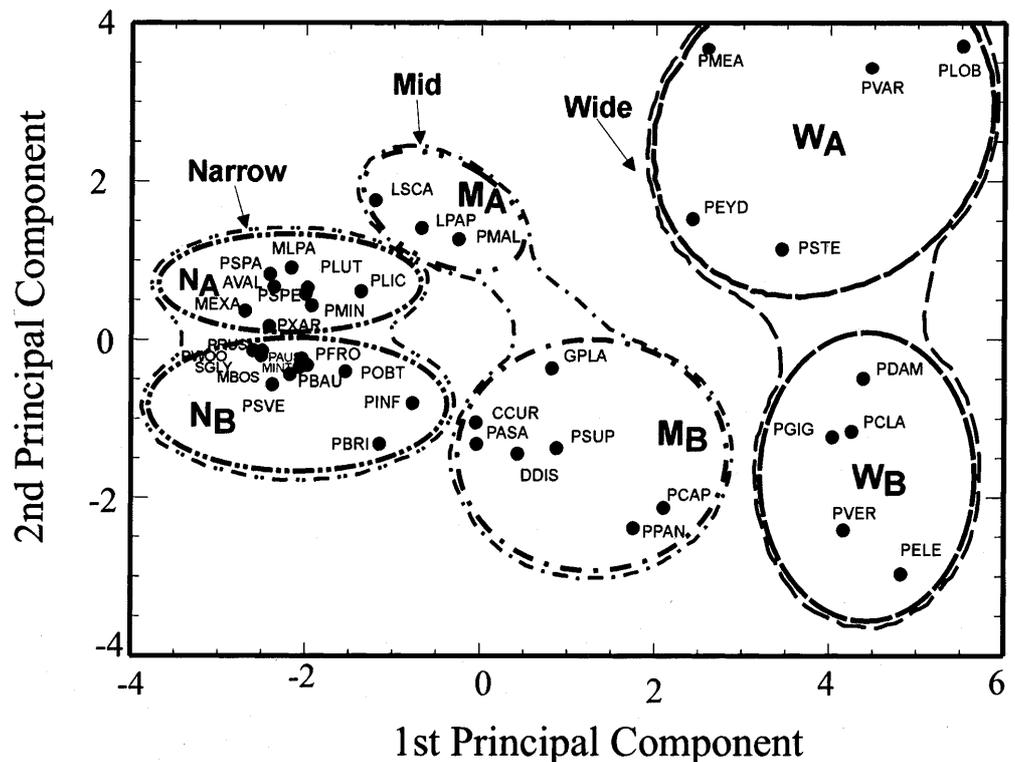
The PCA analyses uncovered three main spatial groupings of coral species spatial distributions, i.e., wide (W), medium (M) and narrow (N), throughout the east Pacific biogeographic region, and each main group was comprised of two subgroups A and B (Fig. 10). The widely distributed species are characterized by occupying many localities ( $\geq 10$  locales) and are relatively abundant at occupied localities. Species with medium distributions are characterized by occupying about half of the localities (i.e., 5–9 of 14 locales) and are marginally abundant at occupied localities. Narrowly distributed species are characterized by occupying few localities and are relatively rare where they are found.

These analyses are reviewed in light of the limited population-dynamic data available on east Pacific coral species (Table 2). For the wide distribution component, we found that these corals parsed into two main subgroups, here referred to as  $W_A$  and  $W_B$ . The  $W_A$  group consisted of five species that occupied from 10 to 13 locales at relatively high levels of abundance. Population-dynamic data were available for *Porites lobata*, *Psammocora stellata* and *Pavona varians* of the  $W_A$  group. In general, the population dynamics of members of the  $W_A$  group was characterized by species with low to medium frame-building potential, low to medium growth rates, medium competitive ability, and year-round spawning. In contrast, the  $W_B$  group also consisted of five species whose population dynamics were characterized by species with low to medium to high frame-building potential, high to medium growth rates, high to medium competitive ability, and wet-season spawning. For the narrow distribution component, we found that these corals also parsed into two subgroups, here referred to as  $N_A$  and  $N_B$ . The  $N_A$  group was characterized by high to medium resilience, while members of the  $N_B$  group were characterized by low population resilience. The mid groups, i.e.,  $M_A$  and  $M_B$ , had population dynamic characteristics falling between the wide and narrow clusters.

