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# Transoceanic dispersal and cryptic diversity in a cosmopolitan rafting nudibranch

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**Abstract.** The aeolid nudibranch *Fiona pinnata* (Eschscholtz, 1831) is an obligate rafter that occurs exclusively on macroalgal rafts and other floating substrata, and has a seemingly cosmopolitan marine distribution. Mitochondrial (mtDNA) and nuclear DNA sequence data were generated from specimens collected worldwide to test for global connectivity in this species. Phylogeographic analyses revealed three divergent mtDNA lineages, two of which were abundant and widespread. One of these lineages has an apparent circumequatorial distribution, whereas the other may have an antitropical distribution within the Pacific Ocean. Low genetic divergences within each lineage suggest that rafting can mediate dispersal across transoceanic scales. A third, highly divergent, lineage was detected in a single Indonesian specimen. Broadly concordant phylogeographic relationships were detected for the nuclear ITS1 region, with distinct tropical versus antitropical lineages observed. The substantial genetic divergences and largely allopatric distributions observed among the *F. pinnata* lineages suggest that they represent a species complex.

**Additional keywords:** biogeography, connectivity, cryptic species, marine, mollusc.

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## Introduction

The wide distributions of numerous marine taxa, coupled with the lack of conspicuous barriers to gene flow in the marine environment, have led to the assumption that gene flow is higher in oceans than in terrestrial environments (Mayr 1954; Palumbi 1992; de Vargas *et al*. 1999). Furthermore, dispersal potential in the sea has often been assumed to reflect larval mode and duration (Scheltema 1971; Strathmann 1985; Hedgecock 1986; Jablonski 1986), with long-lived planktonic larval stages suggested to suppress opportunities for allopatric speciation (Shuto 1974; Collin 2001). However, recent molecular evidence derived from a variety of widespread marine taxa has revealed that 'cryptic' speciation is quite common in the sea, and several apparently widespread marine taxa (including both benthic and planktonic lineages) have been demonstrated to represent species complexes (Knowlton 1993; Lessios *et al*. 2001; Wilson *et al*. 2007; Schwaninger 2008; Goetze 2011; Churchill *et al*. 2014; Schiffer and Herbig 2015). Furthermore, it is becoming increasingly clear that developmental strategy and larval lifespan are not always good predictors of species distributions and levels of gene flow (Sponer and Roy 2002; Waters and Roy 2004; Nikula *et al*. 2010). Indeed, recent reviews of marine biogeographic literature suggest that rafting ability, rather than larval longevity, may be a key factor underpinning successful transoceanic dispersal (Thiel and Gutow 2005*a*, 2005*b*; Levin 2006; Thiel and Haye 2006).

Although some organisms naturally occur worldwide without the influence of anthropogenic translocation (Macaya and Zuccarello 2010; Procheş and Ramdhani 2013), recent biogeographical studies employing molecular tools have debunked the supposed cosmopolitan status of several marine invertebrates, showing instead that these seemingly ubiquitous species are actually composed of multiple cryptic lineages with regionally restricted distributions (Klautau *et al*. 1999; Schroth *et al*. 2002; Eberl *et al*. 2007; Zulliger and Lessios 2010). For example, cryptic diversity has been uncovered in several widespread pleustonic cnidarians, including *Aurelia aurita* (Dawson and Jacobs 2001) and *Physalia physalis* (Pontin and Cruickshank 2012), as well as in noted rafters such as *Membranipora* bryozoans (Schwaninger 2008), *Rhabditis* nematodes (Derycke *et al*. 2008), and *Amphipholis* brittle stars (Sponer and Roy 2002).

The aeolid nudibranch *Fiona pinnata* (Eschscholtz, 1831) is the sole recognised representative of family Fionidae. This species has been recorded worldwide over a broad latitudinal range and is thus recognised as a cosmopolitan species, as based on morphologically similar specimens recorded from numerous distinct regions. This species exhibits an extremely rapid growth rate and its free-swimming veliger larvae take only five days to hatch under laboratory conditions (Holleman 1972). Upon colonisation of a buoyant object, post-metamorphic individuals cannot swim or even float by themselves (Willan 1979), thus

making *F. pinnata* an obligate rafter. Given that this invertebrate has planktotrophic larvae and is frequently observed rafting at sea (Bushing 1994; Aliani and Molcard 2003; Thiel and Gutow 2005*b*), it is conceivable that *F. pinnata* populations worldwide are so well mixed that they can be considered a single cosmopolitan species. Indeed, passive rafting has been invoked to explain the broad distributions of several nudibranch taxa (Jensen 2005; Carmona *et al.* 2011; Martynov and Schrödl 2011). However, this suggested connectivity has yet to be robustly tested with molecular tools. This study therefore undertakes a global analysis to elucidate genetic relationships across the range of this ubiquitous nudibranch. By investigating these global patterns we can explore the extent of genetic connectivity over transoceanic scales.

