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ORIGINAL ARTICLE

Phylogeography of related diadromous species in continental and island settings, and a comparison of their potential and realized dispersal patterns

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ABSTRACT

Aim To compare patterns of potential and realized dispersal in ecologically similar and phylogenetically related amphidromous shrimps (Atyidae) in continental and island-dominated landscapes.

Location Eastern Australia and the Caribbean region.

Methods Population genetic and phylogeographic analyses of mitochondrial DNA data for *Australatya striolata* from eastern Australia (a continental landscape) and *Atya scabra* from the Caribbean (an island-dominated landscape).

Results *Australatya striolata* contained two highly divergent genetic lineages in eastern Australia, corresponding to the disjunct northern and southern populations, respectively. These lineages probably represent allopatric cryptic species, both of which were found to have genetically homogeneous population structures within their regions of occurrence. *Atya scabra* was genetically homogeneous throughout the Caribbean. Recent population expansions were detected for *Atya scabra* in the Caribbean, but not for northern or southern *Australatya striolata*.

Main conclusions The findings of this study are consistent with previously reported patterns of genetic population structure in amphidromous species in both continental and island-dominated landscapes, suggesting that *potential* for widespread dispersal is typically matched by *realized* patterns of panmixia. We therefore raise the hypothesis that landscape setting (i.e. continent or island-dominated) does not influence dispersal patterns in amphidromous species. Further studies, especially of population genetic patterns of amphidromous species on continents, are needed to test this idea. Interestingly, results of the genetic neutrality tests led us to hypothesize that demographic and drift-mutation equilibrium is attainable although not always evident for amphidromous species on continents, but is not attainable for those species distributed across island settings.

Keywords

Amphidromy, *Atya scabra*, Atyidae, *Australatya striolata*, Caribbean, eastern Australia, juvenile-return anadromy, mitochondrial DNA, population history, riffle shrimp.

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INTRODUCTION

The importance and mechanisms of dispersal have long been subjects of evolutionary and ecological research (e.g. Bilton *et al.*, 2001; Bohonak & Jenkins, 2003). The often reported mismatch between *potential* (i.e. assumed or predicted dispersal ability based on traits) for widespread dispersal and *realized* (i.e. empirical) patterns of geographically restricted dispersal and gene flow by stream invertebrates has been explained by high variance in rates and scales of dispersal either among species within a common landscape or within contrasting landscape settings for closely related taxa

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(De Meester *et al.*, 2002; Bohonak & Jenkins, 2003; Hughes *et al.*, 2008). Whilst these dispersal patterns have been considered mainly for invertebrate species capable of overland dispersal (e.g. insects, Hughes *et al.*, 2008; microcrustaceans, De Meester *et al.*, 2002), other stream invertebrate groups, notably various species of caridean shrimp and gastropod (and numerous species of fish), are amphidromous and putatively capable of extensive dispersal by larval movement through the sea (Myers, 1949). Amphidromy is a distinct form of diadromy (McDowall, 2007): adults live and reproduce in freshwater reaches of river systems; eggs or larvae are transported downstream to marine habitats where they undergo early development before returning upstream as post-larvae to freshwater adult habitats (Myers, 1949). We note that the amphidromous life history can be defined also as a subset of anadromy (i.e. juvenile-return anadromy; Bell, 2009), with 'amphidromy' and 'juvenile-return anadromy' being synonymous terms (Bell, 2009). Amphidromy is thought to confer considerable potential for oceanic dispersal by larvae in these species, with this expectation shown to be matched by phylogeographic studies that demonstrate widespread genetic continuity at island and archipelago scales (e.g. Chubb *et al.*, 1998; Fièvet & Eppe, 2002; Berrebi *et al.*, 2005; Hoareau *et al.*, 2007; Cook *et al.*, 2008a, 2009; Page *et al.*, 2008; Crandall *et al.*, 2010).

Interestingly, amphidromous species are considerably less prevalent elements of continental freshwater faunas relative to tropical islands (McDowall, 2004, 2010). The combined influence of steep stream gradients, swiftly flowing water and short river systems, typical of high island rivers, appears to be a key element for successful amphidromy (McDowall, 2010). The mechanistic reasons for this may be linked to the effect of these factors on larval survival (Iguchi & Mizuno, 1999; Bell, 2009), with survival of drifting larvae being greatest in shorter, steeper systems that rapidly transport larvae to marine habitats, and survival diminishing in longer, low gradient systems within which larvae have increased risks of predation or starvation. Indeed, fitness costs associated with failed reproduction and recruitment may increase in an upstream direction even within relatively small rivers on islands (Bell, 2009). Consequently, it has been suggested that large rivers, such as those typical of continents, may exert selection pressures that favour the abandonment of amphidromy, with some studies reporting instances where amphidromous-freshwater life history transitions have occurred on continents (e.g. Cook *et al.*, 2006; Page & Hughes, 2007). Some of these derived freshwater species have evolved abbreviated larval stages, or even abandoned planktonic larval stages, and thereby reduced larval dispersal to guard against mortality by strong water flow (e.g. Hughes *et al.*, 1995; Bauer, 2011a; see also Crandall *et al.*, 2010). Whilst amphidromous species on continents have not taken the drastic evolutionary step of changing their life history to be pure freshwater residents, it is possible that similar dispersal limitation strategies, such as retention in the estuary of the natal river, enable amphidromous species on continents to guard against larvae being 'lost' to ocean currents (Schmidt *et al.*, 2011). Indeed, Benstead *et al.* (2000) reported multiple larval stages of caridean shrimps within estuaries of two rivers from Puerto Rico, suggesting that a proportion of larvae may use retention strategies and undergo early development within estuaries even on islands.

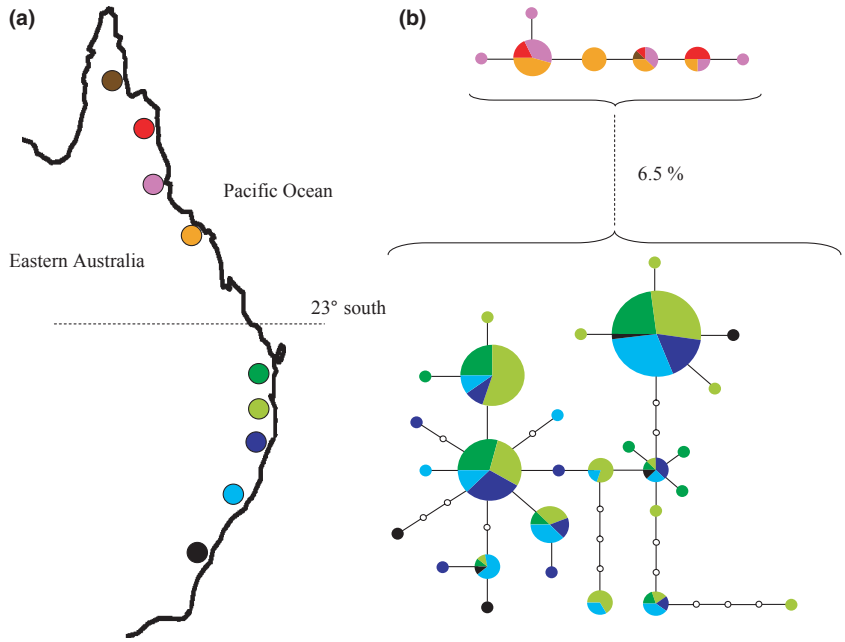

Figure 1 (a) Map of eastern Australia, showing the locations sampled for *Australatya striolata*. Colours at sample sites relate to colours in the haplotype network. (b) Haplotype network for *A. striolata*, sampled from eastern Australia. Circles relate to haplotypes, with colours indicating the geographic origin of the haplotype. Small unfilled circles are unsampled haplotypes and the size of the circle relates to the relative frequency of the haplotype in the sample.

Whilst this trait may represent phenotypic plasticity on islands, we speculate that larval retention may be selected for in continental landscape settings and that we may therefore detect genetic population heterogeneity [i.e. significant population genetic differentiation and isolation-by-distance (correlation between genetic and geographic distance)] among rivers in continental landscapes.

In this study we assessed nucleotide variation within the cytochrome *c* oxidase subunit I (COI) mitochondrial DNA (mtDNA) gene for two closely related atyid shrimps, *Australatya striolata* (McCulloch & McNeill, 1923) from eastern Australia (Fig. 1a) and *Atya scabra* (Leach, 1815) from the Caribbean region (Fig. 2a), to examine phylogeographic patterns and dispersal in the different landscape settings inhabited by the species. The COI mtDNA genetic marker is used widely in studies of dispersal, gene flow and molecular biogeography in invertebrates, including population genetic patterns in amphidromous shrimps (e.g. Bebler & Foltz, 2004; Cook *et al.*, 2008a; Page *et al.*, 2008; Dennenmoser *et al.*, 2010) and amphidromous gastropods (Myers *et al.*, 2000; Bebler & Foltz, 2004; Crandall *et al.*, 2010). We predicted that *potential* for widespread dispersal throughout the Caribbean region would be matched by *realized* extensive dispersal and genetic continuity in *Atya scabra*, as islands dominate this landscape. In contrast, we predicted that despite having potential for widespread dispersal, *Australatya striolata* in eastern Australia would have significant genetic population heterogeneity among river systems, reflecting the possibility that an evolutionary shift from a dispersive to a dispersal-limited strategy would enable this species to persist in large continental rivers.

MATERIALS AND METHODS

Biology of the study species

Atya scabra and *Australatya striolata* are closely related species of shrimp within the Atyidae, which is a globally distributed family with greatest species diversity in tropical and subtropical climatic zones. *Australatya striolata* was formerly contained within the genus *Atya* (McCulloch & McNeill, 1923; Chace, 1983), indicating morphological similarities between the two species, and molecular phylogenetic research demon-

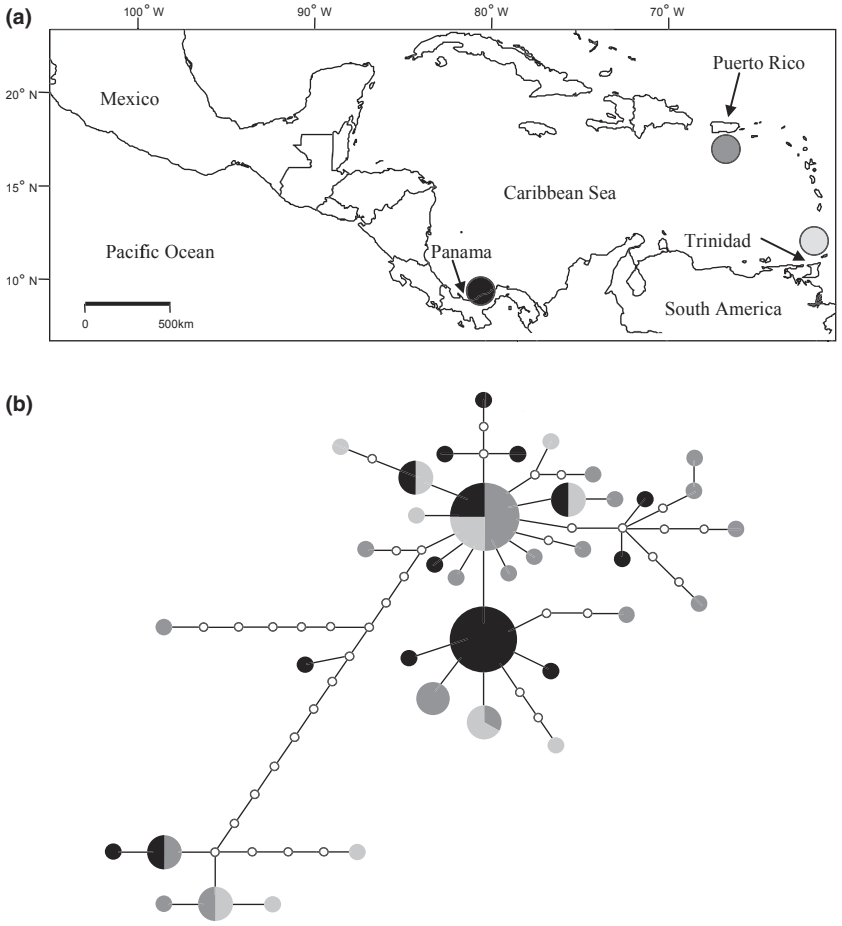

Figure 2 (a) Map of the Caribbean region, showing the three locations sampled for *Atya scabra*: Panama, Puerto Rico and Trinidad. Shading (i.e. black, grey or white) at sample sites relates to colours in the haplotype network. (b) Haplotype network for *A. scabra*, sampled from the Caribbean. Circles relate to haplotypes, with shading indicating the geographic origin of the haplotype. Small unfilled circles are unsampled haplotypes and the size of the circle relates to the relative frequency of the haplotype in the sample.

strates that it is a member of the *Atya* and *Atya*-like clade within the Atyidae (Page *et al.*, 2008). *Atya scabra* and *Australatya striolata* are both amphidromous and have strong habitat preferences for riffles (i.e. fast flowing, often steep sections of stream) where they filter feed (Hobbs & Hart, 1982), although they can also feed by scraping biofilms from benthic surfaces. *Atya scabra* has an extensive distribution, encompassing river systems throughout the Caribbean region (i.e. islands of the Greater and Lesser Antilles and eastern Central America), eastern South America, the Cape Verde Islands and western Africa (Hobbs & Hart, 1982). *Australatya striolata* is widely distributed in eastern Australia, from Cape York Peninsula to north-eastern Victoria, although this distribution is apparently not continuous; northern and southern populations are separated by a stretch of unsuitable adult habitat in central Queensland (Smith, 1994; Fig. 1a). *Atya scabra* and *Australatya striolata* thus have close systematic and ecological affinities and very broad distributions within their respective global regions of occurrence.

Sequence data

Australatya striolata from 22 rivers in eastern Australia were genotyped for the COI mtDNA gene, yielding a total of 188 individuals (GenBank accession numbers JN016250–JN016437; Fig. 1a), although sample sizes for each river varied (Table 1). Twenty-one published COI mtDNA sequences of *Atya scabra* from Rio Maymes, Puerto Rico (GenBank accession numbers EU005086, 087, 090, 091, 092, 095, 106, 108, 130, 131, 150, 153, 162, 165, 171, 181, 209, 210; Cook *et al.*, 2008a) were added to sequence data for this species from Panama ($n = 19$) and Trinidad and Tobago ($n = 12$) (T.J. Page, B.D. Cook, C.M. Pringle, A. Binderup, L.S. Torati and J.M. Hughes, unpublished data; GenBank accession numbers JF810968–JF810990), totalling 52 sequences from three widely spaced populations in the Caribbean region (Fig. 2a, Table 1; genotyping methods described in Cook *et al.*, 2008a). The primers ASTR-F: 5′-CCGAGCAGAACTAGGTCAACCAGG-3′ and ASTR-R: 5′-GGTGTCTACATCTATTCCTACAG-3′ were used for the southern populations of *Australatya striolata*, and NAST-F: 5′-GGAGCCCCAGATATGGCCTTCCC-3′ and NAS T-R: 5′-CCTACAGTAAATATATGGTGTGCTC-3′, for the northern populations. Polymerase chain reactions (PCRs) contained approximately 40 ng of template DNA, 0.4 μM of each primer (3.5 pmol μL^{-1}), 0.2 mM dNTP (Astral Scientific, Sydney, Australia), 2 mM $MgCl_2$, 1.25 μL of 10× polymerase reaction buffer and 0.25 unit of *Taq* polymerase (Fisher Biotech, Perth, WA, Australia), adjusted to a final volume of 12.5 μL with ddH2O. The thermal-cycling profile for both primer sets followed: 5 min at 94 °C; 35 cycles of 30 s at 94 °C, 30 s at 50 °C and 50 s at 72 °C; an additional extension phase of 5 min at 72 °C; and a final hold stage at 4 °C. PCR product was purified with the exonucleoase I-shrimp alkaline phosphatase method, using 2.5 μL PCR product, 2.0 μL shrimp alkaline phosphatase (Promega, Sydney, NSW, Australia) and 0.5 μL exonucleoase I (Fermentas, Glen Burnie, MD, USA), and a two-step thermal-cycling profile: 35 min at 37 °C, 20 min at 80 °C. Sequencing reactions contained 0.5 μL purified product, 0.32 μL forward primer (3.5 pmol μL^{-1}), 2 μL BigDye v1.1 (Applied Biosystems, Melbourne, Vic., Australia) and 2 μL 5× sequencing buffer (Applied Biosystems), and the following thermal cycling conditions were used: 1 min at 96 °C, 30 cycles of 10 s at 96 °C, 5 s at 50 °C, 4 min at 60 °C and a hold period of 4 °C. Sequencing was conducted on a 3130xl Capillary Electrophoresis Genetic Analyzer (Applied Biosystems) at Griffith University and sequences were aligned and edited using SEQUENCHER v. 4.1.2 (Gene Codes, Ann Arbor, MI, USA). An exemplar of each haplotype was sequenced in the reverse direction to verify bases at polymorphic sites. Sequences were translated to amino acid using MEGA2 v. 1.01 (Kumar *et al.*, 2001) to check for pseudogenes and other nucleotide anomalies.

Data analysis

Haplotype (h) and nucleotide (π) diversity and mean pairwise nucleotide differences (k) were calculated for each species in ARLEQUIN v. 3.5.1.2 (Excoffier & Lischer, 2010) to obtain measures of molecular diversity. The parameters D (Tajima, 1989) and F_S (Fu, 1997) were calculated in DNASP v. 5.0 (Librado & Rozas, 2009) to test for evidence of non-neutrality in the mtDNA data. These analyses also indicate population expansions if the resulting values are significantly negative. F_S tests the haplotype frequency distribution in a sample with that expected under neutral evolution and mutation drift equilibrium. An excess of haplotypes in the sample, typically observed in star phylogenies (i.e. radiation of many recently evolved and closely related haplotypes), would give a significantly negative F_S and be indicative of recent population growth. The D statistic is based on the fact that under neutral evolution the number of segregating sites and the average number of nucleotide differences are correlated. Significantly negative D values are observed when there is an excess of segregating sites (e.g. more single segregating sites than expected), as expected in a rapidly growing population. To test whether the empirical D and F_S values were significantly different from zero, we compared them to simulated distributions of these statistics generated using 10,000 coalescent model simulations in DNASP that incorporated the observed number of segregating sites in the empirical data. These analyses were performed only for sampled populations where the sample was at least 10 individuals, although for regional-scale analyses all individuals were included. Genealogical relationships among the haplotypes for each species were constructed using statistical parsimony in the software package TCS (Clement *et al.*, 2000). The program MEGA2 v. 1.01 (Kumar *et al.*, 2001) was used to calculate K2P (Kimura, 1980) divergence between and within the northern and southern populations of *Australatya striolata*, using 1000 bootstrap replicates. This measure of genetic distance is calculated using a simple evolutionary model that assumes equal base frequencies, one transition rate and one transversion rate.

Table 1 Sample locations, sample sizes, molecular diversity (± SE) and results of neutrality tests (*P*-values in parentheses) for northern and southern populations of *Australatya striolata* from eastern Australia and for *Atya scabra* from the Caribbean region. Region codes for *Australatya striolata* are: CYP, Cape York Peninsula; NWT, northern Wet Tropics; SWT, southern Wet Tropics; NCQ, North Central Queensland; SUN, Sunshine Coast; Gold, Gold Coast; NCNSW, north coast New South Wales; CCNSW, central coast New South Wales; SENSW, south east New South Wales. Results for *D* and F_S that were statistically different from zero are indicated in italics. Overall results for each species with all populations pooled are indicated by bold font.

Species	Region	River	*N*	No. of haplotypes	*h*	π	*k*	*D*	F_S
Australatya	CYP	McIllwrath Range	1						
striolata	NWT	Hutchinson Creek*	4						
(northern)	NWT	Ellis Beach	1						
	NWT	Palmer Creek	2						
	SWT	Damper Creek*	15	7	0.781 ± 0.102	0.011 ± 0.006	5.590 ± 2.844	*−0.081 (0.012)*	0.076 (0.698)
	NCQ	Ollera Creek*	5						
	NCQ	Cedar Creek*	5						
Overall			**33**		**0.790 ± 0.045**	**0.007 ± 0.004**	**3.420 ± 1.794**	***−0.105 (0.004)***	**−0.270 (0.665)**
Australatya	SUN	Maroochy River*	16	8	0.842 ± 0.075	0.008 ± 0.005	4.000 ± 2.110	−0.091 (0.711)	−0.021 (0.386)
striolata	SUN	Mooloolah River*	17	6	0.816 ± 0.061	0.007 ± 0.004	3.882 ± 2.050	−0.065 (0.800)	−0.055 (0.761)
(southern)	GOLD	Logan River*	18	9	0.882 ± 0.051	0.009 ± 0.005	4.601 ± 2.369	−0.088 (0.358)	−0.087 (0.398)
	GOLD	Coomera River*	13	7	0.910 ± 0.049	0.007 ± 0.004	3.692 ± 1.995	−0.069 (0.616)	0.010 (0.393)
	GOLD	Nerang River	4						
	GOLD	Mudgeeraba River	4						
	GOLD	Tallebudgera Creek	5						
	GOLD	Currumbin Creek	5						
	NCNSW	Tweed River*	12	8	0.894 ± 0.078	0.008 ± 0.005	4.424 ± 2.347	−0.083 (0.593)	−0.008 (0.239)
	NCNSW	Richmond River*	12	5	0.833 ± 0.069	0.007 ± 0.004	3.833 ± 2.072	−0.095 (0.911)	0.021 (0.798)
	CCNSW	Bellinger River*	15	7	0.857 ± 0.065	0.009 ± 0.005	4.610 ± 2.396	−0.097 (0.556)	−0.070 (0.624)
	CCNSW	Wilson River*	15	6	0.810 ± 0.078	0.008 ± 0.005	4.248 ± 2.231	−0.086 (0.767)	−0.037 (0.748)
	CCNSW	Manning River*	13	8	0.923 ± 0.050	0.008 ± 0.005	4.051 ± 2.161	−0.088 (0.635)	0.129 (0.230)
	SENSW	Hunter	2						
	SENSW	Shoalhaven	4						
Overall			**155**	**28**	**0.851 ± 0.018**	**0.008 ± 0.004**	**4.104 ± 2.056**	**−0.100 (0.110)**	**−0.659 (0.077)**
Atya scabra	Panama	Bocas del Toro	19	16	0.965 ± 0.036	0.009 ± 0.005	5.146 ± 2.608	*−0.096 (0.079)*	*−0.089 (0.002)*
	Puerto Rico	Río Manatí	21	19	0.991 ± 0.018	0.012 ± 3.566	7.314 ± 3.566	*−0.108 (0.049)*	*−0.068 (< 0.001)*
	Trinidad	Paria River	12	11	0.985 ± 0.040	0.012 ± 0.007	7.000 ± 3.539	−0.088 (0.479)	*0.148 (0.026)*
Overall			**52**	**38**	**0.984 ± 0.008**	**0.011 ± 0.006**	**6.396 ± 3.079**	***−0.115 (0.017)***	***−0.466 (< 0.001)***

*Populations of *A. striolata* from rivers marked with an asterisk only were included in pairwise analyses of Φ_{ST}. *N*, number of individuals genotyped; *h*, haplotype diversity; π, nucleotide diversity; *k*, number of pairwise differences; *D*, Tajima's *D*; F_S, Fu's F_S.

Pairwise analyses of inter-population genetic subdivision for each species were implemented in ARLEQUIN (Excoffier & Lischer, 2010) using Φ_{ST} (an index of population genetic differentiation that incorporates both the frequency and divergence of haplotypes) and 1000 permutations of the observed genotypes to assess statistical significance. These analyses were performed only for sampled populations where the sample was at least ten individuals, although for northern *A. striolata*, populations with four or more individuals were assessed (Table 1). Isolation by distance (i.e. correlations between genetic and geographic distance) was tested for each species using Mantel tests in PASSAGE v. 1.0 (Rosenberg, 2001).

RESULTS

Two lineages were detected within *Australatya striolata* from eastern Australia, corresponding to their northern and southern regions of occurrence, respectively. The K2P divergence between these lineages was 6.5 ± 1.0%, which was almost ten times greater than their respective within-group values (i.e. 0.7 ± 0.02% and 0.8 ± 0.02% for the northern and southern populations, respectively). Cross-region pairwise analysis of Φ_{ST} indicated very strong genetic differentiation between northern and southern *A. striolata* (i.e. all inter-region pairwise Φ_{ST} values > 0.875, all P values < 0.001). We therefore considered the northern and southern lineages of *A. striolata* as distinct taxa in subsequent population-level data analyses.

Measures of molecular diversity were highest for *Atya scabra* from the Caribbean, and lowest for northern *Australatya striolata* (Table 1). The neutrality tests indicated mostly significantly negative values for *Atya scabra*, and non-significant results for southern *Australatya striolata*. Northern *A. striolata* had significantly negative values for Tajima's D and non-significant values for Fu's F_S (Table 1). The haplotype networks for each of the three taxa indicated an absence of phylogeographic structuring, although they differed from one another in their structure: *Atya scabra* had a star genealogy (i.e. radiation of many recently evolved and closely related haplotypes) and many individuals (i.e. 52%) represented by a unique haplotype; northern *Australatya striolata* had a linear network with only 9% of individuals represented by a unique haplotype; and southern *Australatya striolata* had roughly equal proportions of internal and exterior genealogical bifurcations with most individuals belonging to one of a few haplotypes that dominated the sample (i.e. only 12% of individuals had a unique haplotype).

No population genetic differences were detected within *Atya scabra* among the three Caribbean regions (Panama versus Puerto Rico, $\Phi_{ST} = -0.015$, $P = 0.653$; Panama versus Trinidad, $\Phi_{ST} = 0.004$, $P = 0.306$; Puerto Rico versus Trinidad, $\Phi_{ST} = -0.021$, $P = 0.669$). Similarly, no population genetic differences were found among populations for either the northern or southern taxa within *Australatya striolata* (within northern region: six among-population pairwise analyses, mean $\Phi_{ST} = -0.035$, mean $P = 0.524$; within southern region: 36 among-population pairwise analyses, mean $\Phi_{ST} = -0.042$, mean $P = 0.766$). It was not possible to test for isolation by distance (IBD) within *Atya scabra* or northern *Australatya striolata*, as the number of populations and individuals per population sampled, respectively, were not large enough. Genetic and geographic distances were not correlated for southern *A. striolata* ($r = 0.256$, $P = 0.884$).

DISCUSSION

The mismatch between potential and realized dispersal and gene flow patterns in stream invertebrates has been explained by differences in dispersal traits among taxa in common landscapes and contrasting landscape settings for closely related taxa (e.g. De Meester *et al.*, 2002; Bohonak & Jenkins, 2003; Hughes *et al.*, 2008). For amphidromous species within landscapes dominated by islands, high potential for widespread larval dispersal through marine habitats has been accompanied by high rates of genetic connectivity at island (e.g. Fièvet & Eppe, 2002; Berrebi *et al.*, 2005; Cook *et al.*, 2008a, 2009, 2010) and archipelago scales (Chubb *et al.*, 1998; Page *et al.*, 2008; Crandall *et al.*, 2010). Our analyses for *Atya scabra* from throughout the Caribbean, which also indicated an absence of population genetic structure, support the assertion that for amphidromous species 'almost anything appears possible' with respect to inter-island dispersal (R. McDowall, pers. comm., cited in Whittaker & Fernández-Palacios, 2007, p. 51). Covich (2006) noted the importance of amphidromy and other dispersive strategies (e.g. aerial dispersal, rafting) in the structuring of freshwater faunal communities of islands, although a recent study has shown some limits to inter-archipelago dispersal at very large geographic scales (i.e. western Pacific versus eastern Pacific; > 2000 km) for the gastropod *Neritina canalis* (Crandall *et al.*, 2010). Population heterogeneity in the species, however, was not accompanied by strong phylogeographic subdivision (i.e. several haplotypes were shared among the regions and region-specific haplotypes were only several base pairs different from one another), and the closely related species *Neripteron dilatatus* was genetically homogeneous at this very large scale (Crandall *et al.*, 2010).

As amphidromous species are considerably less prevalent in rivers within continental landscapes relative to landscapes dominated by islands, we examined the idea that the maintenance of amphidromy on continents may be accompanied by the evolution of dispersal-limitation strategies, as shown for other freshwater species on continents derived from amphidromous progenitors (e.g. Cook *et al.*, 2006; see also Crandall *et al.*, 2010). We therefore thought we might find molecular evidence for restricted gene flow among rivers in *Australatya striolata* in eastern Australia. In contrast, we could not reject genetic panmixia within either the northern or southern taxon. Similarly, no evidence for genetic population structure was found for the amphidromous fish *Prototroctes maraena* from southern Australia (Schmidt *et al.*, 2011) or for the amphidromous shrimp *Cryphiops caementarius* in Chile (Dennenmoser *et al.*, 2010). Furthermore, the one-dimensional dispersal habitat of continental coastlines does not appear to result in

the evolution of stepping-stone populations structures in southern *A. striolata* (this study), *P. maraena* (Schmidt *et al.*, 2011), or *C. caementarius* ($r = -0.529$; $P = 0.142$, our analysis using data from Dennenmoser *et al.*, 2010). Whilst variable patterns of dispersal and population structure have been found in anadromous species (Quinn & Myers, 2004), the results of this study and others (e.g. Chubb *et al.*, 1998; Myers *et al.*, 2000; Berrebi *et al.*, 2005; Cook *et al.*, 2008a, 2009; Page *et al.*, 2008; Crandall *et al.*, 2010; Dennenmoser *et al.*, 2010; Schmidt *et al.*, 2011) demonstrate that widespread dispersal potential appears to be matched by realized dispersal over large geographic extents for amphidromous species in both island and continental landscape settings. Further studies of population genetic structure of amphidromous species with continental distributions are needed, however, to test this supposition. Interestingly, some catadromous species in eastern Australia, including Australian bass *Macquaria novemaculeata* (Chenoweth & Hughes, 1997), have greater population structure than *A. striolata* (i.e. stepping-stone population structure), whereas other catadromus species, including the eel *Anguilla australis*, are panmictic over much larger geographic extents (Dijkstra & Jellyman, 1999). Catadromy therefore reflects a range of realized dispersal patterns, similar to anadromy (Quinn & Myers, 2004), whereas amphidromy appears to be an unvarying life history that facilitates widespread dispersal and gene flow.

As shown at the island scale in Puerto Rico (Cook *et al.*, 2008a), *Atya scabra* has molecular signatures indicative of a recent Caribbean-wide population expansion, in keeping with the idea that disturbance regimes on tropical islands facilitate periodical extinction, recolonization and population growth cycles (Cook *et al.*, 2008a, 2010). Similar results were found for amphidromous gastropods in the Pacific (Crandall *et al.*, 2010). These results contrast patterns of nucleotide variation found for the Puerto Rican freshwater crab *Epilobocera sinuatifrons*, which is a purely freshwater (non-migratory) species, in which demographically stable populations were indicated (Cook *et al.*, 2008b). This suggests that life history traits allow *E. sinuatifrons* to resist disturbances; perhaps its ability to burrow allows connection to ground waters during droughts and refuge from spates during hurricanes. Interestingly, molecular signatures for population growth were not found for *Australatya striolata* (this study) or for *P. maraena* (Schmidt *et al.*, 2011) in eastern Australia. Although the northern *A. striolata* had a significantly negative value for Tajima's *D*, we suggest this does not reflect a recent population expansion, because the F_S value is non-significant and the geneaology was not star-shaped (i.e. was not composed of many recently evolved and closely related haplotypes). Rather, we suggest that small sample sizes have produced the significantly negative *D*, whereby segregating sites that were found only once may be under-represented in the sample. The life history and ecology of *Australatya striolata* in eastern Australia is very similar to that of *Atya scabra*, suggesting that intrinsic differences between the landscape settings have facilitated different population histories for these species. Interestingly, *C. caementarius* from Chile has molecular signatures of recent population growth ($F_S = -0.396$, $P < 0.001$; our analysis of data from Dennenmoser *et al.*, 2010). The distribution of *Atya scabra* extends from the Caribbean region southwards to eastern South America (Chace & Hobbs, 1969). We speculated that the molecular signatures of evolutionary recent population growth in this species we report for the Caribbean region would also be evident within continental regions of its distribution. We therefore hypothesize that demographic and drift-mutation equilibrium is attainable although not always evident for amphidromous species on continents, but is not attainable for those species distributed within island-dominated landscapes.

The strong genetic divergence we report between northern and southern populations of *Australatya striolata* suggests this taxon is composed of two cryptic allopatric species, separated by more than a 500 km stretch of coastline from which the genus is apparently absent (Smith, 1994; this study; Fig. 1b). All three genera of atyid shrimp in eastern Australia, therefore, contain cryptic species (see Cook *et al.*, 2008c). *Australatya striolata* is a habitat specialist as an adult, found only in fast flowing streams and riffle habitats draining coastal mountain ranges (Smith, 1994); habitat types that are absent from the semi-arid plains of central Queensland. However, Dennenmoser *et al.* (2010) did not find genetic differentiation in *C. caementarius* over an extensive geographic break between estuaries in Chile, a distance of about 700 km. It is therefore likely that a strong marine biogeographic boundary explains allopatric diversification of the two lineages within *A. striolata*, rather than large distances between suitable adult habitat in the northern and southern regions, respectively. At 23° S the south-flowing East Australian Current (EAC) diverges to a more easterly flow (Burrage *et al.*, 1996; Fig. 1a), facilitating a biogeographic boundary for various marine species (e.g. Chenoweth *et al.*, 2002; Haig *et al.*, 2010). It is possible that this marine biogeographic barrier along a one-dimensional dispersal habitat in marine waters of eastern Australia has restricted range expansion in *A. striolata* over evolutionary time scales. Differences in various morphological characters are reported between the northern and southern populations of *A. striolata*, with morphological traits of the northern lineage reflecting adaptations to faster current velocities (Smith, 1994). It is possible that the northern lineage is a more recently derived lineage than the southern taxon on account of its lower levels of molecular diversity. We therefore suggest that the northern lineage reflects a past long-distance colonization event from the south, followed by allopatric divergence, adaptation to the local flow environment and probably cryptic speciation.

Finally, we reiterate some conservation issues for amphidromous species (e.g. Pringle, 1997; Greathouse *et al.*, 2006; Cook *et al.*, 2009), particularly the point made by Bell (2009), who suggested that the majority of drifting larvae that survive probably come from adult habitat in relatively downstream reaches of rivers. For example, it was estimated that 75% of surviving larvae within the amphidromous goby *Sicydium*

punctatum originated within only 2 km of the coastline (Bell, 2009). Thus, lower reaches of rivers may therefore be more important areas than upper reaches of rivers for conservation of amphidromous species (Bell, 2009; noted also by Iguchi & Mizuno, 1999). We note that many populations of *A. striolata* occur many tens of kilometres of river distance (e.g. up 100 km) from the coastline in upper catchment areas. Whilst adults of some amphidromous shrimps reportedly migrate to more downstream reaches before releasing larvae (Ideguchi *et al.*, 2007; Bauer, 2011b), or release larvae during periods of high stream flow (Bauer, 2011b), we speculate that smaller coastal rivers and downstream tributaries of large rivers contribute disproportionately more to population maintenance in *A. striolata* relative to headwater reaches of large rivers. This supposition requires validation by future research aimed at identifying the dominant source areas of surviving larvae of amphidromous species in continental river systems.

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