### Discussion and research directions

Several lines of evidence suggest that the “impassable” east Pacific barrier has been frequently breached by diverse taxa and is therefore best regarded as a filter bridge, following GG Simpson’s schema (McKenna

**Fig. 10** Results from the principal components analysis of the coral species relative abundances at localities matrix given in Table 1, showing distinct separation of coral species that have wide (*W*), mid (*M*), and narrow (*N*) spatial distributions in the eastern and east-central Pacific Ocean



1973). Numerous Indo-Pacific reef-associated species, e.g. corals, mollusks, crustaceans, echinoderms and fishes, inhabit the east Pacific, and the majority of these species (those studied) have teleplanic larvae capable of long distance dispersal. Developmental stages of cnidarians, polychaete worms, sipunculans, gastropods, decapod crustaceans, echinoderms, and fishes have been collected alive in epipelagic waters between the Line Islands and east Pacific. The cnidarians included pocilloporid larvae, which settled and grew for a few weeks until they were killed in a laboratory accident (R.H. Richmond, pers. comm.). These dispersing larvae have been found at various distances across the east Pacific filter bridge, in the east-flowing NECC and in west-flowing NEC and SEC waters. Several new records of Indo-Pacific mollusks, echinoderms and fishes have been reported in the east Pacific following ENSO events. Demonstrated massive, high velocity west to east advection during ENSO periods provides a physical explanation for the increased appearance of Indo-west Pacific immigrants in the east Pacific at such times. Molecular studies based on allozyme differences have demonstrated little or no genetic divergence among disjunct populations of crabs, a sea star (*Acanthaster*), sea urchins and fishes, suggesting significant genetic interchange. It is likely that some Indo-west Pacific species have been transported into the east Pacific during the 1997–98 ENSO event. Every effort should be made to document the arrival of immigrants, noting the timing, geographic position, developmental stages and condition, and to monitor their populations to better define the critical factors surrounding metamorphosis,

settlement, and interactions with resident east Pacific species.

Notwithstanding these significant advances, numerous important questions relating to various details of dispersal and colonization still remain. For example, the efficacy of rafting needs to be studied in more detail. The ability of coral larvae to settle and survive on floating objects can add substantially to dispersal capabilities (Jokiel 1990a). Corals settling on pumice can move over great distances (thousands of kilometers) for at least a few years if food resources and environmental conditions are adequate (Jokiel 1990b). Live colonies of *Pocillopora damicornis* (ca. 10 cm diameter) have been observed on sunken tree trunks in Panamá (Glynn, pers. obs.), and a small colony of *Pocillopora* sp. was found attached to clumps of floating *Sargassum* at Gorgona Island, Colombia (Prahl 1988). Pumice recovered in the Hawaiian Islands with two attached colonies of *Pocillopora* sp., the larger colony 2–3 years of age, likely originated from the Revillagigedo Islands (west México) and drifted to Hawaii in the NEC (Jokiel 1984). While diverse larval stages have been captured near the east and west boundaries of the Pacific filter bridge, where transoceanic currents first encounter shallow shelf habitats, the actual arrival of dispersing stages known to have crossed the open ocean has not been reported. Thus, it has not been possible to establish the nature of the dispersing organisms, i.e. whether by drifting larvae or the rafting of settled stages, or the identity of the transporting currents. Here, as in most studies, the NEC, SEC and NECC are assumed to be the most likely currents facilitating dispersal. However, it is possible

that the EUC, originating west of the Line Islands and surfacing immediately west of the Galápagos Islands, and the SECC, moving in an easterly direction through French Polynesia, may also play a role in dispersal. Perhaps related to these southerly routes are four fossil zooxanthellate coral genera (*Stylophora*, *Pocillopora*, *Leptoseris*, *Porites*) that have been collected from seamounts of the Sala y Gomez and Nazca ridges, centered at 25–30°S. The dredge collection (HD-73) containing these corals is from the “Shoal Guyot”, 205–227 m depth at 85°25′W, 25°44′S (Allison et al. 1967). These ridges belong to the Nazcaplatensis Province, which extends from Easter Island in an east to northeast direction across 30° latitude. The E-most end of the ridge lies about 730 km from the Peruvian coast and 1600 km south of the ETP reef coral region. As noted earlier, the cool Peru–Chile Currents may have impeded colonization of the northwest South American coast. Remarkably, some of the seamounts of the Nazca and Sala y Gómez ridges are drowned atolls of Miocene age, ranging from 250 to 1200 m in thickness (Parin et al. 1997). This suggests an important early biogeographic link between the south Pacific and southeast Pacific regions.