## Materials and methods

### Sample collection

Eighty-four ethanol-preserved individuals of *Fiona pinnata* were used in molecular analyses (Table 1), representing 15 sampling locations worldwide (Fig. 1). Animals were collected from offshore floating rafts or from fresh beach-cast wrack,

**Table 1. Sample details for *Fiona pinnata* specimens collected worldwide**

Museum codes: AK, Auckland War Memorial Museum; AM, Australian Museum; CASIZ, California Academy of Sciences; MMF, Museu de Historia Natural do Funchal; UF, Florida Museum of Natural History; ZSM, Zoologische Staatssammlung Munchen

| Locality | Voucher | Raft substrate | Code |
|---|---|---|---|
| Zavora Beach, Mozambique | AM C.476792 | Beach-cast driftwood | MZB |
| Dunedin, southern New Zealand | AM C.476807–476827 | Floating and beach-cast kelp (*Durvillaea* and *Macrocystis*) | NZS |
| Ohui Beach, northern New Zealand | AK118314 | Beach-cast storm debris | NZN |
| Goat Island, northern New Zealand | AM C.476793 | Floating plastic | NZN |
| North Stradbroke Island, Australia | AM C.477132 | Beach-cast cuttlebone | ASI |
| Heron Island, Australia | AM C.477130 | Floating plastic | AHI |
| Heron Island, Australia | AM C.477131 | n/a | AHI |
| Indonesia | AM C.477133 | Rompong (deep-water FAD) | ISU |
| Wakayama, Japan | AM C.476794 | Beach-cast bamboo shoot | JWA |
| North Pacific Gyre (32°03′N, 153°10′E) | AM C.476795 | Floating plastic | NPG |
| French Frigate Shoals, Hawaii | UF 415673, UF 427012 | Floating plastic | HFF |
| Georges Island, Alaska | CASIZ 088586 | Not recorded | AGI |
| Santa Cruz Island, Galapagos | CASIZ 172044 | Floating buoy | GSC |
| Coquimbo, Chile | AM C.476797–476806 | Floating kelp (*Durvillaea* and *Macrocystis*) | CCO |
| Madeira Island, Portugal | MMF 29835 | Floating buoy | PMI |
| Azores, Portugal | ZSM Mol20120145 | Floating plastic | PAZ |
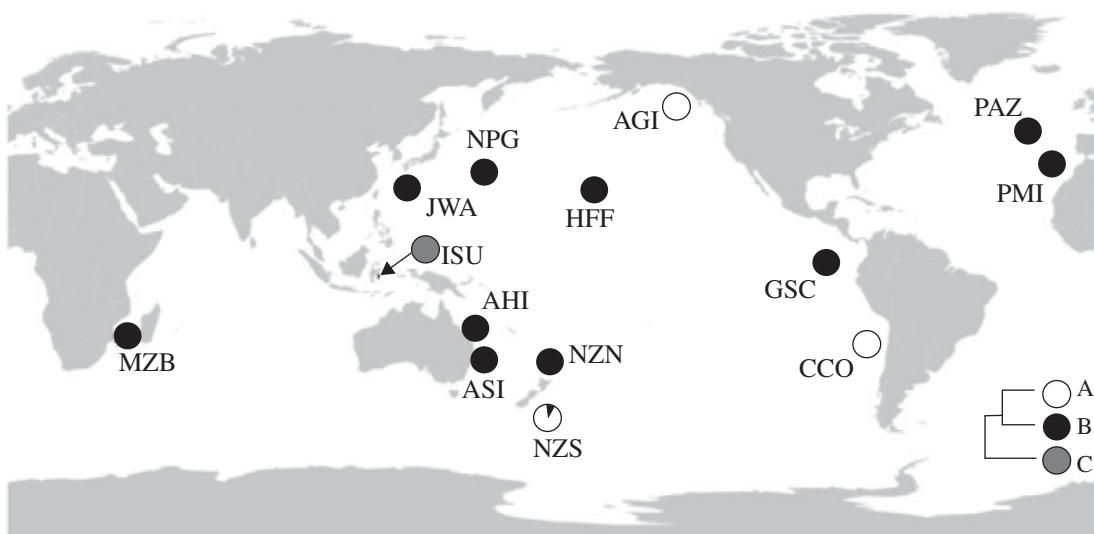


**Fig. 1.** Global sampling of *Fiona pinnata*. Lineage A, B, and C symbols for each sample locality are taken from Fig. 2 and a simplified representation of their phylogenetic relationships based on both COI (Fig. 2) and ITS1 (Fig. 4) is shown. Sampling localities are as follows: MZB, Mozambique (*n* = 1); NZS, Dunedin (*n* = 39); NZN, Opoutere (*n* = 2) and Goat Island (*n* = 3); ASI, Stradbroke Island (*n* = 2); AHI, Heron Island (*n* = 1); ISU, SE Sulawesi (*n* = 1); JWA, Japan (*n* = 3); NPG, North Pacific Gyre (*n* = 2); HFF, French Frigate Shoals (*n* = 2); AGI, Alaska (*n* = 1); GSC, Galapagos (*n* = 1); CCO, Coquimbo (*n* = 20); PMI, Madeira Island (*n* = 1); PAZ, Azores (*n* = 5).

and were generally found in association with their primary prey, goose barnacles of the genus *Lepas*. Many of these samples were sourced from museum collections (Table 1), having already been taxonomically identified by museum experts. Additional specimens we have collected from New Zealand have been identified by malacologist Richard Willan (Fraser *et al.* 2011).

