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High Gene Flow Due to Pelagic Larval Dispersal Among South Pacific Archipelagos in Two Amphidromous Gastropods (Neritomorpha: Neritidae)

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1 **High gene flow due to pelagic larval dispersal among South Pacific**
2 **archipelagos in two amphidromous gastropods**
3 **(Neritomorpha: Neritidae)**

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1 ABSTRACT

2 The freshwater stream fauna of tropical oceanic islands is dominated by
3 amphidromous species, whose larvae are transported to the ocean and develop
4 in the plankton before recruiting back to freshwater habitat as juveniles.
5 Because stream habitat is relatively scarce and unstable on oceanic islands, this
6 life history would seem to favor either the retention of larvae to their natal
7 streams, or the ability to delay metamorphosis until new habitat is encountered.
8 To distinguish between these hypotheses, we used population genetic methods
9 to estimate larval dispersal among five South Pacific archipelagos in two
10 amphidromous species of Neritid gastropod (*Neritina canalis* and *Neripteron*
11 *dilatatus*). Sequence data from mitochondrial COI revealed that neither species
12 is genetically structured throughout the Western Pacific, suggesting that their
13 larvae have a pelagic larval duration of at least eight weeks, longer than many
14 marine species. Additionally, the two species have recently colonized isolated
15 Central Pacific archipelagos in three independent events. Since colonization,
16 there has been little to no gene flow between the Western and Central Pacific
17 archipelagos in *Neritina canalis*, and high levels of gene flow across the same
18 region in *Neripteron dilatatus*. Both species show departures from neutrality
19 and recent dates for colonization of the Central Pacific archipelagos consistent
20 with frequent extinction and recolonization of stream populations in this area.

- 1 Similar results from other amphidromous species suggest that unstable
- 2 freshwater habitats promote long-distance dispersal capabilities.

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Introduction

The life histories of marine and freshwater animals are generally very different: marine animals often have planktonic larvae that are potentially dispersive (Thorson, 1950), while freshwater animals typically develop in benthic or brooded egg capsules, probably to reduce dispersal and downstream loss from adult habitat (Holthuis, 1995; Bohonak and Jenkins, 2003). Notable exceptions to this ontogenetic trend can be found in diadromous species, which may reproduce in freshwater before recruiting to marine habitats (anadromy), or reproduce in the ocean before recruiting to freshwater habitats (catadromy). Amphidromy is a lesser-known type of diadromy that has evolved independently in several families of decapod crustaceans, gastropod mollusks and teleost fishes (Myers, 1949; Holthuis, 1995; McDowall, 2004). While the adults of amphidromous species live and reproduce in streams, rivers, or estuaries, their planktotrophic larvae are released downstream to the ocean, where marine salinities are required for their successful development (Anger *et al*, 1990; Diesel and Schuh, 1998; Crandall, 1999; Diele and Simith, 2006). Following metamorphosis and recruitment to river mouths, juveniles migrate upstream to freshwater habitats (Schneider and Frost, 1986; Blanco and Scatena, 2005; Torres *et al*, 2006).

1 Amphidromous species dominate the fish, decapod, and gastropod
2 stream fauna on tropical oceanic islands, most likely because they are the only
3 lotic species capable of regularly colonizing these habitats (Resh and de Szalay,
4 1995; McDowall, 2004). However, while a community ecologist would view
5 them as freshwater animals (e.g. Bandel and Riedel, 1998; Smith *et al*, 2003),
6 their population ecology may be more similar to that of a marine species, due to
7 their pelagically dispersing larvae. Relatively long pelagic larval durations
8 (PLD) have been estimated from laboratory cultures of amphidromous
9 gastropod veligers (40 – 98 days, Holthuis, 1995; Kano, 2006) and the otoliths
10 of amphidromous Galaxiid fishes and gobies (63 – 266 days, Radtke *et al*,
11 1988; McDowall *et al*, 1994; Radtke *et al*, 2001; Hoareau *et al*, 2007b). These
12 PLDs fall at or above the high end of the range found in the planktotrophic
13 larvae of marine invertebrates (7-293 days, Shanks *et al*, 2003) and fish (~ 20-
14 90 days, Brothers *et al*, 1983).

15 Consistent with this high dispersal potential, genetic structure within
16 high-island archipelagos is low or non-existent in amphidromous Neritid and
17 Neritiliid snails (Hodges and Allendorf, 1998; Myers *et al*, 2000; Kano and
18 Kase, 2004), as well as Galaxiid and Sicydiine fishes (Chubb *et al*, 1998;
19 Waters *et al*, 2000; Berrebi *et al*, 2005; Hoareau *et al*, 2007a), suggesting that
20 populations of amphidromous species are genetically structured at scales

1 similar to fully marine species. In contrast, fully lotic species are frequently
2 genetically structured within watersheds or even within reaches (Bunn and
3 Hughes, 1997; Marten *et al*, 2006).

4 Lotic habitats are rare in the South Pacific, occurring only on volcanic
5 islands that are tall enough to generate their own adiabatic rainfall. Given high
6 levels of larval mortality and the effects of diffusion (Cowen *et al*, 2000), it
7 seems unlikely that significant numbers of larvae advected away from their
8 natal archipelago would be able to find suitable freshwater habitat for
9 settlement. Therefore local selection for traits that favor self-recruitment could
10 be particularly strong for amphidromous species (Sponaugle *et al*, 2002;
11 Strathmann *et al*, 2002). Consistent with this prediction, Sorensen and Hobson
12 (2005) found that newly recruited amphidromous gobies had stable isotope
13 signatures that were similar to inshore plankton rather than offshore plankton,
14 suggesting that larvae prefer to stay in coastal waters. Similar homing behaviors
15 have been suggested for the larvae of amphidromous shrimp and snails
16 (Benstead *et al*, 2000; Haynes, 2000). Such larval retention could result in
17 limited realized dispersal and pronounced genetic structure among
18 archipelagos.

19 However, in addition to their rarity, riverine habitats on oceanic islands
20 are inherently unstable. They are characterized by short overall lengths

1 (generally < 5km), with small catchments, and extremely variable flows (Resh
2 and de Szalay, 1995; Craig, 2003). Climactic fluctuations over the past several
3 million years (Hope, 1996) and the rapid erosion and eventual subsidence of
4 individual islands (Whittaker *et al*, 2008) ensure that populations in oceanic
5 island streams will be subject to local extinction and re-colonization over
6 evolutionary timescales (Covich, 2006). These processes can be expected to
7 leave a molecular signature in the form of shallow, star-like genealogies
8 (Slatkin and Hudson, 1991), and estimates for colonization events that greatly
9 post-date the formation of each archipelago (Price and Clague, 2002).

10 Chaotic population dynamics have also been shown to promote the
11 evolution of long-distance dispersal ability (Johnson and Gaines, 1990; Holt
12 and Mcpeek, 1996). Since the planktotrophic larvae of amphidromous species
13 must settle in a rare, unstable habitat, they could be selected for the ability to
14 delay metamorphosis and extend their planktonic life indefinitely (“death
15 before dishonor” hypothesis, Bishop *et al*, 2006, see Elkin & Marshall 2007 for
16 a numerical model). Such a strategy could result in extremely long-distance
17 dispersal, limiting genetic differentiation among archipelagos.

18 In the present study, we assess mitochondrial genetic variation in two
19 amphidromous snail species from the family Neritidae (Gastropoda:
20 Neritopsina). *Neritina canalis* (Sowerby, 1825) and *Neripteron dilatatus*

1 (Lesson, 1830) have planktotrophic larvae, as indicated by the “D” shaped
2 initial region of their opercula (Kano, 2006) and probably share an
3 amphidromous common ancestor (Holthuis, 1995). *Neritina canalis* is found
4 under stones in riffles within a kilometer or two of the sea, and has a range that
5 extends from the Philippines to the Marquesas (Haynes, 2001). *Neripteron*
6 *dilatatus* is able to tolerate relatively high salinities (Liu and Resh, 1997), but
7 has only been collected from rocky substrate in the estuaries of running streams
8 ranging from the Philippines to the Society Islands (Pointier and Marquet,
9 1990; Haynes, 2001). If the larvae of these species have developed behaviors
10 for retention in coastal waters, then we would expect to see genetic structure
11 between or even within archipelagos. Conversely, if the larvae are passively
12 dispersed, but have adapted to extend their pelagic duration until they can
13 recruit to freshwater habitat, then we would expect to see little genetic structure
14 across the South Pacific, with relatively frequent long-distance dispersal and
15 gene flow occurring in the direction of the prevailing currents.

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1 *Materials and Methods*

2 Sampling and Sequencing

3 We collected *Neritina canalis* (n=202) and *Neripteron dilatatus* (n=151)
4 from two or more islands in the West Pacific archipelagos of Vanuatu, Fiji, and
5 Samoa, as well as the Society and Marquesan archipelagos in the Central
6 Pacific (Figure 1, Table 1). We fixed whole specimens in 95% ethanol, with the
7 opercula propped open to allow proper preservation. *N. dilatatus* is not known
8 to be present in the Marquesas (Pointier and Marquet, 1990, T. Eichhorst, pers.
9 comm.), and we did not find it there. We extracted genomic DNA from foot
10 muscle tissue in a 10% Chelex solution (Walsh *et al*, 1991). We initially PCR
11 amplified a 658bp region of mitochondrial Cytochrome Oxidase I with standard
12 invertebrate primers, HCO-2198 and LCO-1490 (Folmer *et al*, 1994). Because
13 these primers amplified with a low success rate (< 50%), we designed an
14 internal forward primer, NerL (5' – ATGTAATTGTRACTGCTCATGC – 3')
15 that amplifies a 520bp region of the gene, in conjunction with HCO-2198.
16 Reactions occurred in 25 µl volumes with 2.5 µl of 10x buffer, 2 µl MgCl₂ (25
17 mM), 2.5 µl DNTPs (8 mM), 1.25 µl of each 10 mM primer, 1 µl of template,
18 and 0.625 units of Amplitaq™ (Applied Biosystems Inc., California, USA).
19 Thermocycling conditions were: initial denaturation 94°C (15s), main cycle
20 94°C (30s), 50°C (30s) and 72°C (30-40s) for 35-39 cycles, then a final

1 extension of 72°C (3-10min). 5µl of successful PCR products were cleaned by
2 adding 0.5 units of Shrimp Alkaline Phosphatase (Biotech Pharmacon,
3 TromsØ, Norway) and 5 units of Exonuclease I (GE Healthcare, Wisconsin,
4 USA), and incubating at 37°C for 30 minutes and 80°C for 15 minutes. We
5 sequenced forward and reverse directions of double-stranded PCR products
6 with Big Dye™(Applied Biosystems Inc.) terminator chemistry on an ABI 377
7 sequencer, and proofread the resulting chromatograms in Sequencher™
8 (Genecodes Corporation, Michigan, USA). Proper translation using the
9 invertebrate mitochondrial code was confirmed using MacClade 4.05
10 (Maddison and Maddison, 2002).