Further, since the recruitment of Indo-west Pacific species has not been observed directly, various risks associated with recruitment, such as the availability of suitable substrata during settlement, and likely high rates of predation and competition, have not been investigated. Even assuming successful recruitment, a number of conditions must be met to ensure colonization, including the establishment and persistence of populations sufficiently large to ensure future reproductive success. The marked fluctuations in population size and local extinctions of east Pacific corals documented in recent years underline the importance of diverse environmental demands upon adult species populations (Glynn 1997). To better understand the dynamic nature of EP coral reef species, long-term monitoring, in particular the assessment of population size and stability, and reproductive and recruitment success in relation to physical and biotic perturbations, is urgently needed. The relatively strong correlation between population-dynamic characteristics and species distribution and abundance for the few species where detailed information is available suggests the need for expanded demographic knowledge for the bulk of ETP species, and the Central and Indo-Pacific species as well if comprehensive comparative biogeographic analyses are to ever be conducted.

Detailed morphometric and genetic comparisons of central (Line Islands, Marquesas Islands) and east Pacific coral species populations are virtually nonexistent. Comparisons of allozyme differences within and between east and central Pacific coral populations would provide information that could be used to gauge their degree of genetic connectivity. Also, newer molecular techniques based on PCR (polymerase chain reaction) have been utilized in some coral studies and may hold promise for more intensive biogeographic investigations. Mitochon-

drial and nuclear marker genes can offer higher resolution than protein electrophoresis, and provide a quantitative measure of patterns of evolution (Romano and Palumbi 1996). Nuclear ribosomal DNA (rDNA) analysis has proved useful for interspecific comparisons and molecular phylogeny in the difficult genera *Porites* (Hunter et al. 1997) and *Montastraea* (Lopez and Knowlton 1997; Medina et al. 1999). The preliminary study of Hunter et al. (1997) in Hawaii is the only one to date that has examined geographic differences between coral populations. And evidence of hybridization in species of *Acropora* has become available from rDNA studies by Odorico and Miller (1997).

Since all coral genera save two (*Cycloseris* and *Dia-seris*) are present in Caribbean and east Pacific fossil assemblages, it is possible that some east Pacific coral species could be descended from Tethys relicts as suggested by Budd (1989). Two candidate species are the extant endemic *Siderastrea glynni* and *Millepora boschmai*, which would offer interesting comparisons with Caribbean and Indo-Pacific congeners.

The high proportion of east Pacific coral endemics, 24.4% (10 out of 41 species), may be somewhat inflated because six of them have only recently been recognized or named. Future collecting efforts may reveal their presence outside of the east Pacific. Three of these species belong to the equatorial east Pacific province (*Siderastrea glynni*, *Pavona* sp. A, *Millepora boschmai*), two are known only from Clipperton, the Revillagigedo Islands and north México (*Pocillopora* sp. A, *Porites* sp. A), and one occurs from the Galápagos Islands to mainland México (*Pocillopora inflata*). If this high level of endemism is substantiated by further study, it would lend support to a model of allopatric speciation in an isolated peripheral area (see Rosen 1988; Jokiel and Martinelli 1992; Veron 1995). Perhaps a suite of ETP corals, originating from central Pacific species by long distance dispersal, has speciated in response to the novel physical and biotic conditions characteristic of the east Pacific region? In conclusion, our analysis suggests that the Modern east Pacific coral fauna may consist of a mixture of elements derived from both dispersal and vicariance events: (1) mostly of Indo-Pacific migrants that reached the east Pacific by long distance dispersal after closure of the Central American seaway, (2) several endemics that evolved relatively recently in the isolated and marginal east Pacific environment, and (3) a few relict species with closest affinity to west Atlantic ancestral stocks.

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