*DNA extraction and sequencing*

A small piece (~2 mm$^3$) of foot tissue was dissected from each specimen and whole genomic DNA was extracted using a Chelex procedure (Walsh *et al.* 1991). A portion of the mitochondrial COI gene was amplified for all 84 specimens by polymerase chain reaction (PCR). Most individuals were amplified for COI using the primers LCO1490 (Folmer *et al.* 1994) and H7005 (Hafner *et al.* 1994), yielding 988 base pairs (bp) of data. However, a fraction of the samples, particularly those from older museum collections, failed to amplify with these primers but successfully amplified with HCO2198 (Folmer *et al.* 1994) paired with either LCO1490 or mtD6 (Simon *et al.* 1994), or with the primer pair CoxAF and CoxAR (Colgan *et al.* 2003), resulting in 454–759 bp fragments (typically >600 bp). A 560 bp portion of the nuclear ITS1 region was sequenced for a phylogenetically and geographically representative subset of twenty-six individuals out of the 84 already sequenced for COI. This nuclear fragment, which consisted of the 3′ end of 18S rRNA, complete ITS1, and the 5′ end of 5.8S rRNA, was successfully amplified using the primers 18S and 5.8S (Armbruster *et al.* 2000). All PCR amplifications were performed in 20-μL volume reactions containing 1 U of *Taq* DNA polymerase (Bioline, London, UK), 1 μL of each primer (10 μM), 4 μL of 5x MyTaq Red Buffer (Bioline), and 1 μL of extracted DNA. Thermal cycling for all reactions was carried out using Eppendorf Mastercycler ep gradient proS machines. PCR conditions for COI consisted of a 3-min denaturation at 94°C, followed by 40 cycles of 45 s at 94°C, 45 s at 45−48°C, 1.25 min at 72°C, and a final extension of 10 min at 72°C. Thermal cycling for ITS1 entailed a 2-min denaturation at 95°C, followed by 40 cycles of 30 s at 93°C, 30 s at either 52−55°C, 1 min at 72°C, and a final extension for 5 min at 72°C. All PCR products were purified with an Omega Ultra-Sep Gel Extraction Kit (Omega Bio-Tek) according to the manufacturer's instructions, and then sequenced in both forward and reverse directions using the original PCR primers at the University of Otago Genetic Analysis Services facility.

*Phylogenetic analysis*

All DNA sequences were assembled and edited using Sequencher 5.0 (Gene Codes Inc.) and then aligned by eye in MEGA 5.05 (Tamura *et al.* 2011). Pairwise COI and ITS1 sequence divergences among *F. pinnata* samples were calculated using the Kimura (1980) 2-parameter model (K2P) of sequence evolution. TCS 1.21 (Clement *et al.* 2000) was used to identify unique sequences and networks for COI and ITS1 sequence data. Six COI sequences were excluded from network analysis due to missing data (i.e. <988-bp fragments). These six sequences included samples from Madeira Island, the Galapagos, the French Frigate Shoals, and both islands of New Zealand.

Phylogenetic analyses of COI and ITS1 data were performed using maximum likelihood (ML) and Bayesian inference methods. The Akaike information criterion (Akaike 1974) implemented in jModelTest 0.1.1 (Guindon and Gascuel 2003; Posada and Buckley 2004; Posada 2008) determined the best-fit model to be HKY+I for COI, and HKY+I+G (Hasegawa *et al.* 1985) for ITS1. COI sequences from two members of the Fionoidea (*Cuthona ocellata*, GenBank accession AY345043; *Tergipes tergipes*, AY345032) were included as outgroups. Due to a lack of published nudibranch ITS1 data, the aeolid nudibranch *Flabellina verrucosa* (AB180834) was used as an ITS1 outgroup, although only ~100 bp of this sequence was readily alignable with *F. pinnata* ITS1 fragments. All *Fiona* DNA sequences new to this study have been deposited in GenBank (accessions KU757489–692).

MEGA was used to construct ML trees in which branch support was evaluated with 1000 bootstrap replicates (Felsenstein 1985). Mr. Bayes 3.1.2 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003) was used to perform Bayesian analyses on COI and ITS1 data, in which the Markov chain Monte Carlo searches ran for 20 million generations and trees were sampled every 100 generations. The first 10 000 trees (i.e. 1 000 000 generations) were discarded as burn-in, and the remaining trees were used to estimate Bayesian posterior probability (PP) values.

A hierarchical AMOVA approach used to test for genetic partitioning of mitochondrial DNA (mtDNA) variation among separate ocean basins was performed using ARLEQUIN 3.1 (Excoffier *et al.* 2005).

## Results

*Global mitochondrial DNA phylogeography*

Eighty-four *F. pinnata* COI sequences yielded 53 distinct COI haplotypes worldwide, distinguishable by 178 variable nucleotide positions. COI sequence divergences within *F. pinnata* ranged from 0.1% to 12.8% (Table 2), and all ingroup sequences were highly distinct from those of Fionoidea outgroups (>17% divergence). ML analysis and Bayesian inference produced similar tree topologies, and both analyses were congruent in the recovery of three distinct lineages (Lineages A, B, C) (Fig. 2) and provided strong support for the combined monophyly of all ingroup sequences (ML: 100%; Bayesian PP: 1.00).

Most samples clustered into one of two widespread mtDNA lineages (mean 6.1% divergence), and the sister relationship of these two genetic groupings (herein called Lineages A and B) was moderately supported (ML: 78%; Bayesian PP: 0.87).

**Table 2.   Genetic divergences within and among *Fiona pinnata* lineages**
COI sequence divergence values were calculated using the Kimura (1980) 2-parameter model of sequence evolution. Intralineage divergence values are italicised. Lineage C is represented by a single divergent specimen collected in Indonesia

|           | Lineage A   | Lineage B   | Lineage C |
|-----------|-------------|-------------|-----------|
| Lineage A | *0.1–2.0%*  |             |           |
| Lineage B | 4.9–7.1%    | *0.1–1.9%*  |           |
| Lineage C | 11.9–12.7%  | 10.2–12.8%  | *n/a*     |

CCO9
CCO13
CCO5
CCO2 (3)
CCO14
CCO10
AGI
CCO12
CCO11
CCO7
CCO6
CCO3
CCO15
CCO1
96  CCO8 (2)
1.00  CCO4
NZS/CCO (3)
NZS10
NZS3
NZS12
NZS11
NZS1 (24)
NZS5
NZS7
78  NZS4 (2)
0.87  NZS2
NZS8
NZS9

Lineage A

PAZ1
PAZ2
PAZ3
PMI
GSC
41  NPG1
0.38  NZN1
HFF1
HFF2
AHI
JWA2
NZS14
100  NPG2
1.00  JWA3
PAZ4
NZS13
JWA1
NZN3
ASI1
NZN/PAZ(3)
NZN2
ASI2
NZS6
MZB
ISU

Lineage B

Lineage C

*Cuthona ocellata*
*Tergipes tergipes*

0.05

**Fig. 2.** Maximum likelihood (ML) phylogeny of *Fiona pinnata* COI sequences. Bootstrap support values above nodes are derived from ML analysis (1000 replicates), and values below nodes are Bayesian posterior probabilities. Numbers in parentheses indicate frequency of haplotype occurrence.

A single Indonesian (Sulawesi) specimen formed a third mtDNA lineage (Lineage C) that was highly divergent from all other ingroup sequences (mean 11.8%).

Lineage A, abundant at temperate latitudes (Chile, southern New Zealand, Alaska), received high bootstrap (96%) and posterior probability support (1.00). Phylogeographic structure was detected within this lineage, with distinct 'New Zealand' and 'Chilean' haplogroups (Figs 2, 3) (mean 1.03% divergence), although one haplotype was shared by both of these sampling regions. The Alaskan haplotype was five mutational steps away from a common Chilean haplotype. Lineage B sequences, although not supported as monophyletic by bootstrap analysis (Fig. 2), clearly formed a divergent haplogroup with respect to Lineage A (Fig. 3). Lineage B was detected primarily in tropical and subtropical regions of the Pacific, Indian, and Atlantic Oceans. Little clear phylogeographic structuring was detected within this tropical lineage (mean 0.83% divergence) although three Portuguese specimens (Madeira Island, Azores) together formed a distinct haplogroup (Fig. 3). Interestingly, one haplotype was shared by geographically remote samples from the Azores and the North Island of New Zealand.

Despite the low genetic divergences detected within Lineages A and B (Table 2), only two COI haplotypes were shared across multiple sampling localities (Fig. 3). Across all localities (but excluding the divergent Sulawesi specimen), AMOVA revealed that a significant proportion (22%; $P < 0.001$) of the total genetic variation was distributed between ocean basins, whereas 61% ($P < 0.001$) was distributed among regional sampling locations within oceans.

### Global nuclear DNA diversity

Analysis of 26 ITS1 fragment sequences revealed 22 unique sequences worldwide. These sequences were distinguished by 53 variable nucleotide positions, with numerous indels also detected. Bayesian and ML topologies were similar to one another, and thus only the ML tree is presented (Fig. 4). Overall, ITS1 sequence divergences ranged from 0.2% to 8.5%, and the Indonesian specimen again showed marked genetic differentiation from all other *Fiona* sequences (5.7–8.5%). Other ITS1 sequences formed a monophyletic group (ML: 96%; Bayesian PP: 0.52), with a clear distinction between temperate (LINEAGE A) and tropical (Lineage B) sequences (maximum divergence 3.0%). The Lineage A grouping of Alaskan, Chilean, and southern New Zealand sequences received moderate bootstrap support (ML: 75%; Bayesian PP: 0.84), as did the Lineage B grouping (ML: 70%; PP: 0.72).

Although there was close correspondence between temperate (A) and tropical (B) lineages across mitochondrial and nuclear datasets, discordant phylogenetic placements were revealed for three southern New Zealand specimens, which grouped with tropical specimens for mtDNA (COI Lineage B), but with temperate specimens for nuclear DNA (ITS1 Lineage A) (Fig. 4).

### Discussion

Both mtDNA and nuclear datasets support the existence of three major genetic lineages within the widespread rafting nudibranch *F. pinnata*. Lineage A and Lineage B are both abundant and widespread, apparently in temperate and tropical/subtropical seas, respectively. Lineage C, by contrast, represents a relatively divergent but apparently geographically restricted lineage, thus far detected only in Indonesia (Sulawesi). Although the nuclear ITS1 phylogeny did not receive strong bootstrap support, lineages differentiated by small numbers of base substitutions are not expected to receive high bootstrap support. Regardless, the statistical parsimony network of ITS1 sequences (Fig. 5) is in strong agreement with the distinct tropical and temperate lineages revealed by phylogenetic analysis of the mitochondrial marker.

Marine invertebrate species generally occur exclusively in either temperate or tropical zones (Hyman 1955), and the geographic distributions of the two widespread mtDNA lineages of *F. pinnata* are seemingly correlated with these distinct zones. Specifically, based on our sampling regime, it seems that Lineage B predominates in the tropics, whereas Lineage A is generally found in the temperate zone. The latter lineage was commonly found on macroalgal rafts in the south-east and south-west Pacific, but also in Alaskan waters, thus suggesting an antitropical distribution in the Pacific Ocean (Hubbs 1952; Briggs 1987). Antitropical distributions are commonly observed in the sea (for a review, see Briggs 1995) and are exhibited by a diverse range of marine taxa including fish (Bowen and Grant 1997; Burridge and White 2000; Grant *et al.* 2005), algae (Peters and Breeman 1992; Graham *et al.* 2007; Macaya and Zuccarello 2010), crustaceans (Nations 1979), and molluscs (Koufopanou *et al.* 1999; Hilbish *et al.* 2000). Such distributions seem likely to reflect the physiological limitations of temperate-zone taxa, but with intermittent dispersal across the tropical zone (e.g. perhaps during Pleistocene cold periods; Lindberg 1991; Crame 1993).

The close genetic relationship between the Alaskan *F. pinnata* sample and those from the temperate Southern Hemisphere suggest that Lineage A might have experienced recent transequatorial dispersal. Indeed, dispersal seems the most plausible mechanism for establishing north–south disjunctions across the tropics (Vermeij 1989; Lindberg 1991; Peters and Breeman 1992; Hilbish *et al.* 2000). The Alaskan haplotype has a particularly close phylogenetic link with Chilean samples (0.6–1.8% divergence for COI), suggesting that this northern temperate lineage likely dispersed northward from the south-east Pacific by crossing the tropics of the eastern Pacific. Although the tropics are considered a strong biogeographic barrier for temperate taxa (Stepien and Rosenblatt 1996), a possible transtropical dispersal route along the eastern rim of the Pacific Ocean may be facilitated by upwelling of cold water along these coastlines, effectively diminishing the width of the tropical belt and permitting occasional migrations of temperate organisms between hemispheres (Lindberg 1991; Briggs 1995). Macaya and Zuccarello (2010) similarly suggested a Southern Hemisphere origin for the widespread kelp *Macrocystis pyrifera*, which is thought to have dispersed into the Northern Hemisphere via transequatorial migration of floating sporophytes. This hypothesis is supported by the observation that macroalgal rafts in the south-eastern Pacific Ocean are generally carried north along the Chilean coast via the Humboldt Current (Macaya *et al.* 2005). *Fiona pinnata* is frequently observed
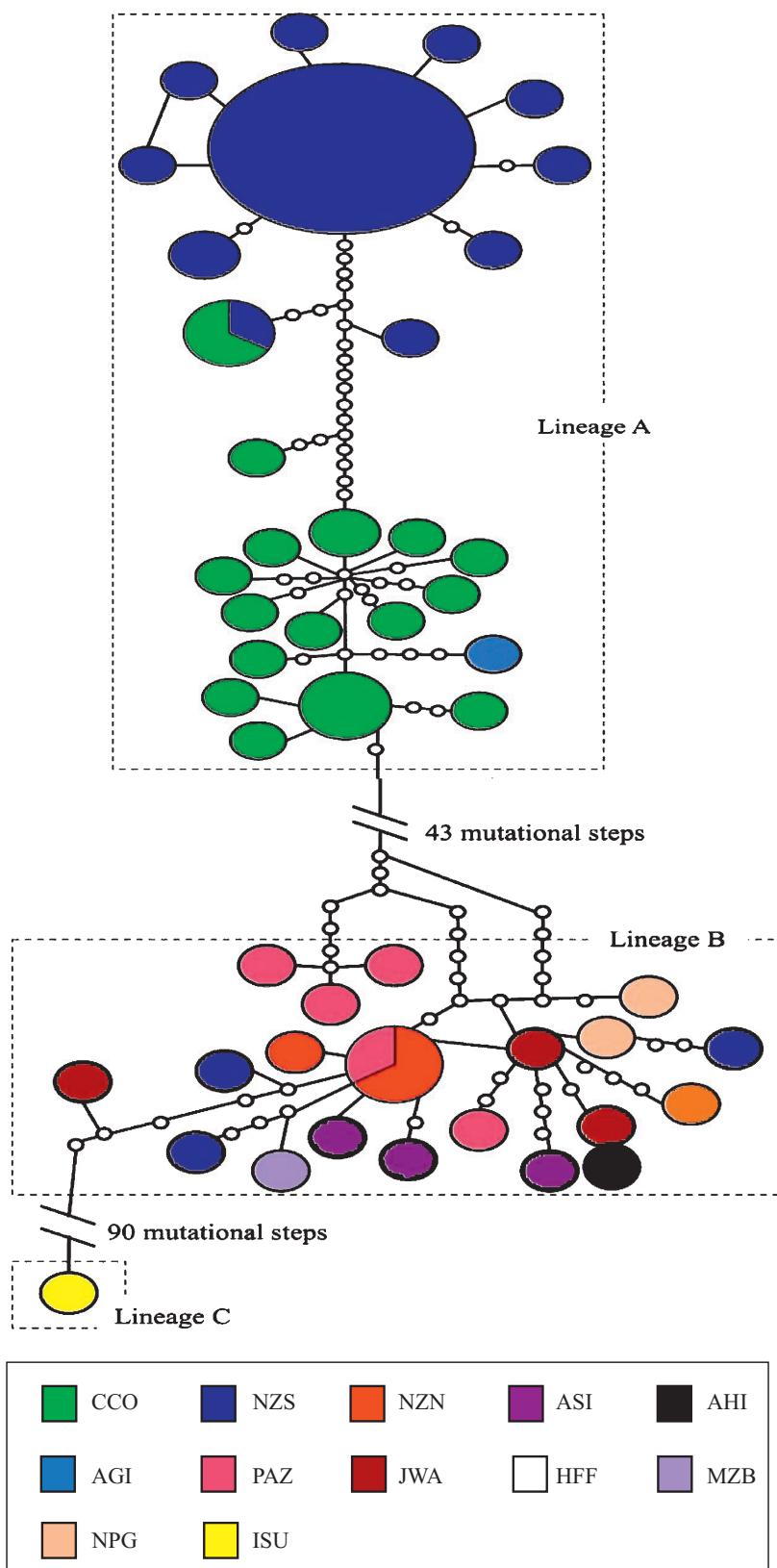
**Fig. 3.** Unrooted statistical parsimony network for *Fiona pinnata* COI. Coloured circles represent unique haplotypes, with sizes scaled to haplotype frequency. Small empty circles represent intermediate hypothesised haplotypes. Haplotypes are coloured according to geographic origins.
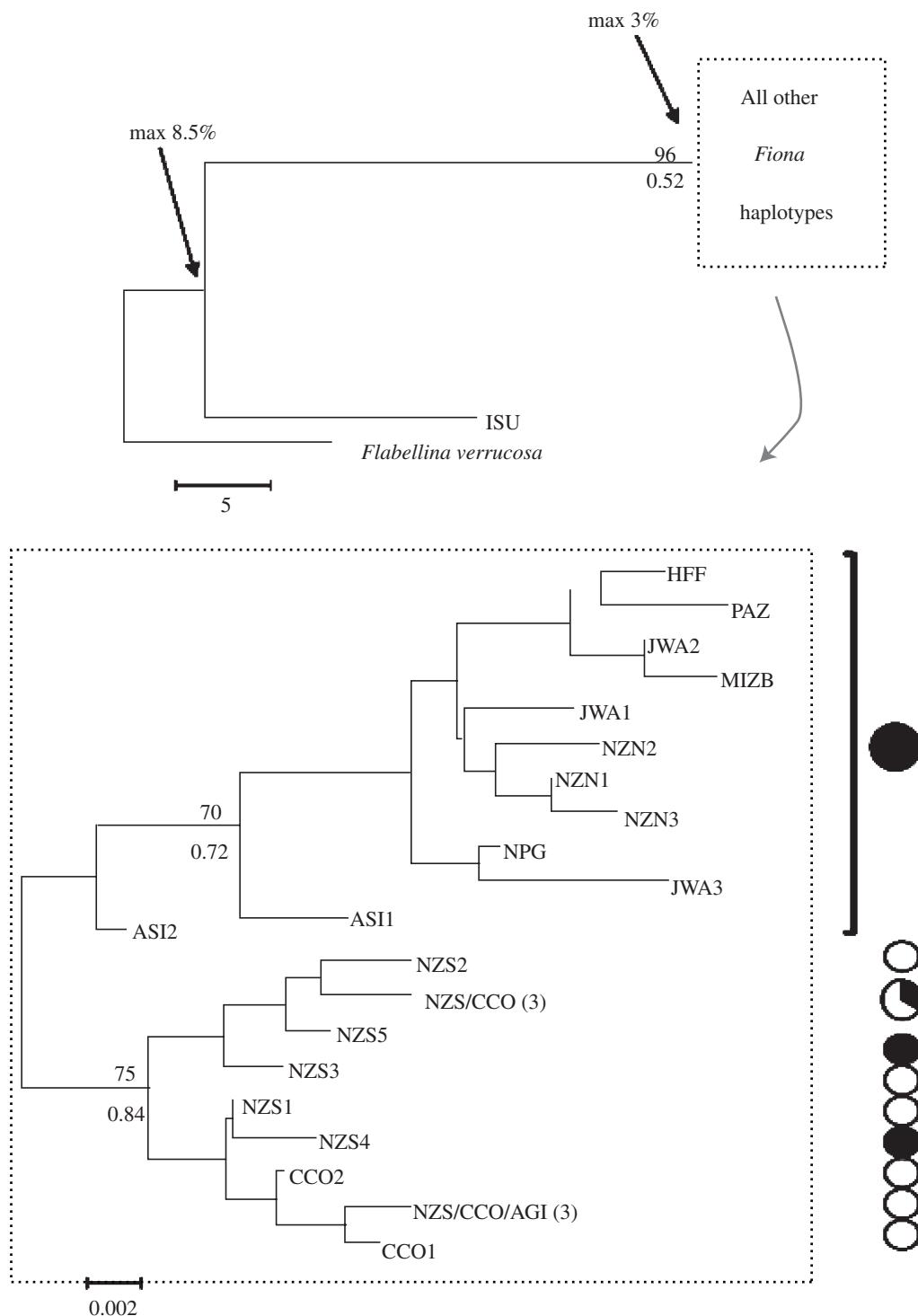
**Fig. 4.** Maximum-likelihood (ML) phylogeny of *Fiona pinnata* nuclear ITS1 sequences. Bootstrap values above nodes are derived from ML analysis (1000 replicates), and values below nodes are Bayesian posterior probabilities. Numbers in parentheses indicate frequency of sequence occurrence. A single Indonesian sequence (ISU; Lineage C) was highly divergent (K2P distance shown) from all other ingroup sequences (top) and is excluded from the main figure. Black and white circles indicate corresponding mtDNA lineages for each sample (white = COI Lineage A; black = COI Lineage B).
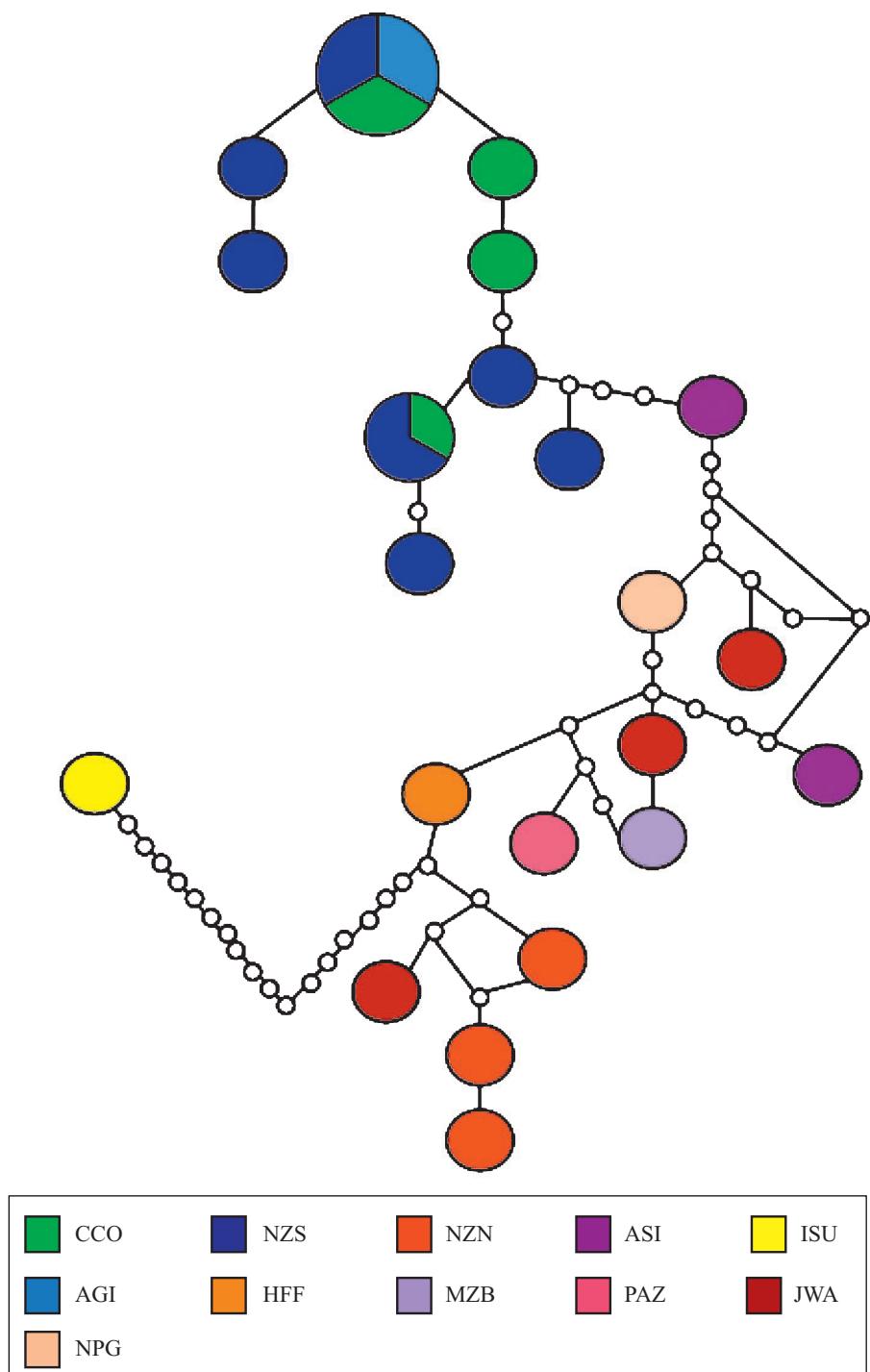
**Fig. 5.** Unrooted statistical parsimony network for *Fiona pinnata* nuclear ITS1. Coloured circles represent unique ITS1 sequences, with sizes scaled to reflect sequence frequency. Small empty circles represent hypothetical intermediate sequences. Sequences are coloured according to geographic origins.

rafting on detached *Macrocystis pyrifera* plants within the eastern Pacific Ocean (Bushing 1994; Hobday 2000; present study), and thus the anti-tropical pattern observed with the temperate lineages of this nudibranch could potentially be linked to the colonisation history and geographic distribution of this buoyant macroalgal host.

Within lineage A, Chilean and southern New Zealand populations were represented by two closely-related COI

haplogroups. This finding is mirrored by phylogeographic divergence recently detected between New Zealand and Chilean populations of *Lepas australis* (Schiffer and Herbig 2015), a rafting species upon which *F. pinnata* feeds. Indeed, it is not surprising to find similar phylogeographic patterns in these codistributed and ecologically similar species (Nikula *et al*. 2010). Despite these broadly distinct regional haplogroups, however, it should be noted that one COI haplotype was shared by both of these regions. It thus appears that passive rafting may facilitate occasional dispersal across the Pacific Ocean, likely driven by the West Wind Drift. Indeed, this strong surface current has previously been inferred to function as a powerful dispersal agent in the Southern Ocean for a variety of buoyant seaweeds and their associated faunal holdfast communities (Helmuth *et al*. 1994; Smith 2002; Waters 2008; Nikula *et al*. 2010).

Lineage distribution patterns appear to be mediated by temperature and ocean currents rather than influenced strictly by latitude alone. This point is illustrated by the fact that the Chilean specimens were collected at ~30°S but grouped genetically with cool-temperate Alaskan and southern New Zealand samples, perhaps due to the temperate influence exerted by the northward flowing Humboldt Current and coastal upwelling events in the Coquimbo region (Brattström and Johanssen 1983; Thiel *et al*. 2007). In comparison, northern New Zealand sampling sites at 36°S are influenced by the warm waters of the East Auckland Current and yielded tropical lineage B. Indeed, much of this region's biota has Indo-Pacific affinities (Pawson 1961).

Despite the fact that the Atlantic and Pacific Ocean basins are semiclosed systems, and interoceanic exchange between the two is believed to occur relatively rarely among marine invertebrates (Hyman 1955), the present study finds that only 22% of the *F. pinnata* COI variation is partitioned between oceans. It is possible that dispersal between ocean basins has been enhanced by anthropogenic processes such as shipping (Sponer and Roy 2002) and introduction of plastics into the marine environment (see also Schiffer and Herbig 2015). For example, the detection of a haplotype shared between New Zealand (Pacific) and the Azores (Atlantic) could perhaps reflect an artificial translocation event (Eberl *et al*. 2007). *F. pinnata* is commonly found in association with its *Lepas* spp. goose barnacle prey, and given that *Lepas anatifera* has been documented on ship hulls (Zvyagintsev and Mikhajlov 1985; Farrapeira *et al*. 2007), anthropogenic translocation cannot be entirely dismissed as a possibility (Schiffer and Herbig 2015). However, there are as yet no definitive records of *F. pinnata* having been translocated via human-mediated dispersal. In contrast, large aggregations of reproductive adults are frequently encountered on floating seaweeds and other buoyant substrates (see Thiel and Gutow 2005*b* for a review), and thus passive rafting, coupled with a planktonic larval stage, seems likely to be the predominant historical mechanism shaping this invertebrate's distinctive phylogeography.

The deep genetic divergence detected between the Indonesian specimen (Lineage C) and all other *F. pinnata* samples strongly suggests that this Indo-Pacific lineage represents a distinct phylogenetic species (Moritz 1994; Morando *et al*. 2003). Furthermore, this individual is potentially ecologically distinct as it was collected at 20-m depth on a rompong (deep-water fish attraction device), an unusual habitat for a taxon that otherwise

seems to occur exclusively on floating objects at the sea surface. To our knowledge, *F. pinnata* has not previously been collected from such a great depth.

In an attempt to establish genetic divergence thresholds among sister species of molluscs, some authors have proposed that a mean COI divergence of ~10% be used as a species delimitation approach (Hebert *et al*. 2003; Malaquias and Reid 2009). However, the application of strict thresholds can be confounded by high variance in rates of molecular evolution among taxa. Indeed, reviews of the literature have uncovered COI distances as low as 3.3–5.1% for well supported sister species of nudibranchs (Pola *et al*. 2007; Turner and Wilson 2008). Accordingly, it seems reasonable to suggest that the three lineages detected within *F. pinnata* represent a cryptic species complex. The clear concordance between data from distinct genetic markers (COI versus ITS1), and across geographic space (tropical versus temperate), broadly supports the notion that *F. pinnata* may comprise three phylogenetically and biologically distinct evolutionary lineages. Nevertheless, the overarching importance of rafting as a dispersal vector is underscored by the wide, transoceanic distributions of the two most abundant lineages of rafting *F. pinnata*.

## Acknowledgements

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