Coral Reefs (2011) 30:937–949
DOI 10.1007/s00338-011-0767-x

REPORT

Vicariance and dispersal across an intermittent barrier: population genetic structure of marine animals across the Torres Strait land bridge

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Received: 23 January 2011 / Accepted: 9 May 2011 / Published online: 28 May 2011
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Abstract Biogeographic barriers, some transitory in duration, are likely to have been important contributing factors to modern marine biodiversity in the Indo-Pacific region. One such barrier was the Torres Strait land bridge between continental Australia and New Guinea that persisted through much of the late Pleistocene and separated Indian and Pacific Ocean taxa. Here, we examine the patterns of mitochondrial DNA diversity for marine animals with present-day distributions spanning the Torres Strait. Specifically, we investigate whether there are concordant signatures across species, consistent with either vicariance or recent colonization from either ocean basin. We survey four species of reef fishes (*Apogon doederleini*, *Pomacentrus coelestis*, *Dascyllus trimaculatus*, and *Acanthurus triostegus*) for mtDNA cytochrome oxidase 1 and control region variation and contrast these results to previous mtDNA studies in diverse marine animals with similar distributions. We find substantial genetic partitioning (estimated from *F*-statistics and coalescent approaches) between Indian and Pacific Ocean populations for many species, consistent with regional persistence through the late Pleistocene in both ocean basins. The species-specific estimates of genetic divergence, however, vary greatly and for reef fishes we estimate substantially different divergence times among species. It is likely that Indian and Pacific Ocean populations have been isolated for multiple glacial cycles for some species, whereas for other species genetic connections have been more recent. Regional estimates of genetic diversity and directionality of gene flow also vary among species. Thus, there is no apparent consistency among historical patterns across the Torres Strait for these co-distributed marine animals.

Keywords Australia · Coalescence · Coral Triangle · Gene flow · Comparative phylogeography · Planktonic larval dispersal

Communicated by Biology Editor Dr. Ruth Gates

Electronic supplementary material The online version of this article (doi:10.1007/s00338-011-0767-x) contains supplementary material, which is available to authorized users.

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Introduction

Absolute vicariance in the marine realm is a rare event (Palumbi 1994), as it depends on major geological restructuring of the landscape such as the movement of continental plates. Indisputably, such vicariant events are important generators of marine biodiversity, for example, geminate species on either side of the Isthmus of Panama have long been recognized (Jordan 1908; Mayr 1954). Some barriers have been more transient, arising from sea level changes, sometimes in combination with locally dynamic geological processes. The imprint of these transient barriers (i.e., an absolute barrier in the past, but without complete impediment to dispersal in the present) can often be detected in the genetic patterns of co-distributed species. For example, Avise and coworkers documented the striking phylogeographic concordance of marine species distributed along the Florida coastline, associated with past sea level changes, climate fluctuations, and contemporary discontinuities in water masses (Avise 2000 and references therein). Similar genetic concordance has been observed across former land

barriers, such as between Atlantic and Mediterranean marine species (Patarnello et al. 2007), and species on either side of the mainland Australia–Tasmania land bridge (Waters et al. 2005, 2007).

It is self-evident that landmasses can create barriers to gene exchange among marine animals. Once the barriers dissipate (due to sea level rise, for example), however, dispersal across the former barrier should lead to gene exchange and degradation of any genetic signal of past vicariance. Why the signatures of vicariance remain for many taxa is puzzling. It may be that marine animals disperse far less then generally assumed, and therefore, historical patterns persist for a long time once genetic differentiation is established. Another possibility is that boundaries between biogeographic regions are anomalous in some way; either dispersal is specifically reduced in such areas (for example, due to currents and water flow) or selection against cross-boundary migrants prevents them from reaching, settling, or reproducing in new destinations (Hellberg 2007). Whether the inherent dispersal and colonization ability of a species affects present-day gene flow across historical barriers is unresolved.

The reefs of tropical Australia together with reefs of the Indo-Malay Archipelago (the "Coral Triangle") contain the greatest concentration of coastal marine biodiversity on earth (Tittensor et al. 2010), with distinct biotas inhabiting the Indian and Pacific Oceans. The exact location and nature of many historic barriers between the Indian and Pacific Oceans are uncertain due to the extremely dynamic geology in this region (Voris 2000). One clear and well-dated barrier is the Torres Strait land bridge (Voris 2000, see Fig. 1). This land bridge connected northern Australia and New Guinea intermittently throughout the late Pleistocene until ~7,000 years ago, after sea levels rose to present levels (Voris 2000; Reeves et al. 2008). Thus, the Torres Strait land bridge offers an excellent setting for exploring how genetic differentiation has been shaped by both recent dispersal and historical vicariance (Chenoweth et al. 1998). There has been a spate of recent studies examining genetic patterns of marine animals distributed across the Torres Strait (Elliott 1996; Begg et al. 1998; Chenoweth et al. 1998; Gopurenko et al. 1999; Lessios et al. 2001; Williams et al. 2002; Chenoweth and Hughes 2003; Uthicke and Benzie 2003; Bay et al. 2004; Dethmers et al. 2006; Duncan et al. 2006; Reid et al. 2006; Imron et al. 2007; Klanten et al. 2007; Lukoschek et al. 2007; Dudgeon et al. 2009; van Herwerden et al. 2009); but there has been no explicit comparison among different species to date.

For marine species with present-day distributions spanning the Torres Strait, there are two possible historical

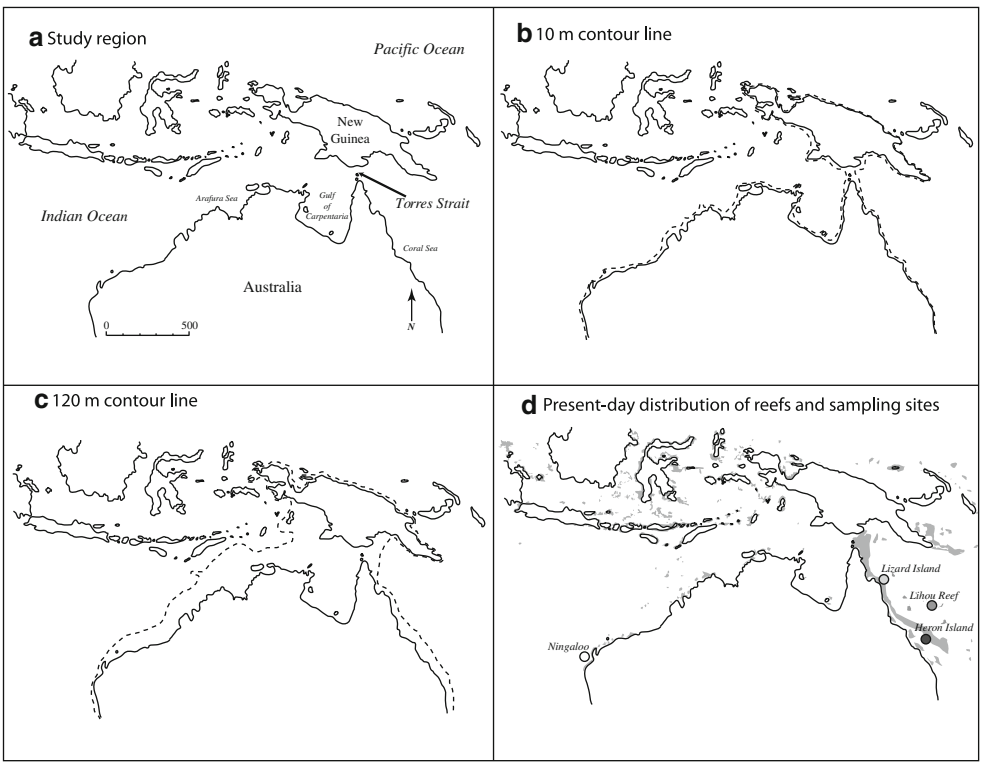

Fig. 1 Australia and New Guinea. **a** study region, **b** the 10-m bathymetric contour is indicated by a *dotted line*; sea level has been at or below this level for most of the late Pleistocene, **c** the 120-m bathymetric contour is indicated by a *dotted line*; this represents the low sea level stand at ~17 kyr, **d** study sites and present-day locations of coral reef; reef areas are *shaded*

scenarios since the inception of the barrier: vicariance caused by the land bridge with persistence of species in both Indian and Pacific Oceans or persistence in one region followed by recent colonization through the Torres Strait (Lukoschek et al. 2007). At the last glacial maximum (LGM), sea level was ~125 m lower than present. The exact geographic distribution of coral reefs (the habitat used by most species considered in the present study) in the Indo-Pacific at that time is uncertain (reviewed by (Montaggioni 2005). Although evidence for reef growth is found at many locations at the conclusion of the LGM, periods of growth were interspersed by reef drownings when sea level rise was too rapid for coral growth to match sea level rise (Montaggioni 2005). For example, the modern Great Barrier Reef (GBR) probably dates to no more than 10 kyr BP, as reef material is missing from the 18–9 kyr interval (Carter and Johnson 1986). Holocene strata in the GBR overlay older reef material from the previous interglacial, ~120 kyr (Marshall and Davies 1984). Similarly, the modern reef of Ningaloo in western Australia is less than 8 kyr and overlays reef strata from the previous interglacial (Collins et al. 2003). Coral reefs have been continuously present along the coastline of western Australia, however, at least since the late Pleistocene (128–121 kyr), albeit with northern contraction during the last glacial (Greenstein and Pandolfi 2008), whereas it is unknown whether there were regional refugia along the east coast of Australia.

To what degree marine animals can disperse across the modern Torres Strait is uncertain, as the oceanography is complex and not yet fully understood. Broadscale currents through this area are highly seasonal, with a complete reversal between summer and winter (Wolanski et al. 1988; Margvelashvili et al. 2008). The average westerly flow is 3-times stronger (0.25 Sv) and is sustained for approximately 3-times as long as the easterly current (Margvelashvili et al. 2008). The water depth in the Torres Strait ranges from 5 to 25 m (Fig. 1), and there are many small reef patches and islands, around which complex eddies can form (Wolanski et al. 1988; Margvelashvili et al. 2008). Overall, this oceanographic profile implies that there is limited sustained through-flow of water through this area. Gene flow through the Torres Strait is therefore likely to be restricted and directionality of dispersal may be seasonal. Genetic surveys taken from sites in the present-day Torres Strait indicate strong genetic affinities with GBR populations for coral trout (van Herwerden et al. 2009) and littorine snails (Reid et al. 2006). For samples from the Gulf of Carpentaria, sea snakes (Lukoschek et al. 2007) and barramundi (Chenoweth et al. 1998) also are genetically similar to GBR samples, indicative of east to west contemporary movement or post-glacial colonization in a westerly direction. In contrast, for sea turtles, Gulf of Carpentaria populations are more similar to western Australian populations than to populations from the east (Dethmers et al. 2006).

In the present study, we evaluate historical and contemporary barriers to movement for marine animals distributed on either side of the Torres Strait. We survey four co-distributed coral reef fishes (see "Materials and methods") for mtDNA variation and compare these results with previously published mtDNA surveys for a variety of marine animals. First, we investigate whether mtDNA variation is consistent with (a) vicariance across the Torres Strait, which would be expected if both western and eastern regional populations persisted since the last marine connection ~120 kyr ago, or (b) post-glacial colonization from either region. Second, in the instance that vicariance is most likely, we examine the age of genetic divergence within species and specifically test whether single or multiple episodes of vicariance typify observed genetic patterns. Finally, we use coalescent approaches to determine whether present-day gene flow is consistently asymetrical in a westerly or easterly direction.

Materials and methods

In the present study, we combine new mtDNA sequence data from four species of coral reef fishes with data gathered from published literature from an additional nine species of marine animals with varying habitat requirements.

Focal study species

The four reef fish species chosen for this study vary in life history traits that may affect dispersal in reef fishes (Riginos and Victor 2001) including egg type, pelagic larval duration (PLD), and larval behavior (see Table 1 and Electronic Supplementary Material, ESM). Based on these qualitative assessments of dispersal potential, we estimated that dispersal is most restricted for *Apogon doederleini*, followed by *Pomacentrus coelestis*, *Dascyllus trimaculatus*, and *Acanthurus triostegus*. Previous genetic surveys for *Apogon doederleini* (Gerlach et al. 2007), *P. coelestis* (Gerlach et al. 2007), and *D. trimaculatus* (Bernardi et al. 2002; Leray et al. 2010) are consistent with these expectations, but for *Acanthurus triostegus* statistically significant genetic structure has been reported over at short distances (Planes 1993; Planes et al. 1998). Thus, we predict that genetic differentiation as estimated by mtDNA should be greatest for *Apogon doederleini*, followed by *P. coelestis*, *D. trimaculatus*, and *Acanthurus triostegus*, but that aberrant results for *A. triostegus* are possible.

Table 1 Mitochondrial DNA surveys of animals distributed across the Torres Strait

Species	Common name	Early life stages and habitat usage	Predicted dispersal	Live on/near coral reefs?	Data reference
Reef fishes					
Apogon doederleini	Doederlein's cardinalfish	Males brood eggs in their mouths; larvae are released and are planktonic for 16–27 days. Adults are free swimming and strongly reef associated	Low	Yes	Present study
Pomacentrus coelestis	Neon Damelfish	Eggs are benthic and larvae can settle on the outer reef in low quality habitat following an 18–20 day PLD. Adults are free swimming and reef associated	Medium	Yes	Present study
Dascyllus trimaculatus	Three-spot damselfish	Eggs are benthic and young recruit to large anemones following a 22–26 day PLD. Adults are free swimming and reef associated	Medium	Yes	Present study
Acanthurus triostegus	Convict surgeonfish	Eggs are pelagic with a long PLD of 40+ days. Adults are reef associated generalists but are often found in high-flow turbid environments such as coastal bays and harbors	High	Yes	Present study
Other vertebrates					
Aipysurus laevis	Olive sea snake	Adults free swimming, found near coral reefs and over soft bottoms; olive sea snakes are viviparous	Low	Yes	Lukoschek et al. (2007)
Stegostoma fasciatum	Zebra shark	Adults are free swimming and reef associated; zebra sharks are ovoviviparous	Low	Yes	Dudgeon et al. (2009)
Chelonia mydas	Green turtle	Adults are pelagic but probably return to natal area to breed and nest	Low	Sometimes	Dethmers et al. (2006)
Mollusks					
Haliotis asinina	Donkey ear abalone	Adults live on shallow hard substrate; lecithotrophic larvae settle after 3–4 days	Low	Yes	Imron et al. (2007)
Echinolittorina trochoides B	Periwinkle	Adults live on shallow hard substrate; planktotrophic larval phase up to 4 weeks	High	Yes	Reid et al. (2006)
Echinolittorina vidua	Periwinkle	Adults live on shallow hard substrate; planktotrophic larval phase up to 4 weeks.	High	Yes	Reid et al. (2006)
Other invertebrates					
Scylla serrata	Mud crab	Adults live in estuaries but migrate offshore to release eggs; planktotrophic larval phase.	High	No	Gopurenko and Hughes (2002)
Diadema setosum-a	Urchin	Adults live on shallow hard substrate; planktotrophic larval phase up to 6 weeks.	High	Yes	Lessios et al. (2001)
Holothuria nobilis	Sea cucumber	Adults live on coral reefs, planktotrophic larval phase greater than 10 days.	Medium	Yes	Uthicke and Benzie (2003)

Field collections and mtDNA sequencing

The study region included western and eastern Australia, with sites on either side of the Torres Strait. Fishes were collected from Heron (23° 26′S, 151° 55′E) and Lizard (14° 40′S, 145° 28′E) Islands in the Great Barrier Reef (GBR), Lihou Reef (17° 25′S, 151° 40′E) in the Coral Sea (eastern populations), and Ningaloo Reef Marine Park (23° 10′S, 113° 45′E) in western Australia (western population) (Fig. 1). A limitation to most studies of coral reef organisms from this region (including the present study) is that sampling locations are distant from the putative barrier of the Torres Strait, with Ningaloo reef and northern GBR as the usual flanking sites. This unsatisfactory sampling design arises from a number of factors that are difficult to circumvent. Reefs are diffuse or poorly developed along coastal Australia west of the Torres Strait (Fig. 1), with soft sediments typifying the Gulf of Carpentaria. The reefs of northern western Australia are poorly surveyed in general due to difficulties with access (requiring permissions from traditional owners) and dangerous working conditions (crocodiles). Although sampling sites adjacent to a suspected barrier are ideal for evaluating the effect of that barrier, the aforementioned considerations constrained out investigation (and many others included in Table 1). Therefore, we cannot decouple the effect of a large geographic distance (Ningaloo to northern GBR) from a historic barrier. From our study sites, tissue samples were collected

on SCUBA or snorkel, with 15–20 individuals collected per species, per site. Fresh tissue was preserved in 100% ethanol and then stored at −80°C.

Total genomic DNA was extracted from muscle tissue using a salt extraction method (Aljanabi and Martinez 1997). Cytochrome oxidase 1 (CO1) and the control region of the mitochondria were amplified in 30-µl polymerase chain reactions (PCR), with each reaction tube containing 1 µl of DNA, 3 µl each of NH_4 buffer and DNTPs (10 mM), 1.5 µl of $MgCl_2$ and 0.2 µl of *Taq*-polymerase (Bioline). CO1 was amplified using the universal fish primers Fish F1, Fish F2, Fish R1, and Fish R2 (Ward et al. 2005). The control region was amplified using the universal primers CR-A and CR-E (Lee et al. 1995). PCR reactions were purified using a standard Exo-SAP protocol (using reagents and specific protocols from New England Biolabs) and outsourced to Macrogen (Korea) for DNA sequencing via capillary electrophoresis. Sequence trace files were manually checked and edited, using Codon Code Aligner v3.0.2.

Data from earlier published studies

In addition to the new mtDNA sequence data generated specifically for this study, we conducted a literature search to identify studies that had sampled marine animals on either side of the Torres Strait and used mtDNA sequences to determine population structure. In order to standardize the analyses across datasets, the published mtDNA datasets were reconstructed using Genbank accession information and information provided in the published papers. Several relevant studies were not included because there was insufficient information to recover the original sequence data.

Phylogeographic, population genetic, and coalescent analyses

For each of the four newly sampled reef fish species, we constructed haplotype networks to visualize the data (although our main conclusions derive from summary statistics and coalescent analyses). Haplotype networks (combined COI and region) were produced in TCS v1.18 (Clement et al. 2000) with a 95% connection limit. Because regional *Apogon doederleini* sequences were highly divergent and reciprocally monophyletic, we were concerned that western and eastern samples might not be sister taxa and that their divergence could be due to factors not associated with vicariance due to the Torres Strait land bridge. To verify that our sampled *Apogon* were sister taxa, we augmented our phylogenetic analyses for *Apogon* by searching Genbank for COI sequences for species within the same genus. All *Apogon* sequences were manually aligned with Se-AL v2.0a11 (Rambaut 1996). A maximum likelihood tree was constructed in PAUP version 4.0b10 (Swofford 1998) using a GTR+G+I model, as selected by Modeltest (Posada and Crandall 1998) using the Akaike information criterion as the most appropriate model of molecular evolution for the data. Branch support was assessed using bootstrapping based on neighbor-joining (with the same GTR+G+I model) and parsimony trees (with maxtree per bootstrap replicate limited to 1,000) in PAUP, and also using the Bayesian approach implemented in MrBayes (ver. 3.1.2, Ronquist and Huelsenbeck 2003) using a GTR model of molecular evolution.

For our reef fish species, we assessed diversity by population and region. DNA polymorphism (number and diversity of haplotypes, polymorphic sites, and π, the average number of pairwise differences) and Tajima's D statistic (as an estimator of deviations from neutral, equilibrium expectations, Tajima 1989) were estimated for all populations sampled using DNAsp v5.00.07 (Rozas et al. 2003). In addition, population structure among all pairs of populations was evaluated using Meirman's F_{ST} (Meirmans 2006), with the significance assessed based on 999 permutations using GenoDive version 2.0b19 (Meirmans and Van Tienderen 2004).

Because exact sampling regimes differed among published studies, all comparisons across species had to be at a regional level. We consider our two regions to be western Australia (west of the Gulf of Carpentaria, with Ningaloo Reef the most commonly sampled) and eastern Australia (east of the Torres Strait, with the GBR region being most commonly sampled). To assess regional gene diversity (proportional to N_e, effective population size) within populations, we estimated π for each sampled population in a given study and then took the regional mean value across the sampled populations; this gave us an average measure of diversity per population per region. For some studies, sampling was diffuse within regions and not linked to specific populations—for instance, the two *Echinolittorina* species consisted of a few individuals from both the west and the east but collected from several locations. For such cases, we analyzed all individuals from a region as a single population (see ESM for sampling schemes in each study). Population structure was estimated using the AMOVA framework (Excoffier et al. 1992) as implemented in GenoDive. For studies where there were multiple populations sampled per region, we estimated Φ_{CT}, the partitioning of variation among regions. For all studies, we estimated Φ_{ST} for the geographically most proximate pair of populations spanning the Torres Strait (based on the 10 m contour, but not sampled from within the Torres Strait itself; a few studies had 1–2 individuals from reef locations within the present-day Torres Strait region). The Torres Strait was chosen as the exact point of demarcation

as it has the shallowest seabed and was the last land area to be inundated. For our fish samples, we used Ningaloo and Lizard Island populations as all four species were sampled from these two locations.

In addition to the standard estimates of genetic diversity and population structure described above, we used a coalescent approach to estimate genetic diversity, divergence time, and migration rates. *IMa* (Hey and Nielsen 2007) is based on a two population model, whereby populations have diverged at the same point in the past but migration since divergence is permitted (Nielsen and Wakeley 2001). This model captures the essential elements of our system, namely two regional populations that have diverged, yet migration between populations can occur. Again, we concentrated on the geographically most proximate pair of populations spanning the Torres Strait for previously published studies and used Ningaloo and Lizard Island populations for our fish species. Initial runs used Bayesian priors of $\theta = [1, 10]$, eastward and westward migration = [0, 10], divergence time = [0, 5], with a burn-in of 1,000,000 steps and a total of 20,000,000 steps using the Computational Biology Service Unit at Cornell University (April 2008 version). Following initial runs, the total number of steps was adjusted such that all ESS estimates were greater than 200 (see *IMa* documentation). For the four fish species, we also conducted a series of runs with maximum divergence time adjusted such that the time period of 1–500,000 years was considered, assuming a molecular clock rate of 1.2% per million years for COI based on several reef fish species separated by the Isthmus of Panama (Bermingham et al. 1997). All running conditions per species were repeated in triplicate, and results were found to be consistent between runs.

Because different mtDNA gene regions have been used in different studies, estimators of $N\mu$ (heterozygosity or gene diversity) such as π or θ will be affected by gene-specific neutral mutation rates (μ) such that relative population sizes between species cannot be inferred across studies. π and θ values, however, can be compared between western and eastern regions within each species. For example, if these values were consistently greater in western Australia, we might conclude that population sizes (and by inference long-term population stability) have historically been greater in the western region. Among the fish species considered here, π and θ values can be compared among species under the assumption of a single common mutation rate for the same gene region (i.e., COI).

We also tested the specific hypothesis that all four reef fish species experienced simultaneous divergence in a hierarchical approximate Bayesian computational framework (Hickerson et al. 2006). Here, data from multiple species are considered in combination and the observed fit to parameters shared among species (such as divergence time) evaluated. A single mutation rate is implicitly assumed, although the exact rate does not have to be specified. The program msbayes (ver. 20081106, Hickerson et al. 2007) was used to simulate data with priors guided by *IMa* results. Divergence time was set to $\tau = [0, 5]$, and simulations were run both with migration fixed at zero and allowed to vary, $m = [0, 10]$, and max θ equal to 50 or 100. Theta values were set both at a maximum equal to 50 and 100. The hyper-parameter Ψ, which reflects the number of discrete divergence events, was allowed to vary between 1 (i.e., simultaneous divergence across species) and 4 (separate divergence time for each of the four species). The top bounds for the ancestral population size relative to current population size was set to 1, matching a scenario of vicariance between regions, and we used 1 million draws per set of simulation conditions and a tolerance of 0.002. The observed data from Ningaloo and Lizard Island populations were compared against simulations using the estimate of Ω as a measure of fit, whereby $\Omega > 0.01$ can be considered as rejecting simultaneous divergence (Hickerson et al. 2006).

Results

MtDNA was sequenced from *Apogon doederleini*, *Acanthurus triostegus*, *Dascyllus trimaculatus*, and *Pomacentrus coelestis* populations from Ningaloo (western Australia), Lizard Island (GBR, eastern Australia), and some additional populations in the GBR and Coral Sea (exact populations varied among species for these latter locations). COI was successfully PCR-amplified and sequenced for all four species, and the control region was also amplified and sequenced for all species except *A. triostegus*. (Multiple attempts at PCR amplification with various primer combinations targeting the control region were unsuccessful for this species.) Sequences have been deposited in Genbank (Acc Nos. JF717878-JF718183). Because of the imbalance in the species representation for control region data, for some analyses we primarily present COI results, so comparisons can be made across fish species. From published literature, we were able to reconstruct datasets for nine species of marine animals; all sources of data are summarized in Table 1.

Haplotype networks showed a range of phylogeographic patterns for the reef fish, ranging from no obvious association with geographic location for *Acanthurus triostegus* and *D. trimaculatus* to reciprocal monophyly between western and eastern populations of *Apogon doederleini* (Fig. 2). The large number of fixed differences between *A. doederleini* clades prompted us to verify that these two clades are sister taxa. Using all *Apogon* COI sequences found on Genbank, we conducted several phylogenetic analyses and in all cases

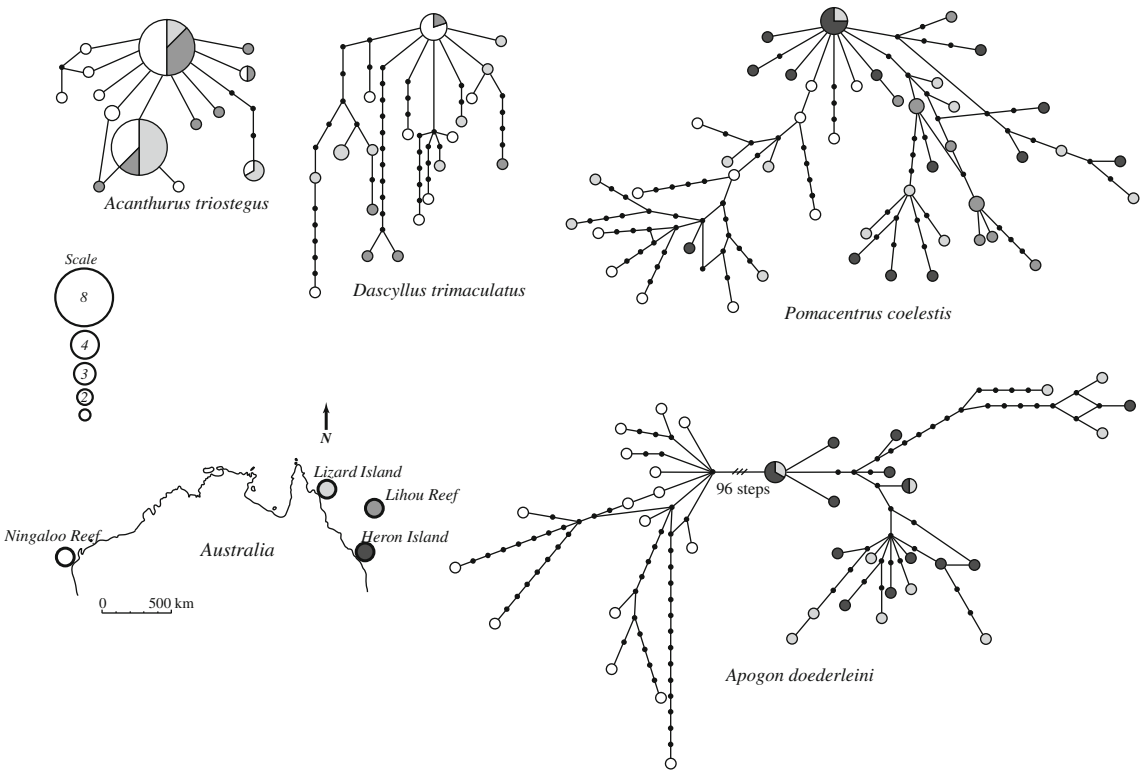

Fig. 2 Haplotype networks for four reef fish species. *Small black circles* indicate haplotypes not observed in our samples. Haplotypes are *shaded* by location and the size is proportional to the observed number. Haplotypes are comprised of concatenated COI and control regions except for *Acanthurus triostegus* where only COI data are included

found high support for the monophyly of our two *A. doederleini* clades; that branch was present in the maximum likelihood tree and had a bootstrap support of 96% from neighbor-joining and a 97% posterior probability in the Bayesian analysis based on 1 million MCMC steps following a burn-in of 11.5 million steps (Figure of phylogenetic tree available in ESM). Although it is possible that the western and eastern forms of *A. doederleini* are different species, they appear to be sister taxa and therefore their divergence time is relevant to this study.

Standard estimators of population diversity among our fish species showed no consistent regional patterns. The population locations with the highest and lowest levels of diversity differed by species and estimator. There were no significant deviations from neutral equilibrium expectations as measured by Tajima's *D*. There was significant genetic differentiation between populations as measured by F_{ST} for many comparisons involving the single western population of Ningaloo with other populations. Estimates of gene diversity and population structure between Ningaloo and Lizard Island fish populations are summarized in Table 2, where there was significant genetic differentiation for *A. doederleini* and *P. coelestis* but not for *D. trimaculatus* or *Acanthurus triostegus*. (Population-specific results for these fish species are available in the ESM.) Table 2 also summarizes the results from species previously studied by other investigators. Many species showed substantial and significant genetic partitioning between western and eastern regions, whereas other species had a complete lack of population genetic structure. Results from the coalescent *IMa* analyses matched standard estimates of population diversity and structure: neither western nor eastern regions were consistently more genetically diverse across species, and many species had significant genetic divergence between regions. Estimates of migration rates and numbers of migrants also differed among species with no consistent directionality inferred.

Due to the common sampling scheme for reef fishes (gene region and populations sampled), we were able to explicitly test the hypothesis of simultaneous divergence across these four species. For all four sets of conditions examined (max $\theta = 50$, 100 and max $m = 0$, 10), the estimated value for Ω was equal to ~ 0.2, substantively greater than the suggested threshold of 0.01 for rejecting a single divergence time (Hickerson et al. 2006).

Discussion

By combining new mtDNA sequence data from four reef fish species with previously published data, we were able to

Table 2 Gene diversity, genetic differentiation, and migration of animals distributed across the Torres Strait

Species	Standard estimates			Coalescent estimates (90% credibility intervals)						
	Gene diversity		Genetic differentiation (F-statistics)	Gene diversity		Genetic differentiation (divergence time scaled by N)	Migration rate		Number of migrants	
	π_{WA} (%)[a, b]	π_{EA} (%)[a, b]	Φ_{CT}/Φ_{ST}[d]	ϑ_{WA}[a, e]	ϑ_{EA}[a, e]	$t\mu$[d, e]	m_{WA}/μ[a]	m_{EA}/μ[a]	Nm_{WA}[a, f]	Nm_{EA}[a, f]
Reef fishes										
Apogon doederleini	0.23	0.34	0.905**	3.54 (0–8.97)	3.74 (0–7.78)	4.02** (0.47–5.00)	0 (0–9.04)	0 (0–9.04)	0	0
Pomacentrus coelestis	0.51	0.30	0.064*	51.37 (12.41–51.37)	51.37 (13.65–51.37)	0.83** (0. 29–1.78)	0 (0–8.94)	4.05 (0.44–9.22)	0	208
Dascyllus trimaculatus	0.09	0.13	0.078	0.33 (0.04–6.38)	0.33 (0.05–6.50)	0.06 (0.00–4.43)	10.0 (0–10)[g]	10.0 (0–10)[g]	3.3	3.3
Acanthurus triostegus	0.37	0.32	0.059	0.50 (0.40–27.08)	21.77 (0.64–27.08)	0.23 (0.15–5.00)	0 (0–9.01)	4.54 (2.32–10.0)	0	99
Other vertebrates										
Aipysurus laevis	0.13	0.06	0.709**/0.409**	2.45 (0.74–26.36)[g]	0.09 (0–2.22)	1.21** (0.50–5.00)	0 (0–9.01)	0 (0–9.01)	0	0
Stegostoma fasciatum	0.15	0.07	0.290**	0.95 (0.18–9.21)	0.24 (0–1.01)	2.29** (0.48–5.00)	6.08 (1.52–10.00)	1.27 (0–8.38)	5.8	0.3
Chelonia mydas	0.83	0.85	0.549**/0.777**	0.47 (0–1.52)	1.87 (0–5.36)	0.62** (0–4.54)	0.06 (0–3.15)	0.18 (0–1.74)	<0.1	0.3
Mollusks										
Haliotis asinina	0.15	0.08	0.956/0.969**	1.12 (0–3.59)	0.17 (0–1.26)	1.36** (0.89–5)	0 (0–0.90)	0 (0–2.27)	0	0
Echinolittorina trochoides B	0.41	0.23	−0.021	62.88 (12.49–62.88)	7.64 (6.89–62.88)	1.20** (0.25–2.94)	0 (0–9.01)	0 (0–8.94)	0	0
Echinolittorina vidua	0.86	0.31	0.767**	95.89 (19.81–95.89)	12.81 (10.98–95.89)	0.99** (0.06–3.08)	0 (0–8.91)	0 (0–8.85)	0	0
Other invertebrates										
Scylla serrata	0.58	0.04	0.848**/0.678**	1.60 (0–3.55)	0.07 (0–0.55)	1.07** (0.10–4.15)	0 (0–1.62)	0 (0–7.48)	0	
Diadema setosum-a	0.15	0.26	0.032	0.27 (0–11.05)	1.06 (0.35–14.48)	0.20 (0–4.46)	0 (0–8.67)	9.29 (2.44–10)	0	9.8

Table 2 continued

Species	Standard estimates			Coalescent estimates (90% credibility intervals)					
	Gene diversity		Genetic differentiation (F-statistics)	Gene diversity		Genetic differentiation (divergence time scaled by N)	Migration rate		Number of migrants
	π_{WA} (%)[a, b]	π_{EA} (%)[a, b]	Φ_{CT}/Φ_{ST}^{d}	$\vartheta_{WA}^{a, e}$	$\vartheta_{EA}^{a, e}$	$t\mu^{d, e}$	m_{WA}/μ^{a}	m_{EA}/μ^{a}	$Nm_{WA}^{a, f}$ $Nm_{EA}^{a, f}$
Holothuria nobilis	0.39	0.46	0.007/0.029	25.76 (14.60–80.83)	36.11 (19.21–80.83)	0.81** (0.53–1.18)	2.42 (1.13–10)	1.29 (0–9.44)	62 47

[a] Specific geographic regions are indicated and can include western Australia (WA) and eastern Australia (EA). Migration (in the conventional sense) is into the population, e.g., m_{WA}/μ is the rate of migration (scaled by the mutation rate) into Western Australia

[b] Average number of pairwise differences; where there are multiple populations sampled per region, π is the average value across the regional populations

[c] Hierarchical AMOVA is used in cases where there are two or more populations per region. Otherwise pairwise Φ_{ST} for the nearest two populations spanning the Torres Strait is reported

[d] * indicates $P < 0.05$; ** indicates $P < 0.01$; based on 999 replicates for AMOVA and log-likelihood tests for $t\mu$. See text for more detail

[e] Based on per-locus estimates. These are not comparable across studies as different studies employed different mtDNA regions; the exception is our new fish data where the same region of COI was sequenced

[f] Number of migrants per generation; the product of most probable point estimates for ϑ and m/μ

[g] Discontinuous posterior probability distribution

examine patterns of genetic diversity and divergence for thirteen species of marine animals across the historic Torres Strait land bridge. We found that there was significant population structure across the Torres Strait for many species, consistent with long-standing vicariance. The degree of genetic structure, however, ranged from very high ($\Phi_{ST} > 0.7$: Table 2, and reciprocal monophyly of mtDNA haplotypes between regions: Fig. 2) to negligible (Φ_{ST} not significant, no phylogeographic structure). Coalescent analyses of reef fish mtDNA data imply that there was no single divergence date across species, a pattern qualitatively matched in previous studies. Estimates of migration similarly varied among species and directionality was idiosyncratic.

Broadscale phylogeographic concordance

The Torres Strait land bridge was an intermittent barrier to dispersal in the late Pleistocene for approximately 90,000–100,000 years, until its most recent inundation ~7,000 years ago (Voris 2000). Evidence that this barrier and/or the large geographic distance between sampling sites (see "Materials and methods") contributed to population structure between western and eastern populations was strong for eight out of thirteen marine animals considered here (i.e., significant Φ_{ST} and matched by significant divergence times in *IMa* analyses: Table 2). For instance, genetic differentiation between Indian and Pacific Ocean populations was high for the reef fish *Apogon doederleini* and strong for *Pomacentrus coelestis*. These results match observations from previous studies representing a diverse cross-section of marine animals with perfect or nearly perfect reciprocal monophyly between western and eastern Australian populations, including coral trout (van Herwerden et al. 2009), sea snakes (Lukoschek et al. 2007), sea turtles (Dethmers et al. 2006), abalone (Imron et al. 2007), a littorine snail (Reid et al. 2006), and mud crabs (Gopurenko et al. 1999). (See also significant Φ_{ST} values for some of these same species in Table 2).

The repeated observation of high population structure (Table 2) across species with widely differing ecologies (Table 1) is the hallmark of past vicariance (Avise et al. 1987; Avise 2000). Thus, our genetic data support a historical scenario whereby regional populations of many species persisted in both Indian and Pacific Ocean reefs through the late Pleistocene and Holocene, although the large geographic distance between sampling points would also be expected to contribute to population structure. If a species had become locally extinct in one region, then colonization would have been within the last 7,000 years, and we would expect to find no appreciable genetic divergence between populations and reduced diversity in the colonized region relative to the source (Hewitt 1996).

Among the five panmictic species (based on *F*-statistics), mtDNA gene diversity was greater (at least two times difference for either conventional or coalescent estimators) in the western region for *E. trochoides B*, greater in the eastern region for *Acanthurus triostegus* and *Dascyllus setosum-a*, and equivalent for *D. trimaculatus* and *H. nobilis.* Whereas we cannot exclude colonization scenarios for these five species, there is no consistent pattern that would indicate that one region historically supported greater species diversity than the other.

Multiple ages of vicariance

Although the pattern of vicariance and secondary contact is common to many species distributed across tropical Australia, the age of divergence between Indian and Pacific Ocean populations appears to differ markedly among species. Because studies compiled from the literature employed different mtDNA gene regions, the estimated divergence times ($t\mu$: Table 2) can reflect gene or taxon-specific mutation rates (μ) and are not comparable. We can, however, make direct comparisons among our surveyed reef fishes under the assumptions of a molecular clock (without using a specific clock rate). The sequenced gene region was the same and the species are from fairly similar taxonomic groups, so the assumption of a common mutation rate is reasonable inasmuch that such an assumption is ever valid. For these reef fish species, coalescent analyses using *IMa* indicated different divergence times, evidenced by peak posterior probabilities for different $t\mu$ values among species (Fig. 3). The hierarchical approximate Bayesian computation framework also allowed us to explicitly reject the hypothesis of simultaneous divergence ($\Omega > 0.01$). In Fig. 3, we have used a molecular clock calibrated for fish COI to illustrate these varying divergence times in years, but regardless of any specific clock employed, these differences among species would remain. If we assume that the clock used is roughly correct, then divergence times for *P. coelestis* and *Apogon doederleini* appear to substantially predate the last glacial cycle.

Prior to the most recent flooding of the Torres Strait land bridge, there would have been a marine connection at approximately 120 kyr and at other older times of high sea level stands (Chappell and Shackleton 1986; Voris 2000). The old divergence of *P. coelestis* and *A. doederleini* between western and eastern Australia implies that Holocene gene exchange has been insufficient to erase signatures of Pleistocene separation times and that regional populations have persisted in isolation from each other for a long time (albeit with some post-divergence gene flow for *P. coelestis*: Table 2). In contrast, the recent west–east divergence for *D. trimaculatus* and possible lack of divergence for *Acanthurus triostegus* (reflected in a flat posterior

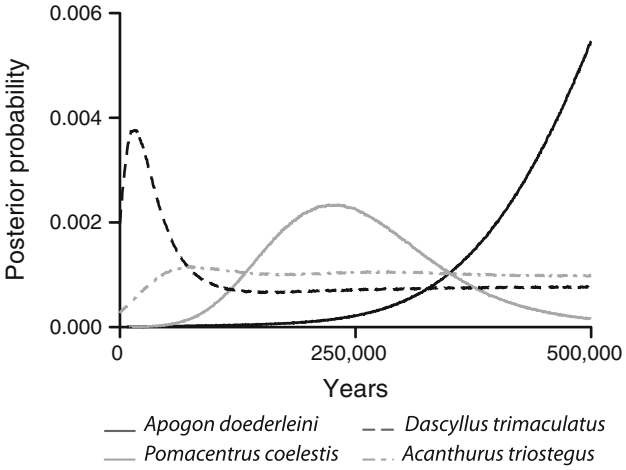

Fig. 3 Posterior probabilities of divergence times between Indian and Pacific Ocean populations of reef fishes based on *IMa*

probability surface: Fig. 3) suggest that there have been strong genetic connections between regions, possibly entailing large-scale colonization in addition to continuing gene flow. One possibility is that *A. triostegus* and *D. trimaculatus* circumvented the Torres Strait barrier via stepping-stone connections north of New Guinea. For these species, recent (Holocene) events obscure the past, and therefore we are unable to make strong inferences about regional patterns of persistence. Similarly, our inference about regional patterns is somewhat hampered as it is based on sampling of a single site in western Australia (Ningaloo) that is quite distant from the Torres Strait itself; Ningaloo is the sampling site for our fishes and western site most proximate to the Torres Strait in most other studies. Thus, we have detected divergence between western and eastern Australian populations and have assumed that vicariance due to the past land bridge is the cause of this divergence and not some other factor, for example, specific to Ningaloo. The studies that have more extensive sampling (multiple populations per region) also showed substantial regional population structure (Φ_{CT}: Table 2), indicating that western and eastern populations of many species are distinct and that there is nothing unusual about Ningaloo as representative of western Australian populations.

Whereas the inclusion of additional loci per species (i.e., nuclear loci) would strengthen the conclusions for individual species (due to the inherent high variance in coalescence times among independently assorting loci), our emphasis was on uncovering regional patterns where species could be considered as independent realizations of shared geographic history. For such a comparative framework, mtDNA sequences deliver substantial information relative to effort and costs.

The overall pattern that emerges from fishes (and is consistent with other species surveyed: Table 2) is that the

Torres Strait and large expanse of northern Australia has been a long-standing potent barrier for some species, whereas for other species these barriers have been transitory, with genetic connections between regions intermittently reestablished during periods of high sea level stands. A similar diversity in phylogeographic patterns has been described for marine species at the Atlantic–Mediterranean transition (Patarnello et al. 2007), where a complete barrier to movement has also been historically intermittent.

Life history traits, divergence times, and gene flow

One of the goals of historical ecology is to investigate how species composition of ecological communities has changed over time and to identify suites of life history traits that have affected community membership (Wares 2002; Hickerson et al. 2010; Tager et al. 2010). Similarly, how life history traits affect dispersal (often inferred from genetic patterns) among established populations is a topic of considerable interest. For marine animals, factors such as pelagic larval duration (PLD), egg type (for reef fishes), and larval feeding mode (for invertebrates) are obvious candidates for predicting dispersal and colonization ability. Species with non-planktonic larvae nearly always have greater population structure than those with planktonic larvae (reviewed by Weersing and Toonen 2009). Egg type and larval feeding mode can be correlated with differing patterns of genetic structure (Watts and Thorpe 2006; Pelc et al. 2009; Riginos et al. 2011), whereas effects of PLD on genetic differentiation are probably less important (Weersing and Toonen 2009).

In the present study, we find that qualitative predictors of dispersal ability match rank order estimates of population genetic structure and gene flow for reef fishes. Among the reef fishes, the only species with a high posterior probability for zero gene flow was *Apogon doederleini*, and this lack of gene flow matched expectations based on larval biology. *A. doederleini* brood their young in their mouths (Takeyama et al. 2007), develop quickly, and larvae orient themselves toward natal reefs (Atema et al. 2002; Gerlach et al. 2007). The predicted high-dispersal species, *Acanthurus triostegus* (planktonic eggs, long PLD), was panmictic, matching predictions based on larval morphology. Unlike allozyme surveys of the same species (Planes 1993; Planes et al. 1998; Planes and Fauvelot 2002), however, we did not detect significant geographic differentiation of mtDNA. For the putative intermediate dispersers, *P. coelestis* and *D. trimaculatus* with benthic eggs and relatively short PLDs, the results were mixed with significant population structure for *P. coelestis* and not for *D. trimaculatus*. *P. coelestis* is known to orient toward reefs, which might contribute to genetic differentiation. Nothing specific has been published about *D. trimaculatus* larval behavior.

Alternative to egg and larval traits affecting genetic patterns, differences in divergence times could reflect the habitat preferences of each study species. In a recent study, Ayre et al. (2009) demonstrated that habitat specificity could be an important determinant of genetic differentiation for intertidal invertebrates. In the case of the Torres Strait, as sea levels rose and covered the land bridge, some species could have recolonized the newly submerged areas before others. Such a pattern has been demonstrated with the Isthmus of Panama, with divergence for coastal species post-dating those species that are limited to deep water or isolated islands (Knowlton and Weigt 1998). *Acanthurus triostegus* are generalists and are often found in turbid, high-flow environments such as coastal bays and harbors (pers. obs). These characteristics may have allowed *A. triostegus* to quickly colonize new habitat. Of the other three fish species, *P. coelestis* has the least specific habitat preferences, as they settle on the outer reefs in low quality habitat (Gerlach et al. 2007), so this species would probably be able to colonize new habitat quickly. *Apogon doederleini* larvae settle deep in the reef (Gerlach et al. 2007) and *D. trimaculatus* settle onto large anemones (Bernardi et al. 2001) or coral heads in the absence of anemones (pers. obs.), indicating greater habitat specificity, especially for *D. trimaculatus* (the habitat specificity of *D. trimaculatus* may explain the lower gene diversity relative to the other fishes: Table 2). Although habitat specificity would predict that *P. coelestis* would be a better colonist than *D. trimatulatus*, we find greater divergence between western and eastern populations for *P. coelestis* as compared to *D. trimaculatus.*

For the reef fishes considered here, there are possible correlations between species characteristics and west–east connections over time; however, it is impossible to make strong inference with only four species. The additional nine marine animals examined represent a diverse array of phyla with a wide variety of traits relevant to dispersal ability and habitat specificity. Our a priori predictions of relative dispersal ability do not match observed genetic patterns and no obvious differences emerge based on coarse habitat type (e.g., coral reef and pelagic). Fine-tuning our predictions regarding dispersal ability or habitat specificity (for instance, restricting analyses to closely related species that differ in single relevant traits, or using quantitative niche predictions) could potentially uncover correlations that are obscured by coarse analyses such as those presented here. Alternatively, it is quite possible that species and community responses to historical barriers and fluctuating local conditions are idiosyncratic and not predictable (Patarnello et al. 2007; Tager et al. 2010). Such a conclusion may be warranted when the predictive characteristics comprise broad categories that cut across evolutionarily diverse taxa.

Acknowledgements Thanks to J. D. Aguirre-Davies and F. MacKenzie for assistance in the field, and two anonymous reviewers for comments. The Computational Biology Service Unit from Cornell University, which is partially funded by Microsoft Corporation, was used for some analyses. Funding for this work was provided by the Australian Research Council (DP0878306 to CR), and the World Wildlife Fund (to EAT). Fishes were collected under permits from the Department of the Environment, Water, Heritage, and the Arts (AUCOM2008042), Great Barrier Reef Marine Park Authority and Department of Environment and Resource Management (G08/28114.1), Queensland Government Dept. of Primary Industries & Fisheries (118636), and WA Department of Environment and Conservation (SF006619). This study complies with Animal Ethics standards for the University of Queensland (permit SIB/817/08/ARC).

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