Gene Flow in Coral Reef Organisms of the Tropical Eastern Pacific

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Abstract

Gene flow can provide cohesion between conspecific populations. In order to obtain an indirect measure of gene flow between coral reef species in the eastern tropical Pacific (ETP) and between these populations and those of the rest of the Pacific we compiled available data from sequences of DNA and microsatellites for corals, gastropods, echinoderms and fishes, and calculated F_{ST} statistics. The ETP consists of a narrow strip of continental shelf along the coast of the Americas and a deeper water gap between the coast and the outer eastern Pacific Islands; a large expanse of deep ocean separates the ETP and the closest islands in the central Pacific. We have, therefore, compared populations in four major directions: (1) between the eastern and the central Pacific, (2) between the coast and the outer islands, (3) among the outer islands, and (4) along the coast and nearshore islands. The available data are biased in favor of showing high levels of gene flow because they contain an excess of transpacific species, which are a minority among ETP biota. Despite this bias, shallow water populations of the ETP are isolated from the rest of the world's oceans. Occasional breaching of the expanse of water between the ETP and the Central Pacific by some species is also possible. Gene flow between the outer eastern Pacific islands and the mainland coast is variable, depending on the species examined. Gene flow among populations at the outer eastern Pacific islands is high except for those at Easter Island (Rapa Nui), in which all but one sampled species show large and significant values of F_{ST} in comparisons with populations from all other islands. Gene flow rates among populations along the ETP coast are high. There is no evident genetic break resulting from the Central American Gap (southern Mexico to the Gulf of Fonseca, Honduras) in any of the sampled species. A trend of isolation by distance along the coast is evident in corals and fishes.

Keywords

Genetic connections • Mitochondrial DNA • Microsatellites • Genetic structure • F_{ST} statistics

16.1 Introduction

Gene flow is the exchange of genes between conspecific populations. It is an important biological process in every species because gene transfer provides cohesion between populations, preventing their independent evolution. The movement of genes over generations assures that new advantageous mutations that arise in one location can eventually spread throughout the species' range. When gene flow becomes restricted populations become "genetically

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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_16

structured", diverging from each other and (if the restrictions become severe and last a long time) possibly turning into separate species. The sharing of genes between populations can also dilute adaptation to local environmental conditions, thus averaging the response to natural selection over the connected populations. It may thus limit the geographic extent over which a species can spread, as peripheral populations are prevented from adapting to conditions at the edge of a species range and then proceed to colonize new, previously unsuitable, areas (Haldane 1956; Case and Taper 2000; Sexton et al. 2009; Dawson et al. 2010).

Genetic exchange is effected by the dispersal of propagules from one population to another, but, as propagules are difficult to follow, most estimates of gene flow do not involve direct observations of such transfers; they rely instead on assessing divergence between populations. This is particularly true for marine organisms in which planktonic larvae maintain genetic connections over very long distances and are virtually impossible to track in the water column. Species with this kind of larvae are expected to show high rates of genetic exchange between populations and thus high genetic homogeneity, although this expectation is not always met. Several studies have indicated that in a number of marine species self-recruitment to the natal population is high, and the dispersal potential expected of their larvae fails to be realized (Jones et al. 1999; Swearer et al. 1999, 2002; Hellberg et al. 2002; Taylor and Hellberg 2003). Such studies have led to doubts that the dogma of near-panmixia in marine organisms is ever realized (Hellberg 2009). Even when local recruitment does occur, however (as it undoubtedly does in most populations), and even if the fraction of the larvae that recruit successfully at a distant locality is small, it may be sufficient to homogenize genetic constitution of populations over large distances.

The position of coral reef organisms of the eastern tropical Pacific (ETP) in the spectrum between panmixia and high genetic structure is the subject of this chapter. We begin by considering geographical and oceanographic features that would be expected to affect rates of contemporary and historical gene flow, then summarize existing data from the literature about genetic connectivity. Not all of the data were gathered to assess population structure, and the organisms for which genetic data exist are far from uniformly spread over taxonomic groups. Nevertheless, a compilation of such data can begin to address the question of whether general patterns exist. In "coral reef organisms" we include all species that are represented by populations resident in coral reefs, even if they are not exclusively found in this particular habitat. As most of these species (even corals) are capable of living outside coral reefs (Robertson 1998; Guzmán et al. 2004), this means that we have attempted to include studies on all organisms that live on hard substrata in the photic zone, except for those limited to the upper intertidal shore line.

16.2 Oceanographic Features of the Tropical Eastern Pacific Relevant to Gene Flow

The ETP (Fig. 16.1) consists of a narrow strip of continental shelf along the coast of the American continent with some islands close to the shore, a deeper water gap between the coast and the outer eastern Pacific Islands (Easter Island, the Galápagos Archipelago, Malpelo Island, Isla del Coco, Clipperton Atoll and the Revillagigedo Archipelago). A large expanse of deep ocean separates the ETP and the closest islands in the central Pacific (the Line Islands, the Marquesas, and Hawaii). Thus, shallow water populations in the ETP can exchange genes in four major directions: (1) between the eastern and the central Pacific, (2) between the mainland coast and the outer islands, (3) among the outer islands, and (4) along the coast and nearshore islands. Potential barriers to gene flow in each direction consist of habitat unsuitable for the establishment of adult populations and of currents that channel the movement of larvae along a particular vector, or that alter environmental conditions as to exceed the tolerances of propagules in a particular area (see Chaps. 3 and 4, Fiedler and Lavín, and Wang et al., respectively). Expanses of deep water that are difficult to cross in a single larval life can be expected to cause the most marked restrictions to the exchange of genes. If impassable, these barriers can prevent the spread of species, thus establishing different biogeographic provinces as determined by patterns of species presence and absence.

Physical barriers that impede gene exchange between populations in the ETP and those in the rest of the world define it as a separate oceanic region. Towards the east, an uninterrupted land bridge has existed for the last 2–3 million years (Coates and Obando 1996). [It has been claimed recently that a nearly complete barrier to water exchange with the Caribbean has existed since the Eocene or early Miocene (Montes et al. 2012) but this claim is incompatible with paleoceanographic (Keigwin 1982; Collins 1996; Haug and Tiedemann 1998; O'Dea et al. 2007), paleontological (Webb 1976; Coates and Obando 1996), and genetic (Lessios 2008) data.] Towards the west lies the widest marine biogeographical barrier on the planet, 4000–7000 km of deep water without any stepping stone habitats on which adults of shallow water marine species can exist (Ekman 1953; Briggs 1974). This ocean configuration, known as the "Eastern Pacific Barrier" (EPB) has been in place for most of the Cenozoic (Grigg and Hey 1992). It is so difficult to cross, that most shallow water benthic genera are represented by different species on its two sides. Had it not been for the small number of "transpacific species", species that span the EPB (Emerson 1978, 1982; Vermeij 1978; Rosenblatt and Waples 1986; Lessios et al. 1996; Robertson et al. 2004; Lessios and Robertson 2006), it would not have figured in a

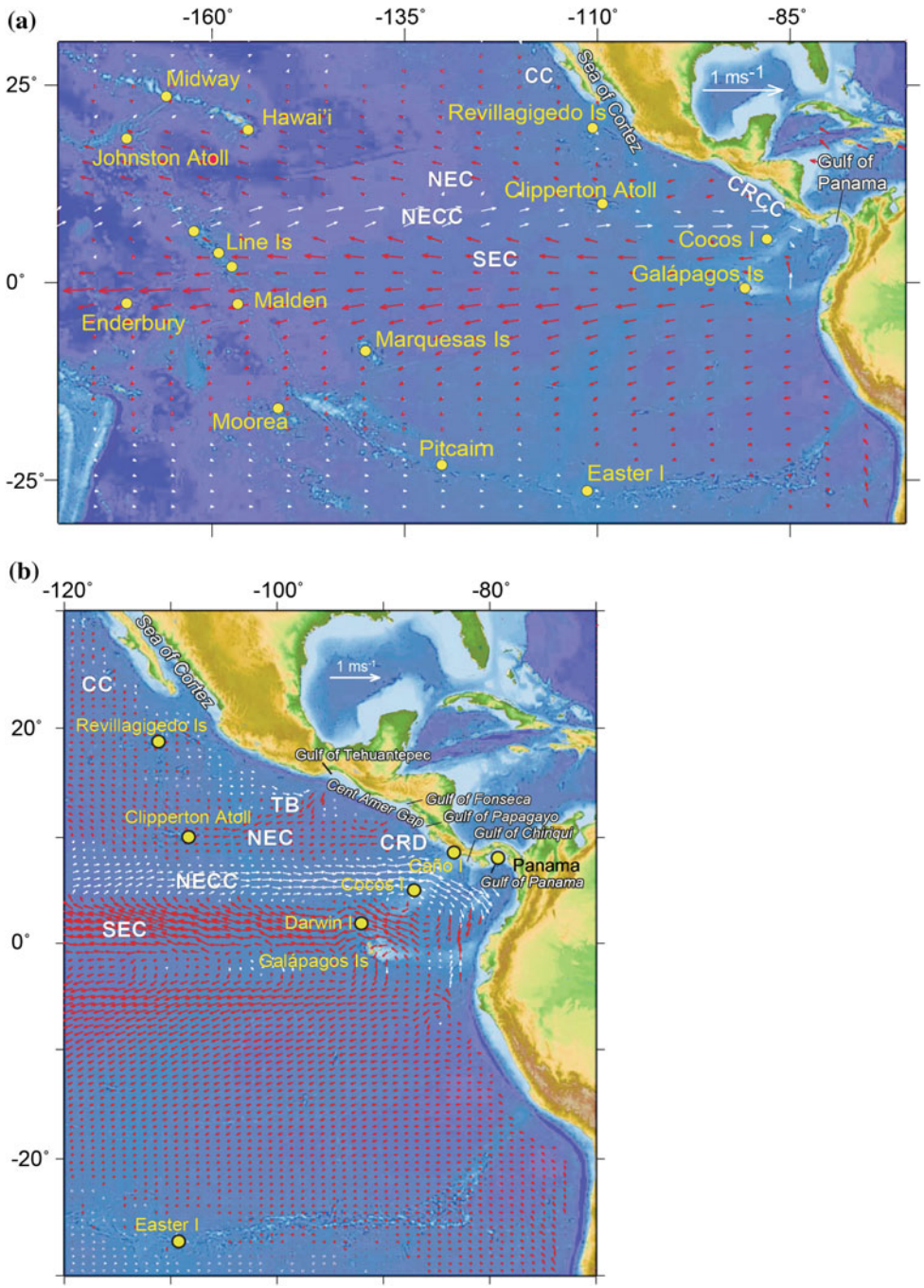

Fig. 16.1 Ten year mean (1993–2003) ocean surface currents in the Central-East Pacific (**a**) and the Eastern Tropical Pacific (**b**). Given are surface current vectors with 1 degree (**a**) or 1/3 degree (**b**) resolution. Basemap generated with ETOPO 2 (USGS). CC = California Current, NEC = North Equatorial Current, NECC = North Equatorial Counter Current, SEC = South Equatorial Current, CRCC = Costa Rica Coastal Current

discussion of conspecific gene flow. The barrier is traversed by the westerly North and South Equatorial Currents and by the easterly North Equatorial Counter Current. The speed of the latter increases greatly during El Niño events, reducing the transit time between the Line Islands and the eastern Pacific to periods that may not exceed the larval duration of a number of organisms (Richmond 1990; Glynn et al. 1996; Glynn and Ault 2000; Robertson et al. 2004). This acceleration of the North Equatorial Counter Current is generally proposed as the conveying mechanism for the dispersal of species from the species-rich central Pacific into the ETP (Dana 1975; Richmond 1990; Robertson et al. 2004) and may also be responsible for recurrent events of gene flow, at least in one direction.