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12 Data Analysis

13 We used Arlequin 3.1 (Excoffier *et al*, 2005) to calculate standard
14 measures of genetic diversity (h , π) for each island deme, and Fu's F_s (Fu,
15 1997), which tests the data for an excess of recent mutations that are indicative
16 of non-neutral processes such as positive selection or population growth. We
17 then visualized the genetic relationships among haplotypes with a minimum-
18 spanning tree (MST) calculated in Arlequin for each species and then re-drawn
19 by hand using Adobe Illustrator™. Each alternative connection identified by

1 the program was evaluated by eye to determine whether it would significantly
2 alter the topology of the MST.

3 We evaluated hierarchical genetic structure among archipelagos using
4 analysis of molecular variance (AMOVA) as implemented in Arlequin 3.1. The
5 data were partitioned into two separate regions, 1) the Western Pacific
6 (Vanuatu, Fiji, Samoa) archipelagos and 2) Central Pacific (Society Islands and
7 Marquesas). We evaluated significance with 10,000 random replicates.

8 Pairwise ϕ_{st} among demes was also calculated with 10,000 random replicates,
9 and the significance of each value was established after a Bonferroni correction.

10 Low levels of genetic structure and haplotypes that are shared between
11 distant populations can be explained either by ongoing gene flow over a
12 relatively long period of time or incomplete lineage sorting following a
13 relatively recent colonization event (Nielsen and Wakeley, 2001). To
14 differentiate between these alternative hypotheses we used the IM program
15 (Hey and Nielsen, 2004) to fit an Isolation with Migration model to the genetic
16 data from the Western and Central Pacific populations of both species. The
17 program uses a Markov Chain Monte Carlo (MCMC) methodology to simulate
18 millions of coalescent genealogies while varying the model parameters,
19 comprising time of population splitting (t), migration rates after the populations
20 split (m/μ), current θ and ancestral $\theta_A (=2N_e\mu)$. The parameter values that are

1 visited most frequently by the program have the highest probability and can be
2 taken as parameter estimates with confidence intervals including 95% of all
3 values visited by the program. These estimates allow comparison of the model
4 parameters between the two species, assuming that they experience a similar
5 substitution rate.

6 The migration rate ($N_e m$) is the product of the parameters m/μ and θ
7 divided by two. This value summarizes the effective number of migrants per
8 generation that move between the populations following their time of splitting,
9 but does not distinguish between constant migration and a few massive
10 dispersal events. Therefore, because IM explicitly estimates genealogies with
11 migration events between populations, we also used it to produce a histogram
12 of the number of independent migration events inserted during each iteration of
13 the Markov chain (Won and Hey, 2005). To get a heuristic estimate of the
14 maximum amount of time since population divergence, we converted the
15 divergence time, t , to years using a relatively slow divergence rate of 1% per
16 million years (based on fossil-calibrated Molluscan rates, Marko, 2002).
17 Finally, we evaluated differences in population size as the proportion of
18 genealogies for which the θ value for one population was larger than the other,
19 expressed as a p-value.

1 synonymous changes were found in *N. canalis*, all of them singletons, and one
2 singleton amino-acid change was found in *N. dilatatus*. Haplotype diversity (h)
3 was high in all demes, with the lowest value for *N. canalis* being 0.912 at
4 Raiatea and the lowest for *N. dilatatus* being 0.871 at Espiritu Santo.
5 Nucleotide diversity was relatively low, ranging from 0.004 to 0.008 in *N.*
6 *canalis* and 0.008 to 0.0013 in *N. dilatatus*. Fu's F_s values were strongly and
7 significantly negative, indicating departures from the neutral expectations for a
8 demographically stable population for all demes in both species except for two
9 *N. dilatatus* demes: Espiritu Santo and Tutuila. Results are summarized in
10 Table 1.

11 Minimum spanning trees for both species contain star polytomies that
12 are also indicative of processes that cause departures from the neutral model,
13 such as selection or population growth (Slatkin and Hudson, 1991). However,
14 the geographic distribution of this variation differs between species (figure 2a,
15 2b). *N. canalis* shows significant population structure. The central star
16 polytomy contains representatives from all five archipelagos (although
17 haplotypes from the Society Islands and the Marquesas occur at a relatively low
18 frequency), a second polytomy contained only haplotypes from the Society
19 Islands, while a third polytomy is almost entirely made up of Marquesan
20 haplotypes (with the exception of one individual from the Societies). Both of

1 these polytomies were rooted at the central polytomy, and none of the 27
2 alternative connections suggested that they are more closely related to one
3 another. In contrast, the MST topology for *N. dilatatus* shows no evidence of
4 regional structure. The large star topology is dominated by a single central
5 haplotype that was found in 36 snails from all four sampled archipelagos. A
6 few less frequent haplotypes that are between 2 and 8 basepair differences away
7 from the central haplotype are at the center of smaller polytomies.

8 We qualitatively detected different patterns of genetic structure in the
9 two snail species. Congruent with the patterns observed in the MSTs, we found
10 strong regional structuring between the Western and Central Pacific populations
11 of *N. canalis*, which explained 11.0% of the genetic variation at the COI locus
12 (Table 2). Regional pairwise ϕ_{ST} values in *N. canalis* revealed no significant
13 structure among the Western Pacific archipelagos of Samoa, Fiji and Vanuatu
14 (ϕ_{ST} ranging from 0 to 0.02, no values significant). However, significant
15 structure was detected in pairwise comparisons between these Western Pacific
16 demes and those from the Marquesas and Societies, respectively (ϕ_{st} ranging
17 from 0.21 to 0.37, $p < 0.0001$, Table 3). In contrast to *N. canalis*, genetic
18 structure in *N. dilatatus* was uniformly non-existent among all archipelagos
19 (global $\phi_{st} = 0.005$, pairwise ϕ_{st} ranging from 0 to 0.04, no values significant),
20 as suggested by the high degree of haplotype sharing.

1 Parameter estimates from three replicate IM runs converged to the same
2 or very similar values for datasets from both species (Table 4). Effective
3 sample sizes (ESS) were all greater than 75, and generally greater than 100.
4 Trend lines for each parameter indicated that the chain was well mixed. For all
5 three replicate runs of the *N. dilatatus* dataset, the posterior distribution for θ in
6 the Western Pacific archipelagos was not complete before it reached the
7 maximum value of the prior distribution, probably due to high levels of gene
8 flow with unsampled populations to the west (Beerli, 2004).

9 IM inferred differing rates of gene flow between the Central and
10 Western Pacific in the two species. In *N. canalis*, the 95% confidence interval
11 for the migration rates ($N_e m$, Table 4) between the West Pacific archipelagos
12 and the Society Islands included the lowest assayed value, and the number of
13 independent migration events reached a modal value at zero, indicating that
14 gene flow in this region is not significantly different from zero in this species.
15 There was a similar result for migration events between the Marquesas and the
16 West Pacific, except that westerly migration events reached their modal value at
17 2 (95% CI 0 to 13), hinting at a small amount of post-colonization gene flow in
18 this direction. In contrast, the migration rate was significantly greater than zero
19 for *N. dilatatus*, and migration events had a modal value of 13 (95% CI – 4 to

1 238) from the Societies to the West Pacific and 3 (95% CI – 1 to 191) in the
2 opposite direction (see supplemental figure 1).

3 The MCMC simulations suggest that the Western Pacific populations of
4 both species have higher effective population sizes than those in the Central
5 Pacific as indicated by their consistently larger θ values ($p < 0.02$ in all cases).
6 In addition, θ values for both contemporary populations of *N. dilatatus* were
7 consistently higher than θ for the ancestral population ($p < 0.001$), indicating a
8 significant increase in effective population size in both populations. This was
9 not the case for *N. canalis*, where θ values for contemporary populations in
10 both Central Pacific archipelagos were not significantly larger than the ancestral
11 population. Divergence time estimates with a heuristic rate of 1%/million years
12 indicate that Western Pacific and Society Archipelago populations of *N. canalis*
13 diverged around 0.6 million years ago (95% CI 0.52 – 1.76 mya), while *N.*
14 *dilatatus* populations diverged significantly later, around 0.3 million years ago
15 (95% CI 0.22 – 0.42 mya). The Western Pacific and the Marquesas populations
16 of *N. canalis* diverged around 0.4 million years ago (95% CI 0.28 – 1.82 mya).

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1 *Discussion*

2 Long-Distance Dispersal Among Western Pacific Archipelagos

3 Although the adults of both *Neritina canalis* and *Neripteron dilatatus*
4 occur only in freshwater streams or their estuaries, neither species showed any
5 evidence of genetic structure within or among the Western Pacific archipelagos
6 of Vanuatu, Fiji and Samoa. The simplest explanations for the absence of
7 genetic structure observed in the Western Pacific are that either both species
8 have maintained high equilibrium levels of gene flow across the Western
9 Pacific ($N_e m > 10$ migrants/generation) for a long period of time, or that they
10 have undergone a recent range expansion through the region, colonizing each
11 archipelago over a relatively short amount of time. Although our present data
12 are unable to distinguish between these two scenarios, long-distance larval
13 dispersal (i.e. dispersal far beyond the mean dispersal distance for these
14 species) must have occurred under both of them.

15 The velocity of the South Equatorial Current is highly variable, but it
16 generally moves southwest through the study region at average speeds no
17 greater than 0.07 m/s (11 year average from Ocean Surface Current Analyses –
18 Real time, <http://www.oscar.noaa.gov>, Bonjean and Lagerloef, 2002). However,
19 climactic fluctuations can periodically produce much faster current velocities.
20 For example, during the 1999 La Niña event, current velocities in the north of

1 the region reached nearly 0.2 m/s. A veliger larva that is released into the South
2 Equatorial Current during such an event would take about 50 days to cross the
3 ~850 kilometers of open ocean that separate Samoa from Fiji or Fiji from
4 Vanuatu, if it were to travel in a straight line. The larvae of both species must
5 therefore be able to delay metamorphosis for at least this long in order to create
6 or maintain the panmixia observed across this region. Similarly, the
7 amphidromous goby *Sicyopterus lagocephalus*, which is known to have a very
8 long pelagic larval duration (133-266 days) was found to be panmictic between
9 the Comoros and Mascarene archipelagoes in the Indian Ocean (Hoareau *et al*,
10 2007a).

11

12 Multiple Colonizations of the Central Pacific

13 While both species were genetically homogenous in the Western
14 Pacific, *N. canalis* exhibited pronounced structure in the Central Pacific.
15 Significantly smaller θ values in the relatively young Central Pacific
16 archipelagos (Table 4), suggest that existing populations of *N. canalis* in the
17 Society Islands and the Marquesas are probably the result of two independent,
18 eastward colonization events from the older archipelagos of the Western
19 Pacific. Analysis under the IM model found that, since colonization, no
20 significant gene flow has occurred between the Society Islands population of *N.*

1 *canalis* and the Western Pacific population, while perhaps only a small
2 westward trickle has occurred between the Marquesas and the West Pacific.
3 The haplotypes shared between Central Pacific and Western Pacific populations
4 are thus most likely the result of incomplete sorting of lineages following
5 colonization, and not ongoing gene flow. Genetic structure or divergence across
6 the large expanses of open water (~2000 km) that lie between archipelagos in
7 the Western and Central Pacific, such as what we found in *N. canalis*, is
8 commonly seen in marine species (Palumbi *et al*, 1997; Bernardi *et al*, 2001;
9 Lessios *et al*, 2001; Crandall *et al*, 2008) as well as an amphidromous goby
10 (Keith *et al*, 2005).

11 It is therefore remarkable that *N. dilatatus* shows no evidence of genetic
12 structure across this span. There are two possible explanations for this pattern:
13 either one population was recently founded by a massive colonization event
14 from the other population, or else there has been ongoing gene flow between
15 the two populations following colonization. Distinguishing between these two
16 models is a classic problem in population genetics that can be addressed with
17 the Isolation with Migration model (Nielsen and Wakeley, 2001; Hey and
18 Nielsen, 2004). Our IM analyses indicate that the Society Islands population of
19 *N. dilatatus* was probably founded by an eastward colonization event, as
20 indicated by its significantly smaller value for θ . This event occurred no more

1 than 420,000 years ago, which is significantly younger than the colonization of
2 the Society Islands by *N. canalis*. However, because IM was unable to reject a
3 model with migration it is possible that *N. dilatatus* has maintained at least
4 intermittent gene flow across the intervening ~2000 km of ocean between the
5 Society Islands and Western Pacific populations ($N_e m > 23.5$ migrants per
6 generation), following this colonization event.

7 It is interesting to note that IM reckoned a higher number of westerly
8 migration events than easterly events. This indicates that, following the inferred
9 eastward colonization event, most of the gene flow in *N. dilatatus* has run
10 westward in the direction of the South Equatorial Current (Table 4). Even at the
11 high speeds estimated for La Niña events (0.2 m/sec, see above), it would take
12 115 days for the South Equatorial Current to transport a larva from the Society
13 Islands to the Samoan archipelago. The possible difference in gene flow across
14 an area that completely lacks freshwater habitats implies that *N. dilatatus* larvae
15 may be able to delay metamorphosis for longer than the larvae of *N. canalis*,
16 and indeed, most marine species.

17

18 Local Extinction and Recolonization

19 Coalescent estimates of population splitting indicate that both species
20 colonized the Central Pacific archipelagos starting no more than 1.82 million

1 years ago, in three independent events. These dates are relatively recent
2 compared to the geologic age of the oldest island in each archipelago (6 million
3 years in the Marquesas, 10 million years in the Society Islands; Craig *et al*,
4 2001). In addition, shallow star polytomies in both minimum spanning trees,
5 and strongly negative values of F_s in all but two island demes indicate non-
6 equilibrium population dynamics such as recent population expansions due to
7 colonization (Slatkin and Hudson, 1991; Fu, 1997). Together, these data
8 support a history of local extinctions followed by re-colonization, as has been
9 suggested for other amphidromous species (Cook *et al*, 2008).

10 These recent dates of colonization could possibly be explained by an
11 absence of suitable habitat in the Central Pacific archipelagos until about a
12 million years ago, or a low probability of eastward colonization (Paulay and
13 Meyer, 2002) due to the prevailing westerly currents of the South Equatorial
14 Current. However, decadal current reversals during El Niño events provide a
15 mechanism for occasional colonization events to occur (Bonjean and Lagerloef,
16 2002; Lessios and Robertson, 2006). Moreover, since islands in these hotspot
17 archipelagos are formed sequentially, they have a large range of ages and
18 therefore offer a wide array of habitats at any one time (Paulay, 1994; Craig *et*
19 *al*, 2001). We therefore find it more likely that each of these species has re-
20 colonized the Central Pacific archipelagos, following local extinction.

1 Consistent with this inference, freshwater stream habitats on oceanic
2 islands are known to be inherently unstable at multiple temporal scales. On a
3 decadal scale, individual streams may dry up due to drought, or be scoured by
4 massive floods, causing local extinction of stream populations (Maciolek and
5 Ford, 1987; Resh and de Szalay, 1995, personal observation). Plio-Pleistocene
6 glacial periods resulted in extended periods of decreased rainfall on the Pacific
7 islands, likely drying up streams throughout the region (Hope, 1996).
8 Fluctuating sea levels during this period would have also alternately created and
9 destroyed riverine habitats (Dickinson, 2004). On still deeper timescales,
10 freshwater habitats on oceanic islands undergo substantial change as erosion
11 modifies steeply profiled streambeds into more mature pool and riffle habitats
12 with relatively broad alluvial estuaries. Ultimately, island subsidence reduces
13 adiabatic rainfall to a point where continuous flow cannot be sustained, and
14 riverine habitats are lost (Craig *et al*, 2001; Craig, 2003).

15

16 The Evolution of Dispersal in Amphidromous Species

17 Species with frequent extinction and recolonization of local populations
18 face two conflicting selective pressures on their dispersal ability (Olivieri and
19 Gouyon, 1997). On one hand, lotic freshwater habitats are rare in the Pacific
20 Ocean, and a larva that recruits to its natal stream should be favored over one

1 that disperses away, as it is unlikely that the dispersive larva will find another
2 stream in which to settle (Strathmann *et al*, 2002). On the other hand, frequent
3 local extinction of stream populations should favor the evolution of larvae that
4 have the ability to delay metamorphosis long enough to find new streams (Holt
5 and Mcpeek, 1996; Elkin and Marshall, 2007). These pressures might not
6 necessarily act in direct opposition. While the former might select for
7 behaviors that favor retention (e.g. utilizing chemical cues to stay near natal
8 habitat, Gerlach *et al*, 2007), the latter might select for developmental and
9 physiological changes that allow for delayed metamorphosis if necessary (as
10 was suggested for habitat specialists in a recent survey of the literature, Bishop
11 *et al*, 2006).

12 While we cannot make any inferences regarding the degree of larval
13 retention with the current dataset, our results show that at least some larvae
14 from both amphidromous gastropod species are able to delay larval
15 metamorphosis for longer than many marine species (>50 days in *N. canalis*,
16 and >115 days in *N. dilatatus*). Other amphidromous species found on oceanic
17 islands have a similarly lengthy pelagic larval duration (Radtke *et al*, 2001;
18 Kano, 2006; Hoareau *et al*, 2007b), an absence of genetic structure across long
19 pelagic distances (Waters *et al*, 2000; Myers *et al*, 2000; Hoareau *et al*, 2007a),
20 and the molecular signature of recent colonization events (Myers *et al*, 2000;

1 Kano and Kase, 2004; Cook *et al*, 2008). The pelagic larva has only been lost
2 from the life history a few times among the extant freshwater Neritids, and only
3 once in an island species (Holthuis, 1995), even though pelagic larvae have
4 been lost multiple times in other families of marine invertebrates (Duda and
5 Palumbi, 1999a; Hart, 2000). Given their unstable habitat, this makes sense,
6 since the evolution of adaptations for larval retention in a freshwater species
7 would lead to its restriction to individual islands and a heightened risk of
8 species extinction (Hansen, 1978; Jablonski and Lutz, 1983).

9 If instability of lotic habitats on oceanic high islands promotes long-
10 distance larval dispersal then we should see the opposite pattern in
11 amphidromous species living in continental watersheds. In these geologically
12 older and more stable lotic environments, selection against dispersal from the
13 natal habitat should be unopposed. Consistent with this prediction,
14 phylogeographic studies of amphidromous Atyid shrimp (Page *et al*, 2005;
15 Cook *et al*, 2006; Page *et al*, 2007) and Galaxiid fishes (Waters and Wallis,
16 2001) from Australia and New Zealand show evidence for multiple losses of
17 amphidromy, with widespread basal amphidromous lineages giving rise to
18 multiple freshwater lineages that are restricted to watersheds. Within the
19 Neritidae, the only genus with benthic development in freshwater (*Theodoxus*)
20 occurs in Eurasia (Bunje and Lindberg, 2007), further supporting the prediction

1 that the relative stability of continental riverine habitats supports the loss of
2 planktonic larvae.

3

4 Conclusions

5 An absence of genetic structure across three archipelagoes in the
6 Western Pacific demonstrates that both *Neritina canalis* and *Neripteron*
7 *dilatatus* have a capacity for long distance larval dispersal that is as good or
8 better than many marine species. Furthermore, these species have colonized
9 Central Pacific archipelagos that lie over 2000 km away from the nearest
10 freshwater habitat. Coalescent analysis suggests that these colonization events
11 occurred independently, and relatively recently in comparison to the age of the
12 archipelagos. Predominantly westward gene flow in *N. dilatatus* appears to
13 have continued following colonization, while it has more or less ceased in *N.*
14 *canalis*. Long-lived larvae, and low levels of genetic structure among oceanic
15 island populations of many amphidromous species, combined with the frequent
16 loss of amphidromy in continental watersheds, support theoretical predictions
17 (Johnson and Gaines, 1990; Holt and Mcpeek, 1996; Elkin and Marshall, 2007)
18 that temporal instability of habitats plays a major role in promoting the
19 evolution of dispersal ability.

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1
2 TITLES AND LEGENDS TO FIGURES

3
4 Figure 1. Map of the South Pacific, showing localities sampled in five
5 archipelagos of high islands. Islands in the Tuamotu archipelago are atolls
6 devoid of running freshwater habitats. Dotted vectors depict 16-year mean
7 surface currents (Bonjean and Lagerloef, 2002) for the period between October
8 and December, when most Neritid egg cases are hatched (Resh and deSzalay,
9 1995).

10

11 Figure 2. Minimum spanning trees for both gastropods. Circles are sized
12 proportionally to the frequency of occurrence, ranging from 1-15 in *N. canalis*
13 and 1-36 in *N. dilatatus*. All haplotypes are separated by one mutational step
14 unless denoted by a higher number of hatch marks.

15

1 Table 1. Summary statistics and neutrality test statistics for each island deme
 2 shown in Figure 1. Haplotype diversity (h), nucleotide diversity (π) and F_s (Fu,
 3 1997) calculated in Arlequin 3.1 (Excoffier *et al.* 2005). Significant values of F_s
 4 ($p < 0.02$) are printed in bold.
 5

			<i>Neritina canalis</i>					<i>Neripteron dilatatus</i>				
Region	Archipelago	Island	n	# haps	h	π	F_s	n	# haps	h	π	F_s
West Pacific	Vanuatu	Espiritu Santo						19	12	0.871	0.009	-3.13
		Efate						23	18	0.941	0.007	-12.76
		Tanna	6	6	1.000	0.004	-2.86					
	Fiji	Viti Levu	17	15	0.985	0.008	-9.95	2	2	1.000	0.012	n/a
		Taveuni	13	10	0.970	0.005	-5.05	23	20	0.976	0.013	-11.60
	Samoa	Upolu	22	17	0.935	0.005	-14.85	23	17	0.937	0.007	-11.02
Tutuila		24	19	0.968	0.005	-19.76	19	11	0.889	0.008	-2.52	
Central Pacific	Society Islands	Raiatea	17	11	0.912	0.005	-6.11	24	16	0.960	0.008	-7.16
		Huahine	18	14	0.967	0.007	-8.73					
		Moorea	25	20	0.970	0.005	-21.20	18	15	0.978	0.011	-7.70
		Tahiti	18	15	0.961	0.006	-11.98					
	Marquesas	Nuku Hiva	23	13	0.921	0.006	-5.07					
		Hiva Oa	19	12	0.924	0.006	-5.53					

6
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1 Table 2. AMOVA results for comparisons among West Pacific and Central
 2 Pacific regions in both species. The West Pacific region includes Vanuatu, Fiji
 3 and Samoan archipelagos. The Central Pacific region includes the Marquesas
 4 and Society archipelagos. Significant values (*) indicate a $p < 0.05$ after 10,000
 5 random permutations of the data.

	<i>Neritina canalis</i>	<i>Neripteron dilatatus</i>
Overall ϕ_{ct} (between regions)	0.110*	0.001 (ns)
Overall ϕ_{sc} (within regions)	0.208*	0.004 (ns)
% Variation:		
Among Regions	10.96%	0.13%
Among demes within regions	18.52%	0.38%
Within demes	70.52%	99.48%

6
7

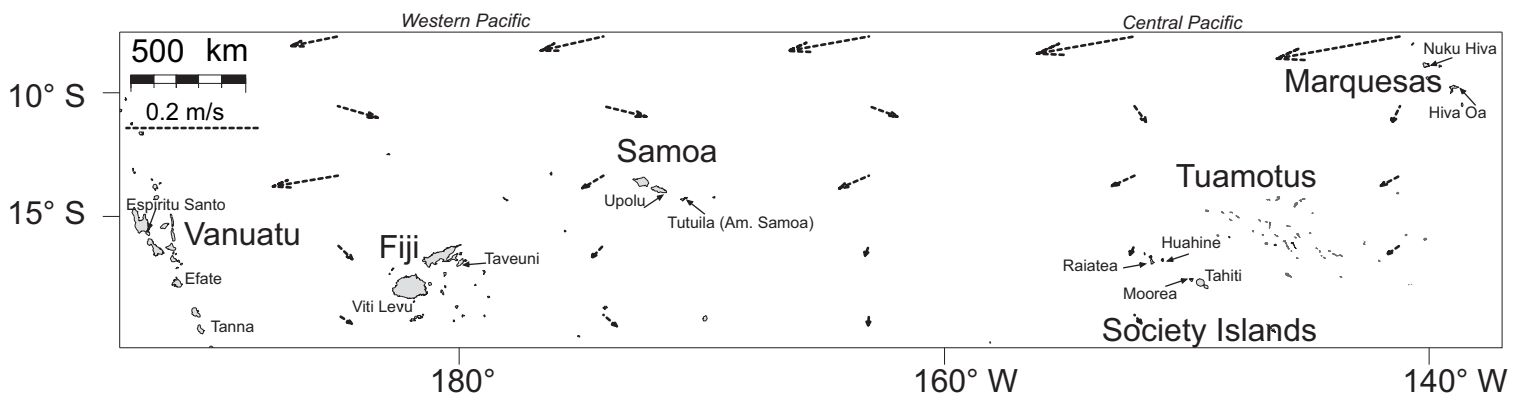
1 Table 3. Pairwise ϕ_{st} values for island demes in *Neritina canalis*. Values in
 2 bold were significant after Bonferroni correction for multiple tests (individual p
 3 < 0.0009).

Locality	3	4	5	6	7	8	9	10	11	12	13
3. Tanna	0										
4. Viti Levu	0.007	0									
5. Taveuni	0.019	0.022	0								
6. Upolu	0.010	0.017	0.018	0							
7. Tutuila	0.006	0.010	0.003	0.000	0						
8. Raiatea	0.323	0.251	0.296	0.294	0.300	0					
9. Huahine	0.244	0.204	0.249	0.253	0.254	0.018	0				
10. Moorea	0.314	0.261	0.303	0.293	0.291	0.000	0.004	0			
11. Tahiti	0.254	0.210	0.252	0.253	0.251	0.000	0.000	0.000	0		
12. Nuku Hiva	0.256	0.225	0.264	0.269	0.269	0.418	0.351	0.420	0.381	0	
13. Hiva Oa	0.363	0.295	0.361	0.363	0.366	0.492	0.418	0.490	0.450	0.024	0

4

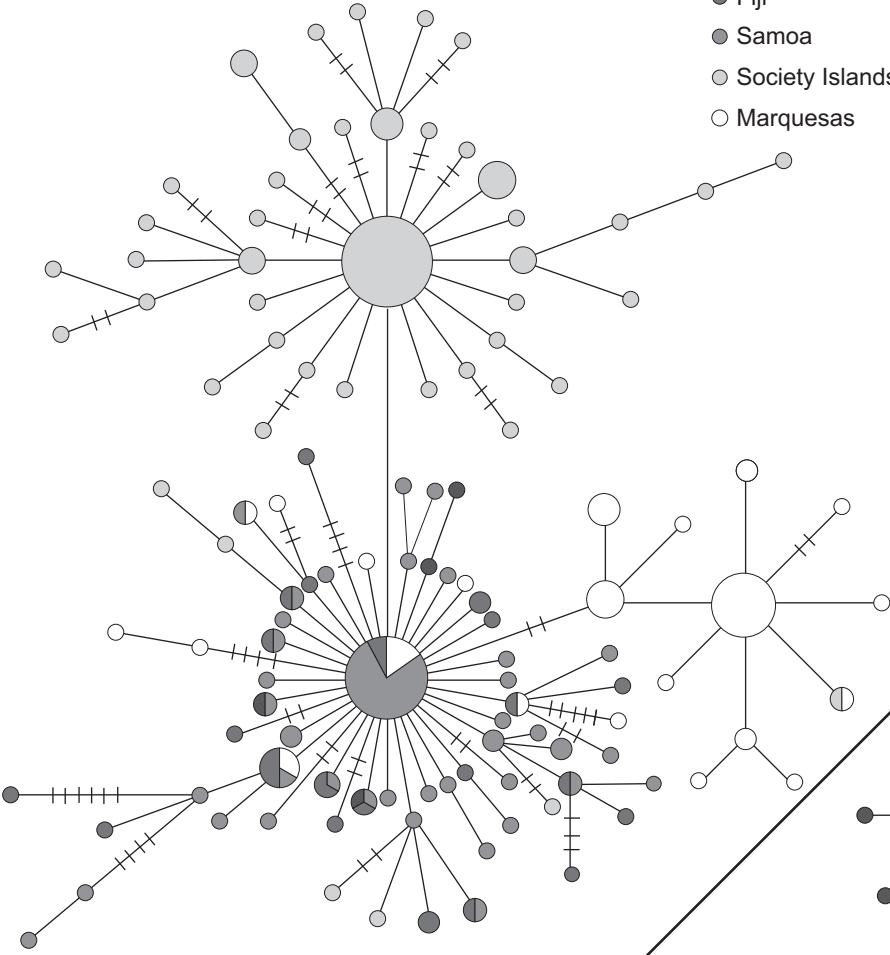
1 Table 4. Mode and 95% confidence intervals for the parameters of an isolation-
 2 with-migration model estimated by IM for Western Pacific populations
 3 (Vanuatu, Fiji and Samoa) and Central Pacific populations of both species.
 4 Confidence intervals for westerly $N_e m$ are given for the parameter m ,
 5 conditional on the modal value of θ for the West Pacific. Time estimates are
 6 scaled by the reciprocal of the per-site mutation rate, $1/\mu$, and estimates of θ are
 7 per site.
 8

	θ West Pacific	θ Central Pacific	θ Ancestral	t_{split}	$N_e m$ (CP \rightarrow WP)	Westward Migration Events	Eastward Migration Events
<i>Neritina canalis</i> – Society Islands and Western Pacific							
Mode	0.375	0.187	0.117	0.0033	0.49	0	0
95% Low	0.252	0.129	0.075	0.0026	0.49	0	0
95% High	0.967	0.310	0.456	0.0088	5.36	2	1
<i>Neritina canalis</i> – Marquesas and Western Pacific							
Mode	0.725	0.060	0.122	0.0020	8.48	2	0
95% Low	0.429	0.029	0.079	0.0014	0.94	0	0
95% High	2.121	0.125	0.381	0.0091	40.5	13	5
<i>Neripteron dilatatus</i> – Society Islands and Western Pacific							
Mode	2.582	0.322	0.071	0.0015	104	13	3
95% Low	1.341	0.168	0.041	0.0011	23.5	4	1
95% High	9.361	1.659	0.130	0.0021	3,830	238	191



a. Neritina canalis

- Vanuatu
- Fiji
- Samoa
- Society Islands
- Marquesas



b. Neripteron dilatatus

