Phylogeography of the New Zealand whelks
Cominella maculosa and *C. virgata*

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"Reality is frequently inaccurate"

– Douglas Adams

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Abstract

Cominella maculosa and *C. virgata* are common rocky shore whelk species from New Zealand. This study used DNA sequences from the mitochondrial gene cytochrome c oxidase subunit 1 (CO1) to expand an earlier unpublished dataset and examine the phylogeographic structure of both species in the Cook Strait region, of *C. maculosa* in the Chatham Islands, and of *C. virgata* in the northern North Island. Both species are found to have a considerable degree of phylogeographic structure, concordant with that reported by an earlier study and for other species with direct development.

South Island sites sampled for *C. maculosa* had several private haplotypes and a high frequency haplotype that is shared with populations from the southern North Island. Together, these formed a 'southern haplogroup'. Low diversity in 'southern' populations may reflect founder effects that would have occurred as part of a southward range expansion during the onset of the present interglacial period. The Chatham Islands samples had two haplotypes that formed a separate sub-group to the 'southern haplogroup', suggesting Chatham Islands populations are moderately isolated from those on mainland New Zealand but may have been founded from 'southern' populations relatively recently.

The high frequency haplotype present in South Island samples of *C. virgata* is absent in Wellington samples but widespread in those from the north-eastern North Island. South Island populations may have been founded from the Hauraki Gulf through human-mediated translocation events. Phylogenetic analyses with a focus on *C. virgata* were conducted using the mitochondrial genes CO1 and 16SrRNA, and the nuclear gene 18S rRNA, to expand an earlier published dataset. The purported northern subspecies *C. virgata brookesi* does not form a monophyletic lineage and voucher specimens fluidly intergrade with the nominal subspecies, with which it is synonymised. A lectotype is designated for *Buccinum lineolatum* Quoy & Gaimard, 1833, for which *Cominella virgata* is a replacement name. Potential causes of the disjunct distribution patterns of *C. virgata* and other mollusc taxa are discussed with particular reference to the formation and timing of marine straits through the Auckland Isthmus and Cook Strait.

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Chapter 1: General introduction

Patterns and causes of genetic connectivity

The suggestion by science-fiction writer Douglas Adams that 'reality is frequently inaccurate' is jest, used here to reflect the incredible diversity in the biological world. Many key definitions in biology are contentious or somewhat subjective, in part because there are so often cases of biological systems that do not fit into a generalisation. The various species definitions (Mayr 1957; Sokal and Crovello 1970; Donoghue 1985) provide a prime example. Herein, a species is defined as a group of individuals and populations capable of interbreeding, but reproductively incompatible and isolated from other such groups (adapted from Mayr 1992: 222).

Biogeography can be loosely defined as the study of patterns and mechanisms behind the historic and contemporary distributions of species (adapted from Craw 1989: 527), whereas phylogeography pertains to the examination of mechanisms behind the extent and geographic distribution of genetic diversity within a species (Avise *et al.* 1987; adapted from Avise 2000: 270; Teske *et al.* 2011).

The parameters of a species' distribution, as well as how individuals and genetic variation are dispersed within, are determined by numerous and complex processes. The extent of a distribution can be determined by targeted sampling, recorded observations from area surveys, and the examination of reference collections from a range of contributors. Discerning past distributions is more difficult due to temporal and spatial gaps both in historic collections and fossil records, as well as due to bias introduced by fossilization processes and sampling (Koch 1978; Crampton *et al.* 2003; Cooper *et al.* 2006). DNA-based methods can be used to infer some historic population characteristics, but these are limited to features such as effective population

size, gene flow and regional affiliations (Hey and Nielsen 2004; Drummond *et al.* 2005; Li and Durbin 2011).

Organisms are seldom evenly distributed across a landscape or seascape and often form groups or aggregate in higher relative densities for the purposes of breeding, predator protection, feeding, and/or accessing favourable habitat (Holmes *et al.* 1994; Parrish and Edelstein-Keshet 1999; Castro *et al.* 2002). The formation of discrete or semi-discrete groups of individuals is often influenced by local geography and limitations to the dispersal potential of the species. A population can be defined from a genetic perspective as a cohesive group of interbreeding individuals that are most likely to mate with others of the same group. This localised pattern of interbreeding and mating isolation means the evolutionary processes of genetic drift, selection and mutation will operate semi-independently from other populations resulting in genetic differentiation among populations and the presence of geographic structuring to genetic variation across a species' distribution.

The rate of intermixing between two populations is dependent on the dispersal ability of the species as well as the presence and permeability of geographic barriers and the ability of migrants to find a mate or access suitable breeding sites. The level of gene-flow determines, in part, the similarity of allele frequencies between populations. Although the possible levels of gene-flow form a continuum, relative gene-flow can be quantified by its effects on genetic diversity. High gene-flow leads to 'panmixia', a single meta-population with little or no allele-frequency differences between regions (Fig. 1.1A). Weak gene-flow over relatively short distances can lead to gradients of allele frequency changes along a geographic transect, known as isolation by distance (IBD). In this pattern of genetic structure, adjacent populations are more closely related to one another than to those further apart (Laikre *et al.* 2005; Fig. 1.1B). Little or no gene-flow leads to discrete populations that have significantly different allele frequencies and unique alleles (Fig. 1.1C). Prolonged lack of migration between populations will result in reproductive isolation, the accumulation of genetic differences and, ultimately, reproductive

