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research paper

Evaluating edge-of-range genetic patterns for tropical echinoderms, *Acanthaster planci* and *Tripneustes gratilla*, of the Kermadec Islands, southwest Pacific

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ABSTRACT.—Edge-of-range populations are often typified by patterns of low genetic diversity and high genetic differentiation relative to populations within the core of a species range. The "core-periphery hypothesis," also known as the "central-marginal hypothesis," predicts that these genetic patterns at the edge-of-range are a consequence of reduced population size and connectivity toward a species range periphery. It is unclear, however, how these expectations relate to high dispersal marine species that can conceivably maintain high abundance and high connectivity at their range edge. In the present study, we characterize the genetic patterns of two tropical echinoderm populations in the Kermadec Islands, the edge of their southwest Pacific range, and compare these genetic patterns to those from populations throughout their east Indian and Pacific ranges. We find that the populations of both *Acanthaster planci* (Linnaeus, 1758) and *Tripneustes gratilla* (Linnaeus, 1758) are represented by a single haplotype at the Kermadec Islands (based on mitochondrial cytochrome oxidase C subunit I). Such low genetic diversity concurs with the expectations of the "core-periphery hypothesis." Furthermore, the haplotypic composition of both populations suggests they have been founded by a small number of colonists with little subsequent immigration. Thus, local reproduction and self-recruitment appear to maintain these populations despite the ecologically marginal conditions of the Kermadec Islands for these tropical species. Understanding rates of self-recruitment vs reliance on connectivity with populations outside of the Kermadec Islands has implications for the persistence of these populations and range stability of these echinoderm species.

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Population attributes are expected to differ according to range position. Differences in abundance, reproduction, and dispersal (connectivity) can often be observed across a species range, and over evolutionary timescales these population attributes are expected to lead to predictable neutral genetic patterns across their range. For

example, the "core-periphery hypothesis" (hereafter CPH) predicts that populations at the periphery of a species range will have lower genetic diversity and be more genetically differentiated as a consequence of smaller effective population sizes (as predicted by the "abundant-center hypothesis") and lower connectivity than core populations (Eckert et al. 2008). Although support for the CPH has been equivocal in the empirical literature (reviewed in Eckert et al. 2008), most tests have focused on terrestrial organisms and thus this theory's relevance in marine systems remains unclear.

Some marine genetic studies support the applicability of the CPH (e.g., urchins, Palumbi et al. 1997; coral, Ayre and Hughes 2004; algae, Faugeron et al. 2004); however, several do not (detailed below). There are many reasons why range-wide genetic patterns of marine organisms may differ from terrestrial organisms (Liggins et al. 2013). Most notably, marine species often have high dispersal potential influencing their ability to colonize, expand their ranges, and maintain connectivity among established populations (Kinlan and Gaines 2003, Mora et al. 2011). Consequently, population abundance remains high toward the range edge of many marine species (e.g., flatfish, Leggett and Frank 1997; mole crab, Defeo and Cardoso 2004; intertidal limpet, Gilman 2005) and genetic diversity as well as connectivity can be maintained in peripheral populations by immigration, contradicting the expectations of the CPH (e.g., barnacle, Dawson et al. 2010; coral, Nakajima et al. 2010; coral reef fishes, Bay and Caley 2011).

For any population to establish and persist, it must rely on some combination of immigration and self-recruitment (Table 1). Peripheral populations are often ecologically marginal (Lesica and Allendorf 1995) and thus by definition have limited reproduction and are heavily reliant on immigration (Barton 2001). For high dispersal marine species, there is the very real possibility that some peripheral populations are sustained by immigration and that self-recruitment is insufficient for long term population persistence. In the extreme, high levels of immigration into peripheral populations may cause levels of genetic diversity to be similar to those of core populations, contradicting the expected pattern of decreased diversity for peripheral populations under the CPH (see "Migration load" scenario in Table 1). Furthermore, frequent immigration and low levels of reproduction and self-recruitment could lead peripheral populations to be less genetically differentiated than core populations also contradicting the CPH (see "Meta-population" scenario in Table 1). Thus, the influence of immigration and local reproductive success, often determined by ecological circumstances, can promote patterns of genetic diversity and differentiation that do not conform to the expectations for a peripheral population according to the CPH.

Here we focus on the Kermadec Islands, a remote chain of eleven volcanic islands (29°15′S–31°21′S and 177°55′W–178°48′W), between Tonga and New Zealand in the southwest Pacific. The islands are geologically young, having originated only 1.8–3 Ma and provide marginal habitat for tropical marine species (Watt 1975). Despite falling within New Zealand's largest marine reserve (Gardner et al. 2006), the transitional coral-algal community of the islands is relatively understudied. Genetic patterns and affinities of the islands' marine biota have mostly been addressed above the species level (e.g., algae, Heesch et al. 2009; coral symbionts, Wicks et al. 2010b), or for subtropical (neritid snail, Spencer et al. 2007) and endemic species (limpets, Wood and Gardner 2007). Recent research has highlighted the diversity and abundance of the tropical marine fauna (Richards and Liggins in press), yet there has

Table 1. Predicted genetic patterns of peripheral *Acanthaster planci* and *Tripneustes gratilla* populations at the Kermadec Islands under extreme competing scenarios. Intermediate scenarios and predictions are possible (i.e., multiple colonization events, low levels of ongoing immigration).

		IMMIGRATION	
		Rare	Frequent
SELF-RECRUITMENT	Minimal	*Ephemeral population – neither immigration or self-recruitment are enough to sustain a population* (not applicable to the current investigation)	*Meta-population – peripheral population relies on immigration for persistence* Genetic diversity – low compared to core populations Genetic differentiation – may differ from core populations Genetic novelty – none
	High	*Colonization – peripheral population is founded by a small group of colonists and is self-sustaining* Genetic diversity – low compared to core populations Genetic differentiation – likely to differ from core populations Genetic novelty – possible especially if colonization is old	*Migration load – peripheral population is maintained by high gene flow between immigrants and local individuals* Genetic diversity – similar to core populations Genetic differentiation – similar to core populations Genetic novelty – none

been little population genetic investigation of resident tropical taxa (but see Vogler et al. 2013, discussed below). Here, we investigate how this island group's characteristics (peripheral and ecologically marginal) influence genetic patterns in two tropical echinoderms: the crown-of-thorns starfish, *Acanthaster planci* (Linnaeus, 1758); and the collector urchin, *Tripneustes gratilla* (Linnaeus, 1758).

Acanthaster planci and *T. gratilla* are common in tropical, shallow reef habitat throughout the Indian and Pacific oceans. *Acanthaster planci* occurs as far south as Lord Howe Island (31°32′S) and the Kermadec Islands (Macauley Island, 30°14′S; Francis et al. 1987). In contrast, *T. gratilla* has been recorded in small numbers in the northeast of mainland New Zealand (C Duffy, New Zealand Department of Conservation, pers comm). Both species broadcast spawn and have high dispersal potential. The pelagic larvae of *T. gratilla* are known to disperse for at least 18 d (Mortensen 1937), and those of *A. planci* typically survive up to 28 d in the pelagic environment (Yamaguchi 1973). Since the first published records of *A. planci* (McKnight 1978) and *T. gratilla* [Farquhar 1897; formerly *Tripneustes variegatus* (Leske, 1778)] at the Kermadec Islands, both species have been repeatedly recorded at the island group (*A. planci*: Schiel et al. 1986, Francis et al. 1987, Cole et al. 1992, Brook 1999, Gardner et al. 2006; *T. gratilla*: McKnight 1968, Schiel et al. 1986, Cole et al. 1992, Gardner et al. 2006), including observations of new recruits (Richards and Liggins in press). *Acanthaster planci* and *T. gratilla* are particularly abundant around the islets of Raoul Island (the northernmost island of the Kermadec Islands); the density of *A. planci* was recently estimated to be >80 individuals per hectare (Richards and Liggins in press) and *T. gratilla* was present in an estimated similar abundance (L Liggins unpubl data). Such densities are typical of both *A. planci* (reviewed in Birkeland and Lucas 1990) and *T. gratilla* (reviewed in Lawrence and Agatsuma 2001) in the core of their ranges. The high dispersal potential of these species and their abundance within a peripheral population suggest the CPH may not apply to the Kermadec populations of *T. gratilla* and *A. planci*. Furthermore, the marginal environment of the Kermadec Islands may cause these populations of

tropical echinoderms to have poor reproduction and self-recruitment, acting as a demographic "sink," which would also disrupt typical expectations for an edge-of-range population under the CPH.

Here we examine genetic patterns of *A. planci* and *T. gratilla* from the Kermadec Islands and compare these observations against the predictions of the CPH. In the context of the Kermadec Islands, the relative influence of immigration (i.e., dispersal to, and survival in, the Kermadec population) and self-recruitment is expected to leave predictable patterns of genetic diversity, genetic differentiation, and genetic novelty (Table 1). A scenario of "Colonization" whereby immigration is rare and self-recruitment is high would result in a population with the expected patterns of the CPH. However, low self-recruitment ("Meta-population" scenario) or high immigration ("Migration load" scenario, Table 1) could cause genetic patterns to deviate from CPH expectations.

Methods

The study region included the known range of the Pacific clade of *A. planci* (Vogler et al. 2008; herein referred to as *A. planci*) and the corresponding range of *T. gratilla* so that the genetic patterns of the Kermadec Islands could be put into a broader east Indian-Pacific ocean context (Fig. 1). Tube feet (*A. planci*) and gonad tissue (*T. gratilla*) were hand collected while on snorkel or scuba from three (LZ, KE, SO) and six (LZ, KE, KV, MO, PG, SO) locations (see Fig. 1 for location details), respectively, to complement existing sequence datasets found on GenBank (Online Appendix 1). The Kermadec samples were taken from reef surrounding islets to the northeast of Raoul Island: Dayrell Island, west of Meyer Island (*A. planci*), Egeria Rock, and east of Meyer Island (*T. gratilla*). Total genomic DNA was extracted from collected tissue using a salt extraction method (modified from Aljanabi and Martinez 1997). The mitochondrial cytochrome oxidase C subunit I (COI) was amplified using COTS_COI_F4734 and COTS_COI_R5433 in *A. planci* (Vogler et al. 2008), and COIp or COIf and COIa in *T. gratilla* (Lessios et al. 2003). Amplicons were purified using Exonuclease I and Antarctic Phosphatase following the Exo-SAP protocol (New England Biolabs) and sequenced by Macrogen (Korea) via capillary electrophoresis.

Sequences were manually checked and edited using CodonCode Aligner v3.7.1.2 (CodonCode Corporation) and aligned with existing COI data sets using Se-AL v2.0a11 (Rambaut 1996). The aligned sequences were translated into amino acid sequences using the invertebrate mitochondrial code to ensure they were not of nuclear origin and a BLAST search against sequences on the GenBank database confirmed their species origin. The primer sequence and regions of insignificant overlap at either end of the sequences were deleted in Se-AL, so that all sequences within each species dataset were of a common length.

To describe patterns of genetic diversity, differentiation, and novelty of the Kermadec populations in relation to other populations across the studied ranges, analysis of DNA polymorphism (polymorphic sites θ, nucleotide diversity π, number of haplotypes *H*, and diversity of haplotypes *Hd*), Tajima's *D* test (Tajima 1989, 1996), pairwise Φ_{ST} (Tamura-Nei corrected), and pairwise F_{ST} measures were carried out using Arlequin v3.5.1.2 (Excoffier and Lischer 2010; all with 10,000 permutations). *P*-values for all pairwise measures were adjusted for multiple comparisons using the method of Benjamini and Hochberg (1995; "BH" or its alias "fdr") implemented in

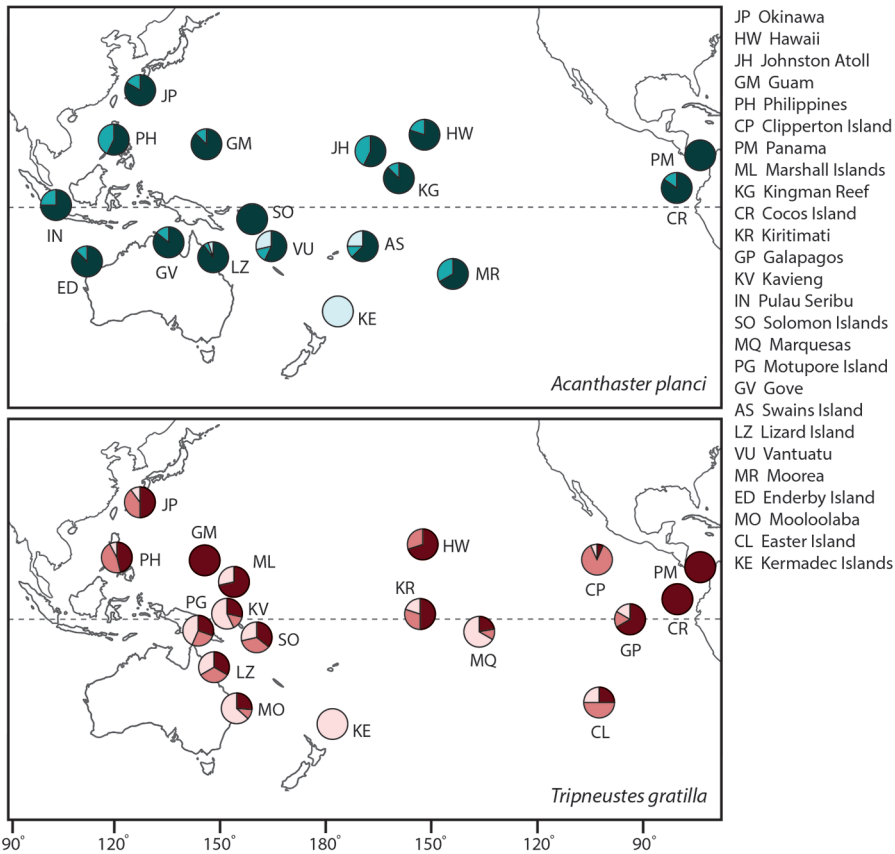

Figure 1. Map of the study locations and their haplotypic composition for *Acanthaster planci* (top) and *Tripneustes gratilla* (bottom). Pies indicate the proportion of individuals that have a haplotype that is shared among locations but not found in the Kermadec Islands (darkest tone), proportion of individuals that have a haplotype unique to their population (medium tone), and the proportion of individuals that share the haplotype found in the Kermadec Islands (lightest tone).

the R statistical package v2.15.2 (R Core Team 2012). To understand the distribution of genetic diversity and regions of genetic disjunction we conducted several analyses of molecular variance (AMOVAs, using Tamura-Nei corrected Φ_{ST}, 10,000 permutations). Hierarchical analyses were conducted using a priori groupings designated according to known biogeographic disjunctions (i.e., east Pacific/central Pacific, the Eastern Pacific Barrier, Ekman 1953; central Pacific/western Pacific + Australia, Drew et al. 2008). Median joining haplotype networks were constructed using Network 4.6.1.0 and Network Publisher 1.3 (fluxus-engineering.com, Bandelt et al. 1999).

To compare how genetic differentiation (untransformed pairwise Tamura-Nei corrected Φ_{ST} and untransformed pairwise F_{ST}) related to geographic distance (untransformed Euclidean distance) and to address how comparisons including the Kermadec populations may deviate from the trend established across other parts of the study region, an Isolation By Distance (IBD, Wright 1943) trend was calculated for each species including all locations, and also excluding the Kermadec population. IBD trends were calculated using reduced major axis regression (Sokal and Rohlf 1981)

and tested using Mantel's permutation test (10,000 matrix randomizations, Mantel 1967), executed by the Isolation By Distance Web Service (Bohonak et al. 2005).

We used simulations to determine whether the haplotypic compositions of the Kermadec populations were likely due to recent immigration events. We conducted 10,000 random draws (of 29 and 7 individuals for *A. planci* and *T. gratilla*, respectively) from a pool consisting of all individuals (and their haplotypes) from across the sampled range of each species, but excluding the Kermadec populations. Each random draw was a simulated immigration event to the Kermadec Islands. The random draws created a null distribution for the expected number of haplotypes in the Kermadec population (given our sample size) and the expected identity of those haplotypes via immigration. The probability of recreating the observed number of haplotypes and haplotype identity of the observed Kermadec populations via immigration alone could then be determined. The simulations were repeated for both species using two weighting systems: unweighted—each individual was weighted equally regardless of population of origin; and weighted—each individual was weighted according to their population of origin based on the predicted IBD trend for all locations excluding the Kermadec population (i.e., the predicted genetic differentiation value for the Euclidean distance between the sample location and the Kermadec Islands as a proportion of the maximum predicted genetic differentiation value for any location, subtracted from 1; all 0 values were adjusted to 0.001).

Results

The final data sets included 151 (622 bp, 17 locations) and 187 (557 bp, 18 locations) COI sequences of *A. planci* and *T. gratilla*, respectively (Table 2, Fig. 1). The *A. planci* data set comprised 43 new sequences from three locations (two previously unstudied: SO, KE) and complementary sequences from the east Indian and Pacific oceans downloaded from GenBank (Vogler et al. 2008, Online Appendix 1). Sequences from GenBank (Lessios et al. 2003; Online Appendix 1) were also used to complement our 77 new sequences of *T. gratilla* from six locations (five previously unstudied: KV, SO, PG, MO, KE). All unique haplotypes represented in the new data sets were uploaded to GenBank (*A. planci*: KF012825-28, *T. gratilla*: KF012802-24).

Haplotype networks (Fig. 2) and AMOVA revealed that *A. planci* had greater genetic structuring across the study region than *T. gratilla* (*A. planci:* global Φ_{ST} = 0.5638, $P < 0.0001$; *T. gratilla:* global Φ_{ST} = 0.2849, $P < 0.0001$, Table 3). The hierarchical AMOVAs revealed the Eastern Pacific Barrier as contributing the most to the genetic structure of both species (*A. planci:* Φ_{CT} = 0.2747, P = 0.0030; *T. gratilla:* Φ_{CT} = 0.1348, P = 0.0128; Table 3). However, once split further into the three a priori designated regions, considerably more genetic structure across *A. planci*'s range could be attributed to among-region differences (*A. planci:* Φ_{CT} = 0.3985, P = 0.0002; Table 3). Haplotype diversity was variable across study locations in both species (Table 2), ranging from 0 (*A. planci*: KE, PM; *T. gratilla*: KE, PM, GM) to 0.95 in *A. planci* (PH) and 1 in *T. gratilla* (GP). Most locations contained unique haplotypes, except KE (both species) and SO, PM in *A. planci*, and GM, ML, CR, PM in *T. gratilla* (see Table 2 and Figs. 1, 2). For both species, the sole haplotype found at the Kermadec Islands was shared (among 4/17 locations in *A. planci* and 14/18 locations in *T. gratilla*, Fig. 2). This haplotype was the most common and central haplotype across the entire study region for *T. gratilla*, and the third most widely shared haplotype for *A. planci*.

Table 2. Summary of included data and genetic diversity statistics for each location studied for *Acanthaster planci* and *Tripneustes gratilla*: number of sequences (n), polymorphic sites (θ), number of haplotypes (H), haplotype diversity [Hd (SD)], nucleotide diversity [π (SD)], Tajima's D statistic and significance (P, no correction). Source (Src) of the CO1 data: a = Vogler et al. (2008), b = present study, c = Lessios et al. (2003).

Code	Location	n	Latitude	Longitude	θ	H	Hd (SD)	π (SD)	Tajima's D	P	Src
Acanthaster planci											
JP	Okinawa	6	36.18	138.25	2	3	0.73 (0.16)	0.0014 (0.0013)	−0.05	0.45	a
HW	Hawaii	5	19.92	−155.60	3	4	0.90 (0.16)	0.0019 (0.0017)	−1.05	0.15	a
JH	Johnston Atoll	7	16.73	−169.54	3	4	0.81 (0.13)	0.0021 (0.0017)	0.40	0.66	a
GM	Guam	8	13.44	144.79	5	5	0.86 (0.11)	0.0030 (0.0022)	−0.17	0.45	a
PH	Philippines	7	13.04	121.71	6	6	0.95 (0.10)	0.0031 (0.0023)	−1.13	0.16	a
PM	Panama	2	8.53	−80.78	0	1	0.00 (0.00)	0.0000 (0.0000)	na	na	a
KG	Kingman Reef	8	6.45	−162.40	12	6	0.93 (0.08)	0.0070 (0.0044)	−0.29	0.40	a
CR	Cocos Island	13	5.52	−87.07	1	2	0.28 (0.14)	0.0005 (0.0006)	−0.27	0.30	a
IN	Pulau Seribu	8	−5.79	105.71	4	4	0.64 (0.18)	0.0016 (0.0014)	−1.53	0.05	a
SO	Solomon Islands	3	−8.24	157.37	2	2	0.67 (0.32)	0.0021 (0.0022)	0.00	0.93	b
GV	Gove	7	−12.35	136.79	2	3	0.52 (0.21)	0.0009 (0.0010)	−1.24	0.12	a
AS	Swains Island	8	−14.27	−170.70	10	6	0.93 (0.08)	0.0067 (0.0042)	0.37	0.67	a
LZ	Lizard Island	19	−14.67	145.46	7	4	0.63 (0.07)	0.0025 (0.0018)	−0.71	0.27	a,b
VU	Vanuatu	7	−15.38	166.96	9	5	0.91 (0.10)	0.0063 (0.0041)	0.33	0.64	a
MR	Moorea	6	−17.52	−149.84	15	5	0.93 (0.12)	0.0104 (0.0066)	−0.10	0.48	a
ED	Enderby Island	8	−20.61	116.53	1	2	0.25 (0.18)	0.0004 (0.0006)	−1.05	0.21	a
KE	Kermadec Islands	29	−29.27	−177.92	0	1	0.00 (0.00)	0.0000 (0.0000)	na	na	b
Tripneustes gratilla											
JP	Japan	10	36.18	138.25	6	6	0.84 (0.10)	0.0036 (0.0025)	−0.50	0.34	c
HW	Hawaii	10	19.92	−155.60	8	7	0.91 (0.08)	0.0035 (0.0024)	−1.47	0.07	c
GM	Guam	2	13.44	144.79	0	1	0.00 (0.00)	0.0000 (0.0000)	na	na	c
PH	Philippines	13	13.04	121.71	13	9	0.94 (0.05)	0.0059 (0.0037)	−1.04	0.16	c
CP	Clipperton Island	15	10.28	−109.22	11	8	0.85 (0.07)	0.0055 (0.0034)	−0.40	0.38	c
PM	Panama	4	8.53	−80.78	0	1	0.00 (0.00)	0.0000 (0.0000)	na	na	c
ML	Marshall Islands	7	7.13	171.18	4	3	0.67 (0.16)	0.0034 (0.0025)	0.80	0.81	c
CR	Cocos Island	10	5.52	−87.07	2	2	0.20 (0.15)	0.0008 (0.0009)	−1.40	0.08	c
KR	Kiritimati	10	1.87	−153.36	7	7	0.91 (0.08)	0.0044 (0.0030)	−0.24	0.42	c
GP	Galápagos	6	−0.82	−91.10	7	6	1.00 (0.10)	0.0046 (0.0033)	−1.01	0.20	c
KV	Kavieng	14	−2.57	150.80	8	7	0.69 (0.14)	0.0026 (0.0019)	−1.70	0.03	b
SO	Solomon Islands	14	−8.24	157.37	13	10	0.92 (0.06)	0.0042 (0.0027)	−1.74	0.03	b
MQ	Marquesas	9	−9.45	−139.39	8	3	0.56 (0.17)	0.0039 (0.0027)	−1.37	0.09	c
PG	Motupore Island	23	−9.51	147.31	12	12	0.81 (0.08)	0.0030 (0.0020)	−1.77	0.02	b,c
LZ	Lizard Island	6	−14.67	145.46	5	5	0.93 (0.12)	0.0034 (0.0027)	−1.34	0.06	b
MO	Mooloolaba	19	−26.68	153.12	6	7	0.61 (0.13)	0.0016 (0.0013)	−1.54	0.05	b
CL	Easter Island	8	−27.12	−109.37	5	6	0.93 (0.08)	0.0033 (0.0024)	−0.42	0.38	c
KE	Kermadec Islands	7	−29.27	−177.92	0	1	0.00 (0.00)	0.0000 (0.0000)	na	na	b

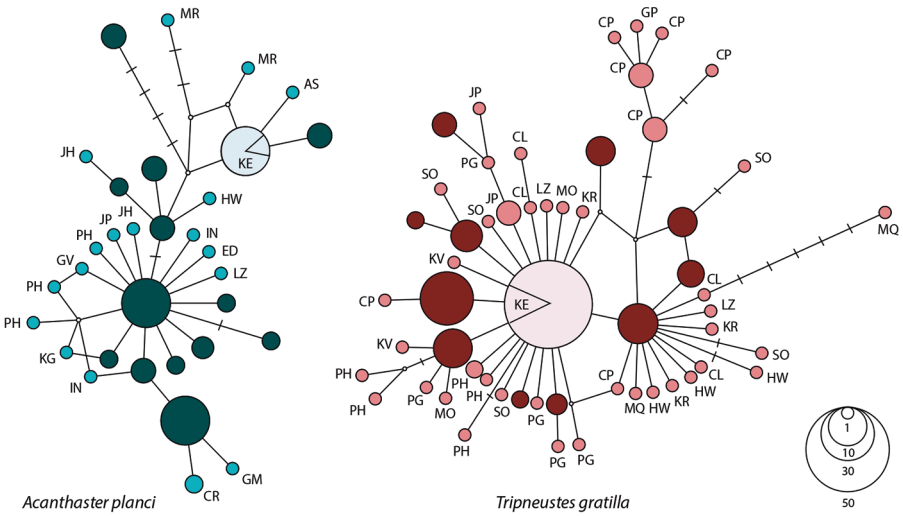

Figure 2. Median-joining haplotype networks for *Acanthaster planci* and *Tripneustes gratilla* displaying which haplotype is found in the Kermadec Islands (lightest tone), which haplotypes are shared among locations but not found in the Kermadec Islands (darkest tone), and haplotypes that are unique to one location (medium tone, also with location code indicated). Hollow circles represent hypothetical historical haplotypes or current haplotypes not sampled; edges between haplotypes or small cross-bars indicate a mutational step. The frequency of each haplotype is indicated by size (see key, bottom right).

There was a significant positive IBD trend across the entire data set for both species based on pairwise Φ_{ST} (Fig. 3) and this trend was stronger and of higher significance once the Kermadec populations were excluded (*A. planci*: all locations, $R^2 = 0.2100$, $P = 0.0010$; excluding KE, $R^2 = 0.3670$, $P < 0.0001$; *T. gratilla*: all locations, $R^2 = 0.0973$, $P = 0.0028$; excluding KE, $R^2 = 0.1530$, $P = 0.0006$). The Kermadec population of *A. planci* was more differentiated from other populations than would be expected based on the IBD trend found throughout the rest of the sampled range, whereas there was no consistent pattern for *T. gratilla* (Fig. 3, Online Appendix 2). IBD patterns based on pairwise F_{ST} were weaker and of lower significance across the entire data set for both species (*A. planci*: $R^2 = 0.0691$, $P = 0.0015$; *T. gratilla*: $R^2 = 0.0380$, $P = 0.0250$; Fig. 3, Online Appendix 2), indicating that the geographic signature of mutation has not been eroded by high dispersal and is informative in these species (Bird et al. 2011).

For *A. planci*, the probability of the Kermadec Islands containing 29 individuals of the same haplotype using a random draw from the existing haplotypes was <0.0001 (individuals were weighted according to population origin, Fig. 4). For *T. gratilla*, the probability of drawing seven individuals with the same haplotype was 0.0008 (Fig. 4), and the probability that the haplotype would have the same identity as that found in the Kermadec Islands was also 0.0008. These results were robust to the method of weighting; in the unweighted comparisons for *A. planci* 29 individuals with the same haplotype were never drawn, whereas for *T. gratilla* the probability of drawing seven individuals with the same haplotype was 0.0001. The haplotype drawn was always the same as that found in the Kermadec population.

Table 3. Analysis of molecular variances (AMOVAs, Tamura-Nei corrected Φ_{ST}) and hierarchical AMOVAs testing the effects of a priori designated barriers on the genetic structuring across the studied ranges of *Acanthaster planci* and *Tripneustes gratilla*. WPac = west Pacific, the Coral Triangle and Australia, including IN, ED, PH, JP, GV, GM, PG, LZ, KV, ML, MO, SO, VU; CPac = central Pacific, including KE, AS, JH, KG, KR, HW, MR, MQ; EPac = east Pacific, including CL, CP, GP, CR, PM. %var = percent variation.

Scenario	Source of variation	df	%var	Φ	*P*
Acanthaster planci					
Sampled populations	Among populations	16	56.38	Φ_{ST} 0.5638	<0.0001
	Within populations	134	43.62		
WPac/CPac/EPac	Among regions	2	39.85	Φ_{CT} 0.3985	0.0002
	Among populations within regions	14	22.82	Φ_{SC} 0.3794	<0.0001
	Within populations	150	37.33	Φ_{ST} 0.6267	0.0000
WPac/CPac	Among regions	1	19.26	Φ_{CT} 0.1927	0.0612
	Among populations within regions	15	40.92	Φ_{SC} 0.5068	<0.0001
	Within populations	134	39.82	Φ_{ST} 0.6018	<0.0001
CPac/EPac	Among regions	1	27.47	Φ_{CT} 0.2747	0.0752
	Among populations within regions	15	38.54	Φ_{SC} 0.5314	<0.0001
	Within populations	134	33.99	Φ_{ST} 0.6601	<0.0001
Tripneustes gratilla					
Sampled populations	Among populations	17	28.49	Φ_{ST} 0.2849	<0.0001
	Within populations	169	71.51		
WPac/CPac/EPac	Among regions	2	11.04	Φ_{CT} 0.1105	0.0030
	Among populations within regions	15	20.23	Φ_{SC} 0.2274	<0.0001
	Within populations	169	68.72	Φ_{ST} 0.3128	<0.0001
WPac/CPac	Among regions	1	9.16	Φ_{CT} 0.0916	0.0065
	Among populations within regions	16	22.39	Φ_{SC} 0.2464	<0.0001
	Within populations	169	68.46	Φ_{ST} 0.3154	<0.0001
CPac/EPac	Among regions	1	13.48	Φ_{CT} 0.1348	0.0128
	Among populations within regions	16	20.98	Φ_{SC} 0.2425	<0.0001
	Within populations	169	65.54	Φ_{ST} 0.3446	<0.0001

Discussion

This study investigated the genetic affinities and relative genetic patterns of an edge-of-range location, the Kermadec Islands, for two common tropical echinoderms. The genetic patterns for both *A. planci* and *T. gratilla* suggest similar processes have shaped their populations around the Kermadec Islands. In both species, the Kermadec populations contained only one haplotype that was shared with other populations (Table 2, Fig. 1). Such a pattern of low diversity is consistent with a self-sustaining population founded by a limited number of colonists ("Colonization" scenario, Table 1). Our resampling results (Fig. 4) indicate it is highly unlikely that the haplotypic compositions of the Kermadec populations could result from contemporary immigration events (i.e., "Meta-population" and "Migration load" scenarios, Table 1).

The Kermadec Populations in an Indo-Pacific Context.—Despite both echinoderm species having only one haplotype within the Kermadec population, the genetic patterns throughout the rest of their ranges varied between species. *Acanthaster planci* had considerably more genetic structuring across its range than

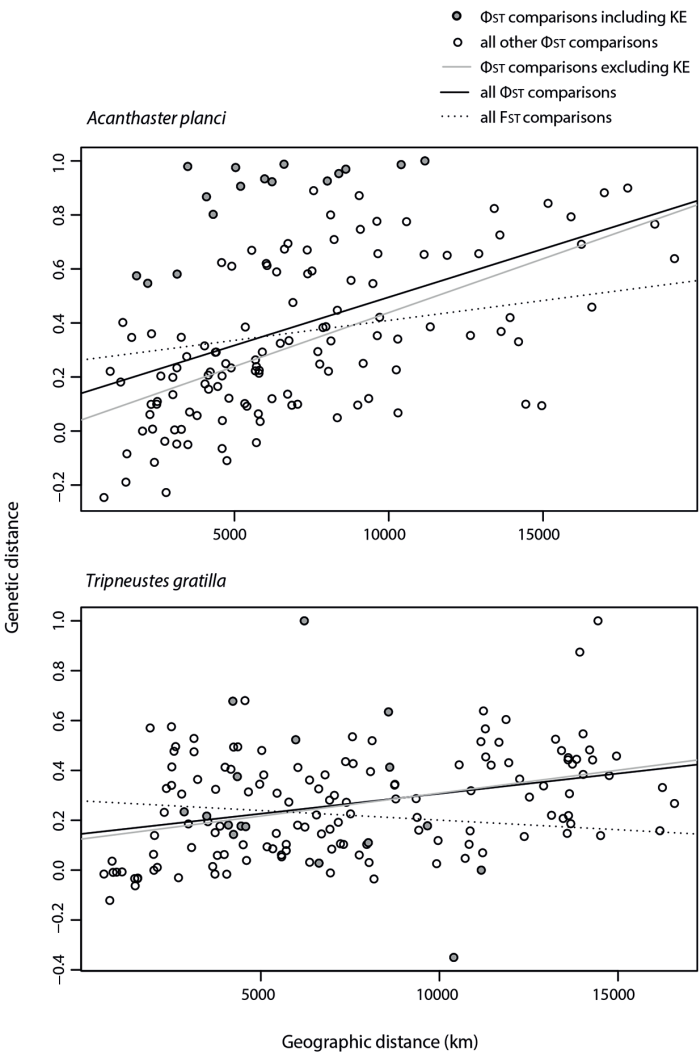

Figure 3. The relationship between genetic differentiation (untransformed pairwise Tamura-Nei corrected Φ_{ST} and untransformed pairwise F_{ST}) and Euclidean geographic distance (kilometers, km) among study locations for *Acanthaster planci* and *Tripneustes gratilla.* The gray filled circles denote pairwise Φ_{ST} relationships between the Kermadec population and other study locations. The black line represents the regression line for all Φ_{ST} comparisons (*A. planci* $R^2 = 0.2100$, $P = 0.0010$; *T. gratilla* $R^2 = 0.0973$, $P = 0.0028$), the gray line represents the regression line excluding the Kermadec population (*A. planci* $R^2 = 0.3670$, $P < 0.0001$; *T. gratilla* KE $R^2 = 0.1530$, $P = 0.0006$), and the dashed line represents the regression line for all pairwise F_{ST} comparisons (*A. planci* $R^2 = 0.0691$, $P = 0.0015$; *T. gratilla* $R^2 = 0.0380$, $P = 0.0250$).

T. gratilla. Recent surveys of *A. planci* based on more variable genetic markers have indicated that island populations separated by approximately 1500 km can be significantly genetically differentiated (Yasuda et al. 2009) suggesting that individuals of this species do not always meet their full dispersal potential (Timmers et al. 2012, Vogler et al. 2013). Comparatively less is known about the scale of genetic structuring and the likely influence of early life history characteristics in *T. gratilla*. However, based on a genetic survey Lessios et al. (2003) described *T. gratilla* as one large

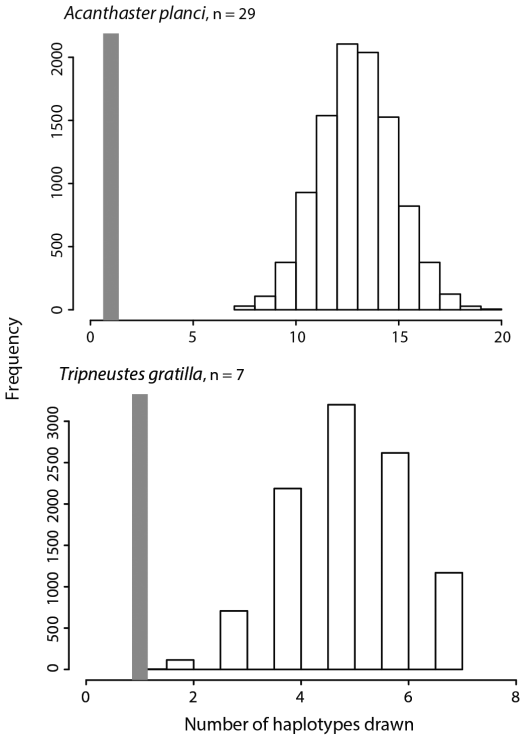

Figure 4. Frequency distribution displaying the number of haplotypes drawn from a pool consisting of all individuals (and their haplotype; weighted according to location) sampled across the study area for both species, but excluding the Kermadec populations. To simulate recruitment events to the Kermadec Islands, 29 individuals for *Acanthaster planci* and seven individuals for *Tripneustes gratilla*, were drawn 10,000 times. The gray line represents the haplotypic composition of the Kermadec populations (i.e., one haplotype).

meta-population throughout the Indo-Pacific, with non-equilibrium local variation likely due to chaotic colonization and local extinction, typical of a high dispersal and high fecundity urchin species.

The genetic affinities (i.e., the shared haplotype) of *A. planci* with American Samoa (AS), Vanuatu (VU), and Lizard Island (LZ), suggest colonization of the Kermadec Islands may have been from these locations, or from a source common to all of these regions (Fig. 1). This finding supports a phylogeographic study conducted by Vogler et al. (2013) that reveals the close genetic relationship that *A. planci* of the Kermadec Islands has with populations of the Central Pacific (specifically Vanuatu and Moorea), the northern Great Barrier Reef (Swains Reef), and Lord Howe Island. Accordingly, descriptions of ocean currents (Schiel et al. 1986, Gardner et al. 2006) and biogeographic similarities of the Kermadec Islands marine fauna suggest connectivity with the north and west (e.g., western and central tropical Pacific for molluscs, Brook 1998; southeastern Australia for corals, Wicks et al. 2010a). In *T. gratilla*, the source of the Kermadec population is difficult to infer based on the data herein, as the haplotype found at the Kermadec Islands is also shared across much of the studied species range (Philippines, PH 122°E to Galapagos Islands, GP 90°W, and the entire studied latitudinal range; Fig. 1). These differing genetic affinities of the two echinoderm

species greatly influence the perceived differentiation of the Kermadec populations as measured by Φ_{ST}. Although the haplotype found in the Kermadec population of *A. planci* is locally shared (with AS, VU, and LZ), pairwise Φ_{ST} values between the Kermadec population and other locations are consistently high because this haplotype is relatively rare. In contrast, pairwise Φ_{ST} values between the *T. gratilla* population and elsewhere are variable owing to the wide distribution and varying frequency of the haplotype shared with the Kermadec population.

The only other location represented by a single haplotype in *A. planci* was Panama (PM), which had two individuals sampled, relative to the 29 individuals from the Kermadec Islands (Table 2). All of the other locations sampled for *A. planci* contained unique haplotypes, and nearby populations of the central Pacific had several unique haplotypes (e.g., AS, MR; Table 2, Fig. 1). Similarly, for *T. gratilla* there were only two locations other than the Kermadec Islands that had one haplotype, both of which had small sample sizes (GM = 2, PM = 4; Table 2). Other peripheral and isolated locations (CL, CP, and JP) sampled for *T. gratilla* had high levels of genetic novelty (4, 13, and 4 unique haplotypes respectively; Table 2 and Fig. 1) some of which are very divergent (see position of unique haplotypes in the network, Fig. 2). The lack of unique haplotypes in the Kermadec Islands could indicate that these populations of *A. planci* and *T. gratilla* are relatively young. The peripheral and isolated location of the Kermadec Islands, their short geological history (1.8–3 Ma; Watt 1975), and continuing active volcanism support this notion of recent colonization, however alternative explanations are possible (discussed below).

Evidence for Self-Recruitment and Little Immigration in an Edge-of-Range Population.—We find no genetic diversity in the Kermadec populations (Table 2), which suggests that bottlenecks have affected both *A. planci* and *T. gratilla*. Such a pattern is reminiscent of contemporary invasion scenarios (Roman and Darling 2007). Colonization of introduced species often involves a small number of initial colonists, causing the colonizing population to be much less genetically diverse than the source population. Our findings contrast with genetic patterns observed following the natural colonization of Krakatau after its 1883 eruption (Barber et al. 2002). Despite the short timeframe, stomatopod populations had high levels of genetic diversity, possibly owing to the central location of Krakatau in the species ranges and consequent high levels of immigration (Barber et al. 2002). In contrast, for the peripheral Kermadec populations, our procedure of taking random draws from the species' sampled ranges confirmed it is highly unlikely that the haplotypic compositions (multiple individuals sharing the same haplotype) could result from contemporary immigration events (Fig. 4). Therefore we can reject a frequent immigration scenario (Table 1).

It is conceivable that larvae of these high dispersal echinoderm species reach the Kermadec Islands, but that their successful immigration is inhibited by high-density blocking (Hewitt 1993), the latent effects of long-distance dispersal, or selection. A pattern of "founder takes all" via high-density blocking of the existing conspecific population has been proposed for several marine colonization scenarios where the standing genetic diversity is maintained despite the arrival of potential immigrants (reviewed in Waters et al. 2013). "Legacy effects" have also been suggested to bias recruitment in larval fish whereby the survival is greater in fish that have undergone a less stressful pelagic larval phase (Shima and Swearer 2010). It is possible

that locally-derived larvae of the Kermadec Islands have greater fitness due to their shorter and potentially less stressful pelagic larval phase (Nosil et al. 2005). Both of these mechanisms could be couched as forms of local selection, as the locally-derived larvae survive in greater proportions than larvae from elsewhere (either by "aggregate" fitness as a consequence of being related to the surviving genotypes, or individual fitness and competitive ability as a consequence of early life experience in the pelagic environment). Although posited as a neutral locus, it is also possible that the mitochondrion, or some genetic element that is linked to the COI haplotype found at the Kermadec Islands is under positive selection. As the mitochondrion is known to have function in metabolism, the haplotype found in the Kermadec Islands may offer some functional benefit in the colder water temperatures (similar examples are reviewed in Galtier et al. 2009). Unfortunately, the influence of such phenomena on the genetic composition of the Kermadec populations is undetectable using our current study design. Acquiring such knowledge would require the capture (and genotyping using multiple unlinked loci) of potential immigrants prior to any form of selection, and/or some proof of a haplotype by environment interaction.

Assuming that the mitochondrion is behaving as a neutral locus, the absence of variation in the Kermadec populations would imply that there has been insufficient time and/or opportunity since colonization for new genetic variants to arise and differentiation to occur (Lesica and Allendorf 1995; Table 1). Although previous studies indicate that *A. planci* and *T. gratilla* have remained abundant around Meyer Island of the Kermadec Islands (*A. planci*: up to 0.008 individuals per m^2 in 1995, Brook 1999; and 0.25 individuals per m^2, Gardner et al. 2006; *T. gratilla*: up to 0.7 individuals per m^2, Cole et al. 1992; and 0.75 individuals per m^2, Gardner et al. 2006), this area is small and may not support a large effective population size. If the Kermadec populations are relatively small and/or experience fluctuating abundance (common in echinoderms, Uthicke et al. 2009) the resultant effective population sizes would maintain low standing diversity in the populations.

Regardless of the timing of colonization or post-colonization mechanisms that keep genetic diversity low, our results suggest both *A. planci* and *T. gratilla* populations are self-recruiting. Thus, while we can only speculate that the peripheral nature of the Kermadec Islands has precluded recurrent immigration (and not selection processes at settlement), the marginality of the islands has certainly not impeded reproduction and self-recruitment following initial colonization. A scenario of "Colonization" (Table 1) followed by self-recruitment and little immigration for *A. planci* is further supported by the findings of Vogler et al. (2013). Using the more variable and faster mutating control region of the mitochondrial locus, the authors found six unique haplotypes from a sample of seven *A. planci* individuals from the Kermadec Islands. None of these haplotypes were shared outside of the Kermadec Islands, and are likely to be locally derived (see Online Appendix 3) indicating *A. planci* has had an isolated demographic history in the Kermadec Islands.

Implications for Range Stability of Tropical Echinoderms at the Kermadec Islands.—Understanding the reproductive capacity and reliance on immigration with regions outside of the Kermadec Islands Marine Reserve is important for predicting the persistence of these species at this locality. Moreover, attributes of peripheral populations (reproduction and connectivity) interact to determine their capacity for local adaptation and species range expansion into other locales (Sexton

et al. 2009). For example, if reproduction is largely unsuccessful within the Kermadec Islands, and the populations are reliant on immigrants from elsewhere in their range, the echinoderms are unlikely to adapt to the marginal conditions of the Kermadec Islands ("Migration load" scenario, e.g., Dawson et al. 2010) and are unlikely to extend their range (Garciá-Ramos and Kirkpatrick 1997, Kirkpatrick and Barton 1997). At the other extreme, if the Kermadec populations are reproductive and have no immigration, their range may be only temporarily limited ("Genetic impoverishment" scenario; Holt 2003). This situation can quickly change with a subsequent immigration event (Gomulkiewicz et al. 1999), and/or the generation of any genetic novelty in the population (Bataillon 2003). While patterns of neutral genetic diversity are not directly related to adaptive genetic diversity (but see Pujol and Pannell 2008), our findings suggest the Kermadec populations are subject to a scenario of "Genetic impoverishment" where local adaptation and subsequent range shifts may only be a matter of time.

Tropical vagrants (and some reproductive populations) are known to occur along the northeast coast of mainland New Zealand (molluscs, reviewed by Powell 1976; marine reptiles, reviewed by Gill 1997; fishes, reviewed by Francis et al. 1999). Most insurgent tropicals are presumed to have originated from Norfolk Island and to a lesser degree, Lord Howe Island (Francis et al. 1999). Although simulations of larval dispersal from Raoul Island to mainland New Zealand indicate that transit times would be in excess of fifty days, dispersal from the southern most island of the Kermadec archipelago (L'Esperance Rock) may be as little as twenty days (Sutton et al. 2012), well within the pelagic larval duration of many benthic reef species. Moreover, fish previously considered endemic to the Kermadec Islands have been found in mainland New Zealand, providing evidence for larval transport from the north (Francis et al. 1999). With changes to ocean currents and global temperatures now considered imminent (Doney et al. 2012), the Kermadec Islands may become an important stepping-stone for tropical marine species into New Zealand.

In conclusion, the genetic patterns found in the Kermadec populations for *A. planci* and *T. gratilla* upheld the expectations of the CPH. Both populations had low genetic diversity, and the *A. planci* population was consistently more genetically differentiated from other populations throughout the sampled range (Fig. 3, Online Appendix 2). Furthermore, we have demonstrated that these populations appear to be self-sustaining. Such conditions would foster local adaptation at the range edge (García-Ramos and Kirkpatrick 1997). With the onset of climate change, the Kermadec Islands may represent a "leading-edge" location for many tropical marine populations, and provide an important dispersal corridor for marine organisms into New Zealand. As such, these populations should be monitored and conserved appropriately.

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