Expanses of deep water narrower than the EPB are also of potential relevance to genetic divergence between conspecific populations of the outer islands of the eastern Pacific and the mainland. Easter Island (Rapa Nui), 4000 km from the coast of Peru, is the most remote of these islands. As its distance from Pitcairn is 1700 km, it can either be considered

as the westernmost island of the eastern Pacific or the easternmost island of the central Pacific. Its marine fauna consists of a mixture of endemic, Indo-West-Pacific, transpacific, and cosmopolitan species, but it also contains several species characteristic of the eastern Pacific (Fell 1974; Rehder 1980; Randall 1998; Glynn et al. 2007). The latter may be the result of larval transport in currents that flow predominantly towards the west (Glynn et al. 2007). The next most remote island, Clipperton Atoll, lies inside the tropics, 1000 km from the coast of Mexico and 4000 km from the Marquesas Islands. It is intermittently bathed by either the easterly North Equatorial Counter Current or the westerly North Equatorial Current and may well represent a stepping stone between the central and eastern Pacific (Glynn et al. 1996; see Chap. 5, Glynn et al.). As at Easter Island, the marine fauna of Clipperton is a mixture of Indo-West and east Pacific species, and also endemics (Glynn et al. 1996; Lessios et al. 1996; Robertson and Allen 1996). The Galápagos Islands comprise the only oceanic Archipelago in the Equatorial eastern Pacific. San Cristóbal, the closest island to the mainland, lies 930 km west of the coast of Ecuador. The Galápagos Islands contain the best studied marine biota among those of the outer islands (e.g., Bowman 1966; Glynn and Wellington 1983; James 1991; Grove and Lavenberg 1997). The marine fauna contains numerous species that are also found on the west coast of America, several species endemic to the eastern Pacific outer islands or just to the Galápagos, and a few Indo-Pacific species (Briggs 1974). The Archipelago is influenced by the Peru Oceanic Current flowing towards the Galápagos from the mainland, the North Equatorial Counter Current bringing water from the central Pacific, the South Equatorial Current flowing in the opposite direction, plus a southerly flowing current during the dry season out of the Panama Bight (Ab bott 1966; Glynn and Ault 2000; Kessler 2006). Isla del Coco is situated 690 km northeast of the Galápagos and 500 km west of Costa Rica. Its marine fauna consists mostly of eastern Pacific species, but there is a small number of outer island endemics and of Indo-Pacific species (Hertlein 1963). The four Revillagigedo islands lie approximately 390 km southwest of the southern tip of Baja California. The shallow water marine species on these islands are mostly a subset of those found on the mainland, but some Indo-Pacific species are also present. The corals show affinities with those of Clipperton (Glynn et al. 1996; Glynn and Ault 2000; Ketchum and Bonilla 2001). The Revillagigedo Archipelago is influenced both by the northerly Costa Rica Current and by the southerly California Current (Glynn and Ault 2000; Kessler 2006; see Chap. 3, Fiedler and Lavín).

Marine populations of the coastal ETP are expected to show more genetic connectivity than those of island populations. This coast, however, is not entirely without potential barriers. Hard substrate bottoms are interrupted by river estuaries and mangrove areas, unsuitable as habitats for adults of many coral reef species. A 1000 km stretch from southern Mexico to the Gulf of Fonseca at the Honduras-El Salvador border (the Central American Gap) is devoid of coral reefs or rocky bottoms, except for a small *Pocillopora* reef in Los Cóbanos, El Salvador (Glynn and Ault 2000; Reyes-Bonilla and Barraza 2003; but see Chap. 5, Glynn et al.). Wind-driven upwelling in the Bay of Panama, the Gulf of Papagayo, and at Tehuantepec (Kessler 2006) may also exclude some species with narrow thermal tolerances, such as *Acanthaster planci* (Glynn 1974). Separate biogeographic provinces along the American coast recognized by some authors (Briggs 1974; Veron 1995; Hastings 2000; but see Robertson and Cramer 2009; Briggs and Bowen 2012) attest to the existance of barriers to dispersal that prevent a number of species from spreading along its entire length. Major currents may be of less importance to dispersal along the coast compared to tidal flux and eddies, likely to spread larvae over moderate distances. Nevertheless, larval connectivity might be influenced by the general circulation pattern from south to north between approximately 20°N and 20°S (Kessler 2006; Fiedler and Lavín (Chap. 3)). The northerly Peru Oceanic and Coastal currents reach almost to the Panama Bight; in this area a reversing gyre moves water towards the north or towards the south, depending on the season. From Costa Rica to Baja California, the current flow along the coast is northward, all the way to the entrance of the Sea of Cortez (Gulf of California). The cold California Current flows southward on the west side of Baja California and limits colonization of most tropical species, thus defining the northern termination of the ETP.

16.3 Data on Gene Flow Between Conspecific Populations in the Eastern Pacific

We have attempted to compile all the existing data published until 2013 that can be used to calculate rates of gene flow among ETP populations of coral reef organisms. Most of these data consist of mitochondrial DNA (mtDNA) sequences. The mtDNA of corals, however, evolves at slow rates and does not provide information useful in comparing conspecific populations (Shearer et al. 2002; Hellberg 2006). Population genetic research of corals has, therefore, had to rely on either sequences of ribosomal internal transcribed spacers (ITS) or microsatellites. We have not included data from isozyme studies because the original data are not readily available, and because many of the organisms for which isozyme data exist have been revisited by studies involving DNA, less subject to the problem of "hidden variation". Most of the studies that generated the data were not designed to address the question of gene flow within the

eastern Pacific; because of this, the sample sizes for each local population are often smaller than necessary for robust statistical analysis. Nevertheless, sequence data from only a few individuals may present a not too distorted view of gene flow (Pluzhnikov and Donnelly 1996). Some of the published studies have included summary statistics that could be used directly. When they did not, we calculated these statistics from raw data downloaded from GenBank. Some studies had to be omitted because authors have not included locality information with the accessioned sequences, making it impossible to use their data to calculate gene flow between local populations.

In order to quantify degree of divergence relevant to gene flow, we used F_{ST} statistics (Wright 1951). F_{ST} is the ratio of genetic variance between populations over the pooled variance within populations. There are two, qualitatively different, ways of calculating F_{ST} statistics. One, as originally conceived by Wright, is based on the frequency of alleles. The other is relevant only to DNA sequences, and is based both on the frequency of haplotypes and on the number of nucleotide differences between them (Hudson et al. 1992). This measure is sometimes referred to as Φ_{ST}. We have used frequency-based F_{ST} for microsatellite data and Φ_{ST} for sequence data. As most of the published studies have not applied corrections to either of these values, we avoided using them in what we calculated from raw data.

F_{ST} is far from a perfect measure of gene flow. Under an island model (in which migration and genetic drift are at equilibrium, and in which migration rates and effective population sizes are equal between all demes), F_{ST} can be used to estimate the number of propagules dispersed from one population to another per generation (Wright 1951). These conditions, however, are rarely met in any species (Whitlock and McCauley 1999), and much less so in marine populations, which are open to immigration of larvae with potentially different genetic constitutions in each generation (Johnson and Black 1984). An additional problem with F_{ST}, particularly for frequency-based data, is that high within-population heterozygosity can create the appearance of no differentiation between populations, even if they share no alleles (Hedrick 2005; Hellberg 2007, 2009). Φ_{ST} can assume negative values if within-population variation is higher than between-population variation. Such negative values are incompatible with the notion that they estimate gene flow. Finally F_{ST} statistics are incapable of distinguishing between recurrent gene flow at low levels among recently separated populations and higher levels of gene flow between anciently separated ones (Hey and Nielsen 2004; Marko and Hart 2012). Despite these problems, F_{ST} is a useful index of genetic differences between populations over and above local variation, differences that increase with genetic isolation, and, unlike more sophisticated statistics of gene flow, it can be applied to all genetic markers. The latter advantage is the main reason why we use it in this chapter. We have arranged the data in tables organized along four axes in which populations can be compared, i.e. between the central and the eastern Pacific, between the outer (oceanic) islands of the eastern Pacific and the mainland, among the outer islands, and among populations distributed along the coast. This, of course, does not imply that the directions in which genes have traveled over the generations are necessarily limited to these axes.

16.3.1 Gene Flow Between the Central and the Eastern Pacific

As few species are shared between the ETP and the central Pacific, the number of studies comparing conspecific populations in the two areas is necessarily limited. Under the island model of Wright (1951), values of $F_{ST} \geq 0.2$ (if calculated from nuclear markers) or ≥ 0.33 (if calculated from mtDNA), which is haploid and maternally inherited) correspond to an estimate of less than one propagule per generation. Accordingly, F_{ST} values that approach these thresholds are held to indicate genetic exchange that cannot overcome the diversifying effects of genetic drift. By this standard, many of the F_{ST} values in Table 16.1 represent a high degree of divergence, indicative of low rates of gene flow over the enormous distances between shallow water habitats in the two oceans. The patterns of genetic exchange, however, differ between species, as would be expected if the EPB is sporadically breached by larvae carried during periods of acceleration of the North Equatorial Counter Current.

Combosch et al. (2008) compared sequences of the internal transcribed spacer (ITS) from the main reef frame-builder of the eastern Pacific, *Pocillopora damicornis,* with sequences from Hawaii and from the western Pacific. Divergence between populations at Hawaii and at Panama was high (Table 16.1) and approximately equal to divergence between populations from the eastern and the western Pacific. Combosch et al. (2008) attributed part of this divergence to introgression of genes from *P. eydouxi* and *P. elegans* into the genome of ETP populations of *P. damicornis,* facilitated by a shift from a brooding reproductive mode in the central and western Pacific to free-spawning of gametes in the ETP (Glynn et al. 1991). This conclusion has been challenged by Pinzón and LaJeunesse (2011), who regard all three morphospecies as a single genetic entity, and consider evidence of apparent hybridization to be artifacts of cloning and sequencing of ITS, due to its representation by multiple copies in the genome (see below). Despite this disagreement, the F_{ST} value between populations of *Pocillopora* on the two sides of the EPB is not large enough to suggest that what is regarded as *P. damicornis* in Hawaii is a different species than the eastern Pacific form. The planulae

Table 16.1 F_{ST} values and approximate distance by sea (in italics) between populations in the eastern and the central Pacific, sampled by various studies

Organism	Reference	Locus	bp or no of loci		F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*
Corals																		
Pocillopora damicornis	Combosch et al. (2008)	5.8S-ITS2	555 bp	Panama (10)	Hawaii (2)													
					0.419	*8400*												
Porites lobata	Forsman et al. (2009) *	18S-5.8S-ITS2	673 bp	Galápagos (15)	Tahiti (9)													
					0.070	*6600*												
				Easter Is. (10)	**0.370**	*4200*												
Porites lobata	Baums et al. (2012)	Microsatellites	12 loci		Midway & NW Islands (84)		Hawaii Central (149)		Hawaii Main (53)		Johnston Atoll (58)		Kingman Rf. (22)		Palmyra (19)		Teraina (10)	
				Clipperton (5)	**0.380**	*6760*	**0.405**	*6200*	**0.406**	*5100*	**0.191**	*6500*	**0.198**	*5860*	**0.117**	*5840*	**0.073**	*5700*
				Darwin, Gal (46)	**0.298**	*8800*	**0.324**	*7900*	**0.315**	*7200*	**0.152**	*8600*	**0.165**	*7800*	**0.116**	*7700*	**0.121**	*7650*
				Wolf, Gal (45)	**0.318**	*8830*	**0.345**	*7930*	**0.342**	*7230*	**0.179**	*8630*	**0.173**	*7830*	**0.124**	*7730*	**0.146**	*7700*
				Marchena, Gal (38)	**0.319**	*8890*	**0.346**	*7990*	**0.344**	*7290*	**0.130**	*8690*	**0.182**	*7890*	**0.110**	*7790*	**0.142**	*7850*
				S. Galápagos (14)	**0.308**	*8940*	**0.336**	*8040*	**0.335**	*7340*	**0.118**	*8740*	**0.151**	*7940*	**0.088**	*7840*	**0.090**	*8000*
				Marino Ballena, CR (32)	**0.319**	*9400*	**0.350**	*8700*	**0.346**	*7800*	**0.161**	*9300*	**0.155**	*8700*	**0.105**	*8650*	**0.120**	*8500*
				Is. Caño., CR (79)	**0.296**	*9400*	**0.323**	*8700*	**0.314**	*7800*	**0.164**	*9300*	**0.154**	8700	**0.116**	*8650*	**0.129**	*8500*
				Golfo Dulce, CR (29)	**0.325**	*9400*	**0.353**	*8700*	**0.350**	*7800*	**0.197**	*9300*	**0.185**	*8700*	**0.150**	*8650*	**0.165**	*8500*
				Is. del Coco (55)	**0.360**	*9220*	**0.388**	*8500*	**0.389**	*7500*	**0.204**	*8900*	**0.189**	*8200*	**0.148**	*8300*	**0.174**	*8100*
				Panama (17)	**0.329**	*9800*	**0.357**	*8900*	**0.359**	*8400*	**0.189**	*9700*	**0.175**	*9000*	**0.138**	*8800*	**0.133**	*8700*
				Ecuador (20)	**0.398**	*10200*	**0.417**	*9600*	**0.442**	*8500*	**0.221**	*9950*	**0.254**	9100	**0.190**	*9080*	**0.221**	*8900*
				Clipperton (5)	Tabuaeran (7)		Kiritimati (49)		Jarvis (12)		Moorea (50)		Hiva Oa (22)		Motane (82)			
					0.107	*5600*	**0.079**	*5400*	**0.110**	*5740*	**0.145**	*5400*	**0.153**	*4000*	**0.151**	*4000*		
				Darwin, Gal (46)	**0.075**	*7500*	**0.106**	*7300*	**0.124**	*7600*	**0.129**	*6600*	**0.132**	*5350*	**0.148**	*5350*		
				Wolf, Gal (45)	**0.073**	*7530*	**0.127**	*7270*	**0.162**	*7630*	**0.133**	*6640*	**0.124**	*5500*	**0.139**	*5500*		
				Marchena, Gal (38)	**0.108**	*7590*	**0.098**	*7430*	**0.098**	*7690*	**0.144**	*6700*	**0.131**	*5500*	**0.138**	*5500*		
				S. Galápagos (14)	**0.059**	*7640*	**0.078**	*7500*	**0.076**	*7740*	**0.119**	*6750*	**0.134**	*5525*	**0.144**	*5525*		
				Marino Ballena, CR (32)	**0.061**	*8400*	**0.098**	*8200*	**0.127**	*8500*	**0.126**	*7800*	**0.138**	*6470*	**0.152**	*6470*		
				Is. Caño., CR (79)	**0.063**	*8400*	**0.124**	*8200*	**0.142**	*8500*	**0.133**	*7800*	**0.126**	*6460*	**0.145**	*6460*		
				Golfo Dulce, CR (29)	**0.096**	*8400*	**0.156**	*8200*	**0.182**	*8500*	**0.158**	*7800*	**0.159**	*6460*	**0.176**	*6460*		
				Is. del Coco (55)	**0.084**	*8000*	**0.150**	*7900*	**0.196**	*8100*	**0.161**	*7300*	**0.170**	*6000*	**0.181**	*6000*		
				Panama (17)	**0.065**	*8600*	**0.132**	*8700*	**0.181**	*8800*	**0.134**	*8200*	**0.154**	*6700*	**0.172**	*6700*		
				Ecuador (20)	**0.220**	*8800*	**0.206**	*8600*	**0.189**	*8800*	**0.187**	*7400*	**0.215**	*6600*	**0.219**	*6600*		

(continued)

Table 16.1 (continued)

Organism	Reference	Locus	bp or no of loci		F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*
Snails																		
Conus ebraeus	Duda and Lessios (2009)	COI	611 bp		Hawaii (17)													
				Clipperton (10)	**0.189**	*5100*												
				Panama (2)	**0.576**	*8400*												
Conus chaldaeus	Duda et al. (2012)				Hawaii (29)													
				Clipperton (9)	0.058	*5100*												
Sea stars																		
Acanthaster planci	Vogler et al. (2008)*	COI	632 bp		Hawaii (2)		Johnston Atol (7)		Kingman Rf. (8)		Moorea (6)							
				Panama (2)	**0.838**	*8400*	**0.775**	*9700*	0.095	*9000*	0.332	*8200*						
				Is. del Coco (13)	**0.906**	*7500*	**0.871**	*8900*	**0.447**	*8200*	**0.669**	*7300*						
Sea urchins																		
Echinothrix diadema	Lessios et al. (1998)	CytB	642 bp		Hawaii (10)		Kiritimati (12)											
				Is. del Coco (15)	0.048	*7500*	−0.032	*7900*										
				Clipperton (6)	−0.061	*5100*	−0.004	*5400*										
Tripneustes depressus/gratilla	Lessios et al. (2003)	COI	640 bp		Marquesas (9)		Kiritimati (10)		Hawaii (10)									
				Clipperton (11)	**0.400**	*3900*	**0.330**	*5400*	**0.380**	*5000*								
				Is. del Coco (10)	**0.410**	*6000*	**0.440**	*7900*	**0.560**	*7500*								
				Panama (4)	**0.380**	*6900*	**0.400**	*8700*	**0.550**	*8400*								
				Galápagos (10)	**0.180**	*5400*	**0.150**	*7400*	**0.230**	*7400*								
				Easter Island (8)	**0.180**	*3700*	0.080	*6000*	**0.110**	*7300*								
Fishes																		
Acanthurus nigricans	Lessios and Robertson (2006)	ATPase8-6	842 bp		Kiritimati (10)		Marquesas (10)											
				Panama (6)	−0.012	*8700*	0.008	*6900*										
				Clipperton (6)	−0.064	*5400*	−0.074	*3900*										
Acanthurus triostegus	Lessios and Robertson (2006)	ATPase8-6	842 bp		Hawaii (5)		Johnston Atoll (4)		Kiritimati (5)		Marquesas (4)							
				Is. del Coco (4)	**0.883**	*7500*	**0.845**	*8900*	0.110	*7900*	0.060	*6000*						
				Revillagigedo (5)	**0.941**	*4700*	**0.915**	*6000*	**0.537**	*5300*	**0.706**	*4400*						
				Panama (5)	**0.898**	*8400*	**0.866**	*9700*	**0.316**	*8700*	0.308	*6900*						
				Clipperton (5)	**0.905**	*5000*	**0.873**	*6400*	**0.328**	*5400*	0.333	*3900*						
Arothron meleagris	Lessios and Robertson (2006)	ATPase8-6	842 bp		Hawaii (3)		Kiritimati (5)		Marquesas (5)									
				Panama (5)	**0.547**	*8400*	**0.625**	*8700*	**0.531**	*6900*								
				Clipperton (5)	0.118	*5000*	0.100	*5400*	0.091	*3900*								
				Easter Is. (3)	−0.001	*7300*	−0.132	*6000*	−0.010	*3700*								
Calotomus carolinus	Lessios and Robertson (2006)	ATPase8-6	842 bp	Revillagigedo (5)	Hawaii (4)		Kiritimati (5)		Marquesas (4)									
					−0.073	*4700*	0.058	*5300*	−0.040	*4400*								
Cantherhinus dumerilii	Lessios and Robertson (2006)	ATPase8-6	842 bp		Hawaii (3)		Kiritimati (5)											
				Clipperton (5)	0.189	*5000*	0.125	*5400*										
Ctenochaetus marginatus	Lessios and Robertson (2006)	ATPase8-6	842 bp		Kiritimati (5)		Marquesas (5)											
				Panama (5)	0.084	*8700*	0.034	*6900*										
				Clipperton (5)	0.050	*5400*	0.032	*3900*										

(continued)

Table 16.1 (continued)

Organism	Reference	Locus	bp or no of loci		F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*
Forcipiger flavissimus	Lessios and Robertson (2006)	ATPase8-6	842 bp		Kiritimati (10)		Marquesas (5)											
				Revillagigedo (3)	0.000	*5300*	−0.133	*4400*										
				Clipperton (5)	−0.064	*5400*	0.000	*3900*										
				Easter Is. (5)	0.041	*6000*	0.083	*3700*										
Heteropriacanthus cruentatus	Lessios and Robertson (2006)	ATPase8-6	842 bp		Hawaii (4)		Kiritimati (10)											
				Revillagigedo (4)	**0.082**	*4700*	**0.299**	*5300*										
				Clipperton (7)	**0.276**	*5000*	**0.343**	*5400*										
				Is. del Coco (11)	**0.288**	*7500*	**0.361**	*7900*										
				Panama (2)	0.065	*8400*	0.212	*8700*										
				Galápagos (9)	**0.122**	*7400*	**0.227**	*7400*										
				Easter Is. (2)	−0.264	*7300*	−0.016	*6000*										
Mulloidichthys vanicolensis	Lessios and Robertson (2006)	ATPase8-6	842 bp		Hawaii (10)		Kiritimati (5)		Marquesas (7)		Moorea (5)							
				Clipperton (9)	**0.306**	*5000*	**0.290**	*5400*	**0.225**	*3900*	0.034	*5400*						
				Easter Is. (5)	0.072	*7300*	0.151	*6000*	−0.010	*3700*	−0.066	*4200*						
Myripristis berndti	Lessios and Robertson (2006)	ATPase8-6	842 bp		Hawaii (8)		Kiritimati (11)		Marquesas (9)									
				Clipperton (6)	0.118	*5000*	**0.376**	*5000*	0.089	*3900*								
				Is. del Coco (3)	0.039	*7500*	−0.180	*7900*	0.226	*6000*								
				Panama (12)	0.022	*8400*	**0.241**	*8700*	0.091	*6900*								
Myripristis berndti	Craig et al. (2007)	CytB	700 bp		Hawaii (147)		Kiritimati (12)		Marquesas (18)		Moorea (18)							
				Clipperton (15)	**0.424**	*5000*	0.083	*5400*	0.333	*3900*	0.189	*5400*						
				Panama (19)	**0.393**	*8400*	0.074	*8700*	0.307	*6900*	0.177	*8200*						
Novaculichthys taeniourus	Lessios and Robertson (2006)	ATPase8-6	842 bp		Hawaii (4)		Kiritimati (6)		Marquesas (5)									
				Clipperton (5)	0.069	*5000*	0.117	*5400*	0.125	*3900*								
				Panama (5)	0.144	*8400*	**0.167**	*8700*	**0.167**	*6900*								
Ostracion meleagris	Lessios and Robertson (2006)	ATPase8-6	842 bp		Hawaii (5)		Kiritimati (4)		Marquesas (5)									
				Panama (4)	0.218	*8400*	−0.013	*8700*	−0.061	*6900*								
				Clipperton (5)	0.375	*5000*	0.305	*5400*	0.167	*3900*								
Scarus ghobban	Lessios and Robertson (2006)	ATPase8-6	842 bp		Kiritimati (10)													
				Panama (10)	**0.169**	*8700*												
Scarus rubroviolaceus	Lessios and Robertson (2006)	ATPase8-6	842 bp		Hawaii (5)		Kiritimati (10)		Marquesas (10)									
				Clipperton (6)	−0.128	*5000*	0.268	*5400*	0.156	*3900*								
				Is. del Coco (3)	−0.154	*7500*	**0.411**	*7900*	0.124	*6000*								
				Panama (10)	−0.028	*8400*	**0.261**	*8700*	0.042	*6900*								

(continued)

Table 16.1 (continued)

Organism	Reference	Locus	bp or no of loci		F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*
Scarus rubroviolaceus	Fitzpatrick et al. (2011)	Microsatellites	15 loci		Marquesas (14)		Big Island (42)		Maui (24)		Oahu (44)							
				Clipperton (6)	**0.170**	*3900*	**0.260**	*4970*	**0.270**	*5140*	**0.250**	*5300*						
				Is. del Coco (51)	**0.140**	*6000*	**0.230**	*7480*	**0.230**	*7610*	**0.220**	*7790*						
				Las Perlas (9)	**0.150**	*6900*	**0.250**	*8530*	**0.270**	*8630*	**0.250**	*8800*						
				Panama coast (7)	**0.170**	*6900*	**0.260**	*8580*	**0.260**	*8680*	**0.250**	*8850*						
Sectator ocyurus	Lessios and Robertson (2006)	ATPase8-6	842 bp		Marquesas (10)													
				Panama (11)	**0.120**	*6900*												
Stethojulis bandanensis	Lessios and Robertson (2006)	ATPase8-6	842 bp		Kiritimati (10)													
				Clipperton (7)	0.030	*5400*												
				Is. del Coco (3)	**0.420**	*7900*												
				Panama (4)	**0.190**	*8700*												
Zanclus cornutus	Lessios and Robertson (2006)	ATPase8-6	842 bp		Hawaii (5)		Kiritimati (4)		Marquesas (5)									
				Revillagigedo (3)	−0.079	*4700*	0.071	*5300*	0.036	*4400*								
				Clipperton (3)	−0.151	*5000*	−0.091	*5400*	−0.084	*3900*								
				Panama (4)	−0.099	*8400*	0.018	*8700*	−0.013	*6900*								

Numbers in parentheses next to locality names indicate sample sizes

Asterisks next to references indicate that F_{ST} was calculated by us from the raw data, because it was not shown in the publication. See Fig. 16.1 for a map of locations. 5.8S-ITS2: ribosomal 5.8S and internal transcribed spacer 2, 18S-5.8S-ITS2: ribosomal 18S-5.8S and internal transcribed spacer 2;COI: Cytochrome Oxidase I, ATPase8-6: mitochondrial ATP synthetase8 and 6, CytB: Cytochrome Oxidase B. Values in *bold*: $p < 0.05$ as determined by 1000 reshufflings of individuals between localities

of *P. damicornis* contain phototrophic *Symbiodinium* endosymbionts, which permit them to generate energy during long-distance dispersal (Baird et al. 2009). Baird et al. (2009) have suggested that species with autotrophic larvae were the only ones capable of recolonizing the eastern Pacific after the formation of the Isthmus of Panama, following the extinction of the earlier western American coral fauna. Presumably, such colonization might have occurred during El Niño events, though there may be constraints in the period of development of zooxanthellate planulae at high temperatures (Yakovleva et al. 2009), which may limit the teleplanic advantages conferred by larval autotrophy.

The study of *Porites* by Forsman et al. (2009) included samples of the massive coral *Porites lobata* from Tahiti and the ETP. As expected, little gene flow was evident in ITS between the central Pacific and Easter Island, one of the most isolated islands in the world (Table 16.1). Surprisingly, however, divergence between populations from Tahiti and the Galápagos was very low, although significant. The low F_{ST} value in this comparison may be due to non-equilibrium conditions arising from a recent influx of larvae. In a study of the same species by Baums et al. (2012), based on 12 microsatellites, samples from Moorea were highly divergent from samples from four localities in the Galápagos Archipelago (Table 16.1). The extensive sampling in this study permits firm conclusions regarding gene flow in this widespread, broadcast spawning coral with autotrophic larvae. Gene flow in *P. lobata* is high within the ETP and within the central Pacific but severely restricted across the EPB, despite occasional low F_{ST} values between some populations from the Galápagos and some of the south central Pacific islands. Principal components and Bayesian STRUCTURE (Pritchard et al. 2000) analysis revealed that colonies at Clipperton Atoll group genetically with those from the central, rather than the eastern Pacific (Baums et al. 2012). Populations at Tabuaeran (Fanning Atoll) and Kiritimati were genetically less differentiated than those of other central Pacific islands from a number of locations in the ETP (Table 16.1).

The only genetic comparisons of transpacific molluscs are for two species of *Conus*. Duda and Lessios (2009) found that populations of *C. ebraeus* at Hawaii were highly differentiated in Cytochrome Oxidase I (COI) from two populations in the ETP (Table 16.1). It appears that Clipperton is a stepping stone to the rest of the ETP, because the sample from this atoll consisted of mitochondrial haplotypes also found in either Panama or Hawaii, plus an additional type otherwise only encountered in Okinawa. These three haplotypes were distantly related, suggesting that they did not evolve in situ, and that the Clipperton population is thus the result of haphazard, infrequent influx of larvae. Analysis of Molecular Variance (AMOVA) found high ($\Phi_{ST} = 0.263$) and significant differentiation across the EPB (Duda and Lessios 2009). In contrast to those of *C. ebraeus*, COI haplotypes of *Conus chaldaeus* from Hawaii and Clipperton were very similar (Table 16.1; Duda et al. 2012).

Data from the corallivorous sea star, *Acanthaster planci,* illustrate that different conclusions about gene flow are sometimes drawn when different genetic markers are used. ETP populations of *Acanthaster* were originally described as a separate species, *A. ellisii,* based on morphological differences (Madsen 1955). Sampled by isozymes, their genetic constitution appeared to be similar to those of the central Pacific, which led Nishida and Lucas (1988) to the conclusion that there was only one species, connected by high gene flow across the EPB. When sequences of the mitochondrial gene COI were subsequently obtained from the entire range of *Acanthaster* (Vogler et al. 2008), they showed that mtDNA of the ETP populations belonged to the same lineage as that of populations from the rest of the Pacific. F_{ST} values between eastern and central Pacific localities, however, are very large in seven out of eight comparisons (Table 16.1), suggesting that there is no gene flow across the EPB.

A number of tropicopolitan sea urchin genera show the deepest divergences between central-west and eastern Pacific extant species (Lessios et al. 1999, 2001; McCartney et al. 2000). There are, however, two exceptions. *Echinothrix* is a genus that, until one of its species, *E. diadema*, was observed at Isla del Coco in 1987, was unknown from the ETP (Lessios et al. 1996). Sequencing of Cytochrome B (CytB) found a higher amount of divergence between populations of *E. diadema* at Isla del Coco and at Clipperton, on the same side of the EPB, than between these populations and those at Kiritimati and at Hawaii (Table 16.1). Lack of divergence between ETP and central Pacific populations is more likely to be the result of recent introduction than of recurrent gene flow. Lessios et al. (1996, 1998) suggested that these populations may have become established during the 1982–1983 El Niño, which also introduced a number of central-west Pacific species of fishes into the ETP (Robertson et al. 2004). The second case of a transpacific echinoid is that of *Tripneustes*. Despite doubts by some taxonomic authorities, *T. gratilla* from the Indo-Pacific and *T. depressus* from the ETP were regarded as separate species. Lessios et al. (2003), however, found that these two putative species shared the same mtDNA clade and are, thus, in all probability conspecific. Sequences of bindin, a nuclear gene responsible for sperm-egg recognition, led to the same conclusion (Zigler and Lessios 2003). Gene flow across the EPB in *Tripneustes* was restricted, as evidenced by high pairwise F_{ST} values between five ETP and three central Pacific locations (Table 16.1).

Fishes are the group that contains the highest number of transpacific species (Robertson et al. 2004), and have thus provided the greatest opportunities for assessing gene flow across the EPB. Data from fishes illustrate great diversity of

evolutionary histories and gene flow rates, diversity that is consistent with "sweepstakes dispersal" between the oceanic regions on either side of the barrier. An isozyme study by Rosenblatt and Waples (1986) indicated little divergence between ETP and Hawaiian conspecific populations of twelve species. More recently, Lessios and Robertson (2006) compared two mitochondrial genes, ATPase8 and ATPase6, in twenty species considered as transpacific on the basis of morphology. Two of these turned out to be anciently separated between oceanic regions, as indicated by reciprocally monophyletic mtDNA clades, and thus should probably be recognized as separate species. Among the other eighteen, F_{ST} between central and eastern Pacific populations ranged from negative values to +0.94. The highest values, indicative of a complete cessation of gene flow, were those between demes of the surgeon fish *Acanthurus triostegus sandvichensis* from Hawaii and Johnston Atoll, and of *A. triostegus triostegus* from the ETP (Table 16.1), but also between *A. triostegus sandvichensis* and *A. triostegus marquesensis* from the Line Islands and the Marquesas (Lessios and Robertson 2006). It would appear, therefore, that there is genetic isolation between the Hawaiian-Johnston subspecies from the other two subspecies. These comparisons illustrate that populations at Hawaii are often isolated not only from those in the ETP, but also from the rest of the Pacific, as Baums et al. (2012) have also found in *Porites lobata*. Thus, data in Table 16.1 in which the central Pacific is represented only by samples from Hawaii may not be indicative of isolation between oceanic regions.

Divergence between populations of *Acanthurus triostegus* from Kiritimati and the Marquesas and from the ETP was generally high, but at the same time suggestive of low levels of gene flow, also evident in the sharing of the most common haplotypes (Lessios and Robertson 2006). Divergence between ETP and central Pacific localities was occasionally high (but inconsistent between comparisons of different populations) in the glass eye, *Heteropriacanthus cruentatus*, in the goatfish *Mulloidichthys vanicolensis* and in the squirrelfish *Myripristis bendti.* Such inconsistencies may well be the result of small sample sizes, because sampling of *M. bendti* CytB of some of the same localities by Craig et al. (2007) did not always produce similar F_{ST} values. Other species, such as the surgeon fish *Acanthurus nigricans*, the parrotfish *Calotomus carolinus,* the surgeon fish *Ctenochaetus marginatus*, the butterflyfish *Forcipiger flavissimus* and the moorish idol *Zanclus cornutus* showed practically no divergence across the EPB (Table 16.1), indicating that there has been either recent or recurrent gene flow. In an analysis of molecular variation (AMOVA) only two of the 18 transpacific species were found to have significantly higher differentiation between oceanic regions than within regions. F_{ST} and AMOVA cannot distinguish between on-going gene flow and recent isolation. For this reason, Lessios and Robertson (2006) employed "IM", an algorithm of Bayesian estimation based on coalescence (Hey and Nielsen 2004), to deduce time of initial separation and degree and direction of subsequent gene flow. Such analyses do not always produce reliable results when they involve a single locus, but they can provide an indication regarding these parameters. Estimated time of initial separation between central and eastern Pacific conspecific populations ranged from 30,000 to 1,000,000 years ago, times more recent than the 3 million year final closure of the Isthmus of Panama (Coates and Obando 1996). These relatively recent estimates indicate that a vicariance scenario, according to which transpacific species are relicts of circumglobal connections that were severed by the rise of the Isthmus (McCoy and Heck 1976; Heck and McCoy 1978), is unlikely. Direction of gene flow deduced by IM was not always from West to East, as might have been expected if the North Equatorial Counter Current were the only means of conveyance. In eight out of the eighteen cases, migration was actually estimated as being higher in the opposite direction. Reconstruction of ancestral genotypes and comparisons of relative genetic diversity suggested that in at least two cases the original range expansion was from the ETP into the central Pacific. Thus, directions of initial colonization and subsequent gene flow do not always coincide.

In conclusion, marine shallow water biota of the ETP is, indeed, isolated from the rest of the world's oceans, but breaching of the EPB is also possible. Such transpacific migrations of larvae most likely are the result of haphazard combinations of factors favorable for migration, such as timing of spawning relative to current speed intensifications, availability of rafting materials, and good fortune in encountering suitable habitat at the end of the dispersal event.

16.3.2 Gene Flow Between the Outer Eastern Pacific Islands and the Mainland Coast

Compared to the distances between the ETP and the central Pacific, those between the American mainland coast and the outer oceanic islands of the ETP (Revillagigedo, Clipperton, Isla del Coco, the Galápagos and Easter Island) are shorter, but far from negligible. The available data on gene flow across this 520–4000 km oceanic divide (Table 16.2) are biased towards showing high rates of migration because, by and large, they come from transpacific species likely to possess traits conducive towards high rates of dispersal.

Data from corals found on at least one island and on the mainland come from studies on *Pocillopora* and *Porites*. In corals, morphological plasticity (Todd 2008) and gene exchange between distinguishable morphs (Willis et al. 2006)

Table 16.2 F_{ST} values and approximate distance by sea (in italics) between populations on the shore and at the outer islands of the eastern Pacific, sampled by various studies

Organism	Reference	Locus	bp or no of loci		F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*
Corals																
Pocillopora type 1	Pinzón and LaJeunesse 2011	Microsatellites	7 loci		Revillagigedo (2)		Clipperton (9)		Galápagos (16)							
				Sea of Cortez (173)	0.121	*700*	0.052	*1600*	0.083	*2200*						
				Banderas Bay, Mex (71)	0.117	*600*	0.021	*1300*	0.089	*2900*						
				Oaxaca, Mexico (15)	0.057	*1700*	0.036	*1700*	0.041	*1800*						
				Panama (22)	0.113	*3800*	0.050	*3400*	0.083	*1500*						
Pocillopora type 3	Pinzón and LaJeunesse (2011)*	Microsatellites	7 loci		Galápagos (3)											
				Panama (26)	**0.239**	*2200*										
Porites lobata	Baums et al. (2012)	Microsatellites	12 loci		Clipperton (5)		Is. delC oco (55)		Darwin, Gal (46)		Wolf, Gal (45)		Marchena, Gal (38)		S. Galápagos (14)	
				Marino Ballena (32)	**0.142**	*2800*	**0.009**	*540*	**0.013**	*1230*	**0.006**	*1240*	**0.046**	*1230*	**0.031**	*1300*
				Is. Caño., CR (79)	**0.173**	*2700*	**0.021**	*520*	**0.018**	*1200*	**0.015**	*1200*	**0.057**	*1200*	**0.057**	*1360*
				Golfo Dulce, CR (29)	**0.190**	*2860*	0.025	*530*	**0.028**	*1230*	**0.014**	*1240*	**0.075**	*1230*	**0.064**	*1300*
				Panama (17)	**0.184**	*3200*	**0.024**	*840*	**0.011**	*1300*	**0.017**	*1300*	**0.082**	*1260*	**0.055**	*1330*
				Ecuador (20)	**0.298**	*3400*	**0.208**	*1000*	**0.145**	*1300*	**0.149**	*1270*	**0.130**	*1100*	**0.150**	*1000*
Sea stars																
Acanthaster planci	Vogler et al. (2008)*	COI	632 bp		Is. del Coco (13)											
				Panama (2)	0.000	*840*										
Sea urchins																
Echinometra vanbrunti	McCartney et al. (2000)*	COI	631		Galápagos (4)											
				Mexico (9)	0.064	*2200*										
				Panama (7)	−0.022	*1500*										
Diadema mexicanum	Lessios et al. (2001)	ATPase8-6	614		Clipperton (12)		Is. del Coco (12)		Galápagos (4)							
				Sea of Cortez (9)	0.000	*1200*	−0.020	*3500*	0.000	*3600*						
				Panama (5)	0.040	*3200*	−0.010	*840*	−0.110	*1500*						
Tripneustes gratilla/depressus	Lessios et al. 2003	COI	640		Clipperton (11)		Is. del Coco (10)		Galápagos (10)		Easter Is.(8)					
				Panama (10)	**0.540**	*3200*	−0.120	*840*	0.170	*1500*	**0.480**	*5100*				
Fishes																
Acanthurus nigricans	Lessios and Robertson (2006)	ATPase8-6	842 bp	Panama (6)	Clipperton (6)											
					−0.082	*3200*										
Acanthurus triostegus	Lessios and Robertson (2006)	ATPase8-6	842 bp		Revillagigedo (5)		Clipperton (5)		Is. del Coco (4)							
				Panama (5)	−0.0006	*3600*	−0.196	*3200*	−0.042	*840*						
Arothron meleagris	Lessios and Robertson (2006)	ATPase8-6	842 bp		Clipperton (5)											
				Panama (5)	0.239	*3200*										
Ctenochaetus marginatus	Lessios and Robertson (2006)	ATPase8-6	842 bp		Clipperton (5)											
				Panama (5)	0.036	*3200*										
Diodon holocanthus	Lessios and Robertson (2006)*	ATPase8-6	842 bp		Revillagigedo (5)		Galápagos (10)		Easter Island (6)							
				Sea or Cortez (20)	0.046	*890*	−0.005	*3700*	**0.442**	*6000*						
				Panama (20)	**0.140**	*3600*	0.036	*1500*	**0.550**	*5100*						

(continued)

Table 16.2 (continued)

Organism	Reference	Locus	bp or no of loci		F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*
Epinephelus labriformis	Craig et al. (2006)	CytB	468 bp		Is. del Coco (11)		Galápagos (35)									
				Lower Cape, Baja Calif. (12)	0.064	*3200*	0.064	*3300*								
				Loreto, Baja California (38)	0.045	*3800*	0.048	*3900*								
				Mazatlan (30)	0.050	*3000*	0.052	*3150*								
				Puerto Vallarta (49)	0.098	*2680*	0.036	*2830*								
				Oaxaca (26)	0.040	*1600*	−0.014	*1850*								
				El Salvador (21)	−0.008	*890*	−0.008	*1500*								
				Panama (46)	0.073	*840*	0.012	*1500*								
Heteropriacanthus cruentatus	Lessios and Robertson (2006)	ATPase8-6	842 bp		Revillagigedo (4)		Clipperton (7)		Is. del Coco (11)		Galápagos (9)					
				Panama (2)	−0.191	*3600*	−0.085	*3200*	−0.085	*840*	−0.141	*1500*				
Myripristis berndti	Lessios and Robertson (2006)	ATPase8-6	842 bp		Clipperton (6)		Is. del Coco (3)									
				Panama (12)	−0.049	*3200*	0.234	*840*								
Myripristis berndti	Craig et al. (2007)	CytB	700 bp		Clipperton (15)											
				Panama (19)	−0.061	*3200*										
Novaculichthys taeniourus	Lessios and Robertson (2006)	ATPase8-6	842 bp		Clipperton (5)											
				Panama (5)	0.063	*3200*										
Ophioblennius steindachneri	Muss et al. (2001)	CybB	630 bp		Clipperton (17)		Galápagos (9)									
				Sea of Cortez (11)	**0.396**	*1700*	?	*3200*								
				Panama (13)	?	*3200*	0.000	*1500*								
Ostracion meleagris	Lessios and Robertson (2006)	ATPase8-6	842 bp		Clipperton (5)											
				Panama (4)	−0.122	*3200*										
Scarus rubroviolaceus	Lessios and Robertson (2006)	ATPase8-6	842 bp		Clipperton (6)		Is. del Coco (3)									
				Panama (10)	−0.083	*3200*	−0.135	*840*								
Scarus rubroviolaceus	Fitzpatrick et al. (2011)	Microsatellites	15 loci		Clipperton (6)		Is. del Coco (51)									
				Panama Coast (7)	**0.080**	*3200*	0.000	*840*								
				Is. Perlas (9)	0.020	*3150*	0.000	*790*								
Stethojulis bandanensis	Lessios and Robertson (2006)	ATPase8-6	842 bp		Clipperton (7)		Is. del Coco (3)									
				Panama (4)	**0.590**	*3200*	**0.376**	*840*								
Zanclus cornutus	Lessios and Robertson (2006)	ATPase8-6	842 bp		Revillagigedo (3)		Clipperton (3)									
				Panama (4)	−0.231	*3600*	−0.180	*3200*								

Numbers in parentheses next to locality names indicate sample sizes

Asterisks next to references indicate that F_{ST} was calculated by us from the raw data, because it was not shown in the publication. COI: Cytochrome Oxidase I, ATPase8-6: mitochondrial ATP synthetase8 and 6, CytB: Cytochrome Oxidase B. Values in *bold*: $p < 0.05$ as determined by 1000 reshufflings of individuals between localities. ?: Sequences necessary for the calculations are not in GenBank

contribute to uncertainties as to which populations belong to the same species. This is particularly true for *Pocillopora* in the ETP. Pinzón and LaJeunesse (2011) sampled individuals of this genus that by morphological criteria belonged to *P. damicornis*, *P. verrucosa*, *P. capitata, P. meandrina*, and *P. eydouxi.* They determined sequences of the internal transcribed spacer 2 (ITS2) and of an unidentified open reading frame in mitochondrial DNA, and they also genotyped seven microsatellite loci. According to all of these markers, *Pocillopora* in the ETP belong to three distinct clades, independently of morphotype. Microsatellites were the only markers sampled in both the islands and the mainland in *Pocillopora* types 1 and 3. They indicate little differentiation between islands and mainland in *Pocillopora* type 1 (the larger values between Revillagigedo and the mainland are based on only two specimens), but substantial divergence between the Galápagos and Panama in *Pocillopora* type 3 (Table 16.2). *Pocillopora* type 2 is endemic to Clipperton. The population of *Porites lobata* at Clipperton sampled with microsatellites by Baums et al. (2012) was strongly differentiated from populations on the mainland (Table 16.2). Populations from Isla del Coco and the Galápagos maintain high rates of gene flow with populations at the mainland, except for the one at the Ecuadorian coast.

There are high rates of genetic exchange between conspecific populations of echinoderms from the islands and the mainland (Table 16.2). *Acanthaster planci* from the ETP, though genetically differentiated from the same species from the central Pacific, was represented by identical COI haplotypes at Isla del Coco and in the Gulf of Chiriquí, Panama. All three species of sea urchins for which data exist were genetically homogeneous between the islands and the coast with one exception. Paradoxically, this exception consists of the transpacific species *Tripneustes gratilla/depressus*, in which populations at Clipperton and Easter Island maintain very little gene flow with populations along western American shores. Other sea urchin species in which larvae from the islands have not established viable populations on the mainland are *Echinothrix diadema*, which has yet to be observed outside Clipperton and Isla del Coco (Lessios et al. 1996), and *Eucidaris galapagensis* at the islands, which is reciprocally monophyletic in COI with respect to the continental *E. thouarsii* (Lessios et al. 1999). It is doubtful that larvae of these species are incapable of crossing between the islands and the continental shore; a more plausible cause of this pattern is that they fail to become established due to ecological factors.

Practically all the existing data regarding fishes at the oceanic islands of the ETP come from transpacific species, and, as expected, indicate high genetic connectivity with coastal populations (Table 16.2). The grouper *Epinephelus labriformis,* though endemic to the ETP, fits the same pattern. The wrasse *Stethojulis bandanensis*, however, shows a high degree of genetic isolation, both at Clipperton and at Isla del Coco. The cosmopolitan puffer *Diodon holocanthus* is the only fish species sampled from both Easter Island and the mainland; like *Tripneustes*, it illustrates that populations at this remote locality are genetically isolated from populations in the rest of the ETP.

Examination of F_{ST} values from species that have been sampled at more than one island suggests that populations at Easter Island and Clipperton Atoll are less connected to populations along the mainland (Table 16.2). Ideally we would like to test statistically whether there is a general trend showing that populations at geographically more remote islands are also genetically more isolated from conspecific coastal populations. As there are few islands, this cannot be done through correlation of genetic and geographic distances; it can be addressed, instead, by comparison of intraspecific divergence between the residents of each island and those of a common locality on the mainland. The only such comparison that provides a sample size sufficient for statistical testing is between populations from Panama and Clipperton, on the one hand, and between Panama and Isla del Coco, on the other. We compared F_{ST} values of the same nine species sampled in all three localities paired by genetic marker. The results indicate that, as expected from relative geographic distances, genetic isolation of populations at Clipperton from those at Panama was significantly higher than isolation of the same nine species at Isla del Coco (Wilcoxon paired sample test, $p < 0.05$).

16.3.3 Gene Flow Between the Outer Eastern Pacific Islands

Although genes are not necessarily transferred directly between the outer islands (mainland populations may act as stepping stones) it is useful to ask how genetically different island populations are from each other. The general picture in comparisons between island populations of various species (Table 16.3) is almost identical to the one presented by comparisons between the islands and the mainland (Table 16.2). There is high genetic connectivity between conspecific residents of most islands, except for those at Easter Island, in which all but one species show large and significant values of F_{ST} in comparisons with populations from all other islands. Clipperton Atoll shows a mixed pattern. Populations of *Porites lobata*, *Tripneustes gratilla,* the blenny *Ophioblennius steindachneri* and the wrasse *Stethojulis bandanensis* are very different from populations from all other islands. Populations of all other species, however, show high rates of gene flow.

16.3.4 Gene Flow Along the Coast of the Eastern Pacific

We would expect to observe the highest rates of gene flow along the American shores of the ETP. This is generally the case. Pinzón and LaJeunesse (2011) found no significant restrictions of gene flow in microsatellites of *Pocillopora* "type 1" in populations spanning approximately 4200 km from the Sea of Cortez to Panama (Table 16.4). Combosch and Vollmer (2011), on the other hand, reported that their microsatellite data of *Pocillopora damicornis* show significant structure at a much smaller scale on the Panamanian coast. This structure is not evident in F_{ST} values, in which only two comparisons between populations are larger than 0.073 (Table 16.4). It is somewhat more evident in R_{ST} [an F_{ST} equivalent that takes the step-wise mutation pattern expected from microsatellites into account (Slatkin 1995)]. AMOVA analysis found significant, but small variation between individual populations and also between populations that were grouped in three areas along the Panamanian coast. High rates of gene flow were found between microsatellite frequencies of most coastal populations of *Porites lobata* by Baums et al. (2012). One exception was the population at Ecuador, which is different from all populations at Costa Rica, though not from the one at Panama (Table 16.4).

In four species of sea urchins, genetic connectivity in mtDNA along the coast is generally high from Mexico to Panama (Table 16.4). As in *Porites*, the population of the echinoid *Arbacia stellata* in the southernmost periphery of the species is highly differentiated from those in the species' center of distribution.

Among the fishes, those with transpacific ranges, *Diodon holocanthus* and *Scarus rubroviolaceus,* show no genetic structure (Table 16.4). This is hardly surprising in the case of the latter, because both sampling localities of this species are situated close to each other in the Bay of Panama, but in the case of *Diodon* they lie 4000 km apart on either side of the Central American Gap. *Epinephelus labriformis* also shows high genetic connectivity over long spans of the coast from Baja California to Panama. The case of the three species of the grunt *Anisotremus* studied by Bernardi et al. (2008) is somewhat surprising. *Anisotremus interruptus* and *Anisotremus taeniatus*, species usually found only in the proximity of hard bottoms, show no significant structure in either mitochondrial CytB or the nuclear S7 region over 4000 km of coastline. *Anisotremus dovii*, on the other hand, even though it prefers sandy and muddy bottoms (and should thus be more continuously distributed along the coast) appears to experience marked restrictions in gene flow between Mexico and Panama, at least in CytB. Only one out of the total twelve CytB sequences sampled in this species is shared between the two locations, which accounts for the high and significant F_{ST} value.

In contrast to the pattern of high gene flow along most of the tropical west coast of America, genetic connectivity within the Sea of Cortez can be quite low in a number of species. Gene flow in the ovoviviparous sea horse *Hippocampus ingens* was high among all populations sampled from Mexico to Peru by Saarman et al. (2010) except for one; the mitochondrial control region of the population from Guaymas in the Sea of Cortez was highly differentiated from that of every other population (Table 16.4). Sequences of the mitochondrial control region of the scarletfin blenny *Coralliozetus micropes* were reciprocally monophyletic between upper and lower Gulf regions (Riginos 2005), a level of divergence that is reflected in the F_{ST} values in Table 16.4. This is also the case in the Cortez triplefin *Axoclinus nigricaudus* (Table 16.4) and in the Gulf of California endemic sand bass *Paralabrax maculatofasciatus* (Stepien et al. 2001; Riginos 2005), but not in the redside blenny *Malacoctenus hubbsi* (Table 16.4). These genetic breaks were attributed by Riginos (2005) to a hypothetical Pleistocene deep water break of the Baja California Peninsula that bisected habitats of hard bottom fishes, as it did of terrestrial mammals and reptiles. IM analyses yielding similar times of divergence between upper and lower Gulf populations of five fish species supported the hypothesis that a historical barrier was responsible for present-day isolation patterns, but environmental differences might also be responsible (Riginos 2005).

Along a linear coast, such as that of the ETP, one would expect a pattern of isolation by distance (Wright 1943), as one population acts as a stepping stone for the dispersal of genes towards others down the line. To determine whether this was the case, we analyzed the data of all species in Table 16.4 for which more than three localities were sampled. We calculated correlations between F_{ST} values and geographical distance along the coast, using Mantel (1967) tests to estimate probabilities of the correlation coefficient. For this analysis, negative values of F_{ST} were replaced by zero, because negative gene flow has no meaning (Hudson et al. 1992). Combosch and Vollmer (2011) found no correlation between genetic differentiation and distance in *Pocillopora damicornis* over the limited geographic extent of their samples, but our analysis of populations from Mexico to Panama of the data of Pinzón and LaJeunesse (2011) shows that such a correlation does exist in *Pocillopora* type 1 ($r = 0.349$, $p < 0.005$). Baums et al. (2012) found a strong isolation by distance trend in *Porites lobata* in the ETP, including the outer islands. The correlation remains significant when only coastal localities are considered ($r = 0.856$, $0.01 < p < 0.025$). In *Epinephelus labriformis*, most F_{ST} values were negative (and replaced by 0), which resulted in a slight, but still significant correlation with geographic distance ($r = 0.051$, $0.01 < p < 0.025$).

Table 16.3 F_{ST} values and approximate distance by sea (in italics) between populations at the outer islands of the eastern Pacific, sampled by various studies

Organism	Reference	Locus	bp or no of loci		F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*
Corals														
Pocillopora type 1	Pinzón and LaJeunesse (2011)	Microsatellites	7 loci		Clipperton (9)		Galápagos (16)							
				Revillagigedo (2)	0.079	*950*	0.176	*3000*						
				Clipperton (9)			0.058	*2100*						
Porites lobata	Forsman et al. (2009)*	18S-5.8S-ITS2	673 bp		Easter Island (10)									
				Galápagos (15)	**0.258**	*3500*								
Porites lobata	Baums et al. (2012)	Microsatellites	12 loci		Is. del Coco (55)		Darwin, Gal (46)		Wolf, Gal (45)		Marchena, Gal (38)		S. Galápagos (14)	
				Clipperton (5)	**0.212**	*2500*	**0.134**	*2100*	**0.160**	*2100*	**0.150**	*2350*	**0.089**	*2500*
				Is. del Coco (55)			**0.048**	*700*	**0.032**	*700*	**0.086**	*690*	**0.087**	*815*
				Darwin, Gal (46)					**0.012**	*37*	**0.030**	*217*	**0.007**	*420*
				Wolf, Gal (45)							**0.048**	*180*	**0.045**	*322*
				Marchena, Gal (38)									**0.026**	*197*
Sea urchins														
Echinothrix diadema	Lessios et al. (1998)	CytB	642 bp		Clipperton (6)									
				Is. del Coco (15)	−0.044	*2500*								
Eucidaris galapagensis	Lessios et al. (1999)	COI	640 bp		Galápagos (7)									
				Is. del Coco (6)	−0.060	*750*								
Diadema mexicanum	Lessios et al. (2001)	ATPase8-6	642 bp		Is. del Coco (12)		Galápagos (4)							
				Clipperton (11)	−0.010	*2500*	−0.130	*2300*						
Tripneustes gratilla/depressus	Lessios et al. (2003)	COI	640 bp		Is. del Coco (10)		Galápagos (10)		Easter Island (8)					
				Clipperton (11)	**0.600**	*2500*	0.110	*2300*	**0.400**	*4100*				
				Is. del Coco (10)			0.250	*750*	**0.490**	*4300*				
				Galápagos (10)					**0.190**	*3500*				
Fishes														
Acanthurus triostegus	Lessios and Robertson (2006)	ATPase8-6	842 bp		Clipperton (5)		Is. del Coco (4)							
				Revillagigedo (5)	0.000	*950*	0.358	*3000*						
				Clipperton (5)			−0.042	*2500*						
Arothron meleagris	Lessios and Robertson (2006)	ATPase8-6	842 bp		Easter Is. (3)									
				Clipperton (5)	0.032	*4100*								
Diodon holocanthus	Lessios and Robertson (2006)	ATPase8-6	842 bp		Galápagos (10)		Easter Isl. (6)							
				Revillagigedo (5)	**0.022**	*3000*	**0.325**	*5000*						
				Galápagos (10)			**0.470**	*3500*						
Epinephelus labriformis	Craig et al. (2006)	CytB	468 bp		Galápagos (35)									
				Is. del Coco (11)	0.045	*750*								
Forcipiger flavissimus	Lessios and Robertson (2006)	ATPase8-6	842 bp		Revillagigedo (3)		Easter Is. (5)							
				Clipperton (5)	0.000	*950*	0.250	*4100*						
				Revillagigedo (3)			0.118	*5000*						

(continued)

Table 16.3 (continued)

Organism	Reference	Locus	bp or no of loci		F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*	F_{ST}	*Distance (km)*
Heteropriacanthus cruentatus	Lessios and Robertson (2006)	ATPase8-6	842 bp		Clipperton (7)		Is. del Coco (11)		Galápagos (9)					
				Revillagigedo (4)	−0.075	*950*	−0.117	*3000*	−0.031	*3000*				
				Clipperton (7)			−0.117	*2500*	0.004	*2300*				
				Is. del Coco (11)					0.048	*750*				
Mulloidichthys vanicolensis	Lessios and Robertson (2006)	ATPase8-6	842 bp		Easter Island (5)									
				Clipperton (9)	**0.179**	*4100*								
Myripristis berndti	Lessios and Robertson (2006)	ATPase8-6	842 bp		Is. del Coco (3)									
				Clipperton (6)	0.360	*2500*								
Ophioblennius steindachneri	Muss et al. (2001)	CytB	658 bp		Galápagos (9)									
				Clipperton (17)	**0.379**	*2300*								
Scarus rubroviolaceus	Lessios and Robertson (2006)	ATPase8-6	842 bp		Is. del Coco (3)									
				Clipperton (6)	−0.193	*2500*								
Stethojulis bandanensis	Lessios and Robertson (2006)	ATPase8-6	842 bp		Clipperton (7)									
				Is. del Coco (3)	**0.783**	*2500*								
Zanclus cornutus	Lessios and Robertson (2006)	ATPase8-6	842 bp		Revillagigedo (3)									
				Clipperton (3)	−0.250	*950*								

Numbers in parentheses next to locality names indicate sample sizes

Asterisks next to references indicate that F_{ST} was calculated by us from the raw data, because it was not shown in the publication. 18S-5.8S-ITS2: ribosomal 18S-5.8S and internal transcribed spacer 2, COI: Cytochrome Oxidase I, ATPase8-6: mitochondrial ATP synthetase8 and 6, CytB: Cytochrome Oxidase B. Values in *bold*: $p < 0.05$ as determined by 1000 reshufflings of individuals between localities

Table 16.4 F_{ST} values and approximate distance by sea (in italics) between populations sampled by various studies along the coast of the tropical eastern Pacific

Organism	Reference	Locus	bp or no of loci		F_{ST}	*Distance* (km)	F_{ST}	*Distance* (km)	F_{ST}	*Distance* (km)	F_{ST}	*Distance* (km)	F_{ST}	*Distance* (km)	F_{ST}	*Distance* (km)	F_{ST}	*Distance* (km)	F_{ST}	*Distance* (km)
Corals																				
Pocillopora "type 1"	Pinzón and LaJeunesse (2011)	microsatellites	7 loci		Mexico															
					Banderas Bay (71)		Oaxalaca (15)		Panama (22)											
				Sea of Cortez (173)	0.080	*600*	0.020	*2000*	0.081	*4200*										
				Banderas Bay (71)			0.032	*1600*	0.075	*3500*										
				Oaxaca (15)					0.039	*2000*										
Pocillopora damicornis	Combosch and Vollmer (2011)	microsatellites	6 loci		Gulf of Chiriqui				Azuero Peninsula						Bay of Panama					
					N. of Is. Coiba (21)		B, Damas (30)		Is. C. Afuera (18)		Achotines (30)		Is. Iguana (23)		Taboga (21)		Saboga (22)		Contadora (25)	
				Uva, G. Chiriqui (23)	0.035	*30*	**0.065**	*54*	0.033	*116*	0.015	*250*	0.039	*300*	**0.087**	*420*	0.019	*415*	0.025	*416*
				N. of Is. Coiba (21)			**0.073**	*20*	**0.229**	*100*	0.001	*200*	**0.048**	*240*	**0.072**	*390*	**0.061**	*400*	**0.039**	*401*
				Bahia Damas, Is. Coiba (30)					0.047	*85*	**0.069**	*180*	**0.045**	*230*	**0.065**	*360*	**0.053**	*370*	**0.060**	*371*
				Is. Canal de Afuera. G. of Chiriqui (18)							0.037	*120*	0.025	*160*	**0.064**	*400*	0.015	*320*	**0.040**	*321*
				Achotines, Azuero Pen. (30)									0.029	*41*	**0.071**	*180*	0.040	*185*	0.031	*186*
				Is. Iguana, B. of Panama (23)											**0.069**	*140*	0.022	*150*	**0.033**	*151*
				Taboga, Bay of Panama (21)													**0.046**	*54*	0.030	*57*
				Saboga, Is. Perlas (22)															**0.000**	*1*
Porites lobata	Baums et al. (2012)	microsatellites	12 loci		Costa Rica															
					Is. Caño (79)		Golfo Dulce (29)		Panama (17)		Ecuador (20)									
				Marino Ballena (32)	**0.003**	*119*	0.008	*150*	**0.008**	*320*	**0.154**	*1020*								
				Is. Caño (79)			**0.006**	*242*	**0.015**	*400*	**0.156**	*1150*								
				Golfo Dulce (29)					0.016	*590*	**0.167**	*1000*								
				Panama (17)							**0.001**	770								
Sea urchins																				
Arbacia stellata	Lessios et al. (2012)	COI	660 bp		Panama (9)		Peru (4)													
				El Salvador (11)	0.179	*1300*	0.108	*1700*												
				Panama (9)			**0.373**	*860*												
Diadema mexicanum	Lessios et al. (2001)	ATPase8-6	614 bp		Panama (5)															
				Mexico (9)	0.020	*4000*														
Echinometra vanbrunti	McCartney et al. (2000)*	COI	631 bp		Panama (7)															
				Mexico (5)	−0.095	*4000*														
Eucidaris thouarsi	Lessios et al. (1999)	COI	640 bp		Panama (4)															
				Mexico (6)	−0.030	*4000*														

(continued)

Table 16.4 (continued)

Organism	Reference	Locus	bp or no of loci		F_{ST}	*Distance* (km)	F_{ST}	*Distance* (km)	F_{ST}	*Distance* (km)	F_{ST}	*Distance* (km)	F_{ST}	*Distance* (km)	F_{ST}	*Distance* (km)	F_{ST}	*Distance* (km)	F_{ST}	*Distance* (km)
Fishes																				
Anisotremus dovii	Bernardi et al. (2008)*	S7	531 bp		Panama (4)															
				Mexico (8)	0.166	*4000*														
		CytB	692 bp	Mexico (8)	**0.304**	*4000*														
Anisotremus interruptus	Bernardi et al. (2008)*	S7	529 bp		Costa Rica (5)		Panama (5)													
				Mexico (6)	0.281	*2600*	−0.014	*4000*												
				Costa Rica (5)			0.091	*300*												
		CytB	750 bp		Costa Rica (5)		Panama (6)													
				Mexico (6)	−0.034	*2600*	0.076	*4000*												
				Costa Rica (5)			0.056	*300*												
Anisotremus taeniatus	Bernardi et al. (2008)*	S7	529 bp		Costa Rica (4)		Panama (7)													
				Mexico (2)	0.000	*2600*	−0.316	*4000*												
				Costa Rica (4)			−0.098	*300*												
		CytB	728 bp		Costa Rica (4)		Panama (8)													
				Mexico (2)	−0.264	*2600*	−0.214	*4000*												
				Costa Rica (4)			−0.095	*300*												
Axoclinus nigricaudus	Riginos (2005)*	dloop	206 bp		Bahia Kino (10)															
				Bahia Los Angeles (10)	**0.350**	*154*														
Coralliozetus micropes	Riginos (2005)*	dloop	206 bp		B. S. L. Gonzaga (6)		Isla Monserat (5)		Punta Chivato (5)											
				Bahia Los Angeles (9)	0.030	*260*	**0.689**	*700*	**0.730**	*260*										
				Bahia San Luis Gonzaga (6)			**0.795**	*660*	**0.838**	*460*										
				Isla Monserat (5)					−0.069	*260*										
Diodon holocanthus	Lessios and Robertson (2006)	ATPase8-6	842 bp		Panama (20)															
				Sea of Cortez (20)	−0.004	*4000*														
Epinephelus labriformis	Craig et al. (2006)	CytB	468 bp		Lower Cape (12)		Mazatlan (30)		Puerto Vallarta (49)		Oaxaca (26)		El Salvador (21)		Panama (46)					
				Loreto, Baja California (38)	−0.018	*400*	−0.001	*590*	−0.006	*800*	0.015	*1800*	0.001	*2500*	−0.011	*4000*				
				Lower Cape, Baja California (12)			−0.020	*270*	−0.013	*490*	0.017	*1500*	−0.003	*2400*	−0.004	*3800*				
				Mazatlan (30)					0.000	*300*	0.015	*1400*	0.014	*2300*	0.006	*3700*				
				Puerto Vallarta (49)							0.008	*1200*	0.014	*2000*	−0.011	*3400*				
				Oaxaca (26)									−0.017	*800*	−0.008	*2200*				
				El Salvador (21)											−0.007	*1500*				

(continued)

Table 16.4 (continued)

Organism	Reference	Locus	bp or no of loci		F_{ST}	*Distance* (km)	F_{ST}	*Distance* (km)	F_{ST}	*Distance* (km)	F_{ST}	*Distance* (km)	F_{ST}	*Distance* (km)	F_{ST}	*Distance* (km)	F_{ST}	*Distance* (km)	F_{ST}	*Distance* (km)
Hippocampus ingens	Saarman et al. (2010)	dloop	359 bp		Mexico						Ecuador				Peru					
					Mazatlan (6)		Salina Cruz (5)		Guatemala (30)		Manta/Salango (17)		Guayaquil (6)		Chiclayo (7)		Pisco (4)			
				Sea of Cortez (10)	**0.168**	*600*	**0.134**	*2000*	**0.210**	*2500*	**0.355**	*4300*	**0.263**	*4300*	**0.342**	*5200*	**0.328**	*6000*		
				Mazatlan (6)			−0.099	*1700*	−0.041	*2100*	0.041	*3900*	−0.108	*4200*	−0.024	*4700*	0.002	*5300*		
				Salina Cruz (5)					−0.030	*420*	0.008	*2300*	0.000	*2700*	0.062	*3100*	0.030	*3900*		
				Guatemala (30)							0.022	*2000*	−0.061	*2300*	0.043	*2600*	0.007	*3500*		
				Manta/Salango (17)									0.097	*330*	0.034	*770*	0.028	*1600*		
				Guayaquil (6)											−0.079	*670*	−0.022	*1500*		
				Chiclayo/Sechura (7)													−0.067	*870*		
Malacoctenus hubbsi	Riginos (2005)*	dloop	206 bp		Bahia Kino (10)															
				Bahia Los Angeles (10)	0.080	*154*														
Scarus rubroviolaceus	Fitzpatrick et al. (2011)	microsatellites	15 loci		Perlas Is. (9)															
				Panama coast (7)	0.000	*58*														

Numbers in parentheses next to locality names indicate sample sizes

Asterisks next to references indicate that F_{ST} was calculated by us from the raw data, because it was not shown in the publication. COI: Cytochrome Oxidase I, ATPase8-6: mitochondrial ATP synthetase8 and 6, CytB: Cytochrome Oxidase B, S7: ribosomal protein S7, dloop: mitochondrial control region. Values in *bold*: $p < 0.05$ as determined by 1000 reshufflings of individuals between localities

Saarman et al. (2010) reported no significant correlation between F_{ST} and distance in *Hippocampus ingens*, which would have been surprising given that sea horses are sedentary and have no larval stage. Our re-analysis of their F_{ST} data, however, shows that the expected relationship does, in fact, exist ($r = 0.441$, $0.01 < p < 0.025$). The difference between their analysis and ours is not only that they (presumably) used negative F_{ST} values, but also because some of the geographic distances they listed in their Table 4 cannot be correct because they show Peru situated north of Ecuador. Thus, the available data are consistent with a general trend of isolation by distance along the ETP coast. Such a correlation, however, is not necessarily the result of genes dispersing via stepping stones, because populations on either side of a barrier are also more distant from each other than populations on the same side of the barrier. Riginos and Nachman (2001), using partial Mantel tests, found that genetic divergence of populations of *Axoclinus nigricaudus* in the Sea of Cortez was caused not only by the distance between localities, but also by a genetic break between the upper and central parts of the Gulf of California.

In conclusion, gene flow rates among populations along the ETP coast are high, at least between central Mexico and the Panamanian coast. There is no evident genetic break resulting from the Central American Gap in any of the sampled species. Populations at the northernmost and the southernmost peripheries of the ETP appear to be genetically more isolated, possibly as the result of historical barriers, or possibly due to ecological conditions unfavorable to tropical species. A trend of isolation by distance is evident in corals and fishes.

16.4 General Conclusions and Future Prospects

The compilation of existing data regarding gene flow of coral reef organisms in the ETP suggests that gene flow within this oceanic region is generally high; this is certainly true along the coast, except perhaps for the northernmost and southernmost limits of tropical species ranges. Documented genetic connectivity is also generally high between populations at the outer ETP islands <1000 km offshore and the mainland, and (in some transpacific species) between the residents of islands in the central Pacific and ETP. These generalizations, however, need to be tempered by the realization that all coral reef organisms in which genetic structure has been sampled to date, except for sea horses, possess planktonic larvae. Large genetic differences among closely situated populations of the same morph of the ovoviviparous intertidal isopod *Excirolana braziliensis* were found in both isozymes (Lessios and Weinberg 1993, 1994) and in mtDNA (Sponer and Lessios 2009). The same may well turn out to be true for coral reef organisms with limited means of dispersal. It would be of interest to obtain data from ascidians, bryozoans, and other organisms with abbreviated larval phases to see how they compare with data from organisms with planktonic larvae. It is also important to sample genetically more species of corals, the ecological engineers responsible for creating the habitats in which other coral reef organisms live. The isolation of the ETP from other oceanic regions, the remote location of its outer islands, and the simple spatial arrangement of its coastal populations, can produce interesting contrasts in patterns of gene flow. Such data can address general population genetic theory in addition to producing information regarding the natural history of the organisms in this ocean.

Acknowledgements We thank G. Bernardi, S. Coppard, L. Geyer, A. Hiller, P.W. Glynn, and C. Riginos for comments on the manuscript.

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