incompatibility resulting in speciation (Rice and Hostert 1993; Palumbi 1994; Cruickshank and Hahn 2014).
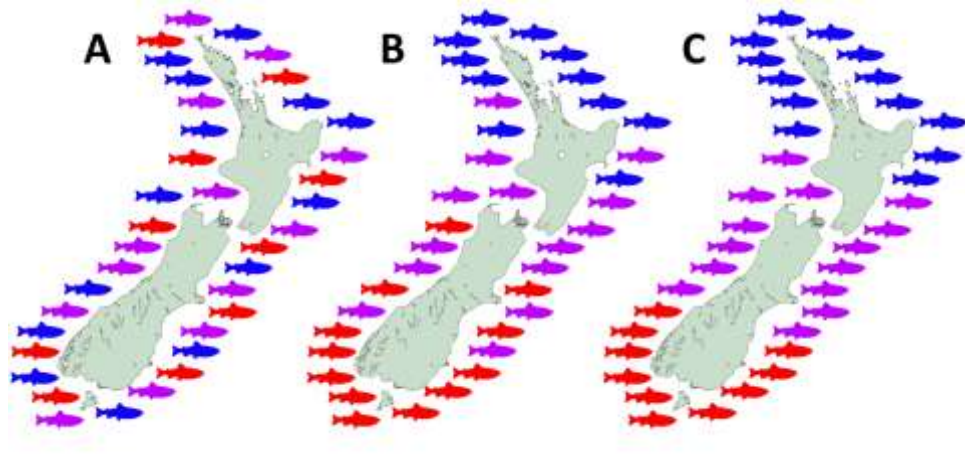
Figure 1.1. Examples of phylogeographic structure assuming differing levels of gene-flow. Different colours represent different haplotypes. **A**) Panmixia. **B**) Isolation by distance. **C**) Distinct populations. Redrawn from Wilcox (2015).

Demographic coupling of populations is different from genetic connectivity between populations, because it is dependent on the proportion of reproductively successful migrants relative to the population sizes (Lowe and Allendorf 2010; Ovenden 2013). In contrast, genetic connectivity is determined by an absolute number of migrants (Ovenden 2013). Very few migrants per generation are needed to constitute 'high' gene-flow and homogenise genetic variation among populations (Mills and Allendorf 1996; Lowe and Allendorf 2010; Ovenden 2013). The fixation index (*F*) is often used to test for genetic differentiation and can be calculated using the equation: $F_{ST} = \frac{1}{4N_e m + 1}$ (Wright 1969; Ovenden 2013), where '*m*' is the proportion of migrants relative to the effective population size (N_e). Higher F_{ST} values denote greater genetic difference between populations (Ovenden 2013).

In marine systems, geographic features such as straits, peninsulas, ocean circulation patterns and rivers can hinder or prevent the movement of individuals between populations, and by extension, limit the level of gene-

flow (Slatkin 1987; Manel *et al.* 2003). How geographic features influence gene-flow depends on species characteristics such as longevity, pelagic larval duration (PLD), swimming ability and orientation, habitat specificity, and tolerances for a range of abiotic factors (Slatkin 1987). Such abiotic factors include habitat availability, temperature, salinity, sedimentation and climate (Slatkin 1987; Bradbury *et al.* 2008).

With geographies changing over time and species continually evolving, observed phylogeographic patterns can be due, in part, to historic barriers to dispersal or species characteristics (Slatkin 1987). It is difficult to infer causality or deconstruct the individual effects of synergistic contributing factors when interpreting phylogeographic data. Identification of potentially congruent or convergent phylogeographic patterns in different species can aid the interpretation of phylogeographic data making it important to examine the growing body of data from regional bio- and phylogeographic studies based a diverse range of species and genetic markers. Dispersal ability and barrier permeability may differ between species or throughout ontogeny, especially for invertebrates, which often have larval morphologies that are quite distinct from the adult form (Ross *et al.* 2009; Gardner *et al.* 2010).

Dispersal as larvae and other pre-settlement processes significantly influence the levels of gene-flow of many benthic marine species (Bradbury *et al.* 2008; Ross *et al*. 2009) but aspects of the larval stage such as positioning in the water column, swimming behaviours, survivorship and distribution are seldom well understood (Ross *et al.* 2009). Early paradigms held that marine habitats are largely open to dispersal between populations because of the lengthy larval duration of many species and capacity of currents to transport larvae long distances (Mayr 1954; Palumbi 1994; Warner and Cowen 2002). However, the prevalence and importance of self-recruitment in populations is becoming increasingly apparent, even among species with considerable dispersal potential (Sponaugle *et al.* 2002; Swearer *et al.* 2002). While the presence or extended duration of a pelagic larval phase often relates to increased gene-flow (Thorson 1950; Mileikovsky 1971) and/or dispersal ability, several factors including competitive exclusion (Waters 2011; Waters *et al.* 2013),

larval retention in local eddies (Chiswell and Roemmich 1998; Chiswell and Booth 1999) and local selection pressures (Gardner *et al.* 2010) make PLD a poor predictor of dispersal ability and/or gene-flow (Bay *et al.* 2006; Haye *et al.* 2014).

Multiple layers of information about the distribution of species have allowed researchers to broadly characterise regional faunas. Elements of distribution patterns or phylogeographic structuring for different species are often similar because they have experienced the same environmental influences and changes (Teske *et al.* 2011). Similarities of distribution patterns have been used to suggest various schemes of biogeographic regions (reviewed by Shears *et al.* 2008). However, the division of an area into biogeographic regions has been a contentious approach as it relies on the classification of non-discrete characters, i.e., species' distributions. After examining well-established distribution boundaries of hundreds of mollusc species in relation to proposed biogeographic areas, several researchers (Dell 1962; Beu 2012; B.A. Marshall pers. comm. 2016) concluded that many of the proposed biogeographic boundaries were poorly supported or could not be precisely localised and are, thus, better viewed as regions with gradients of faunal composition changes.

The extent and significance of overlap between proposed biogeographic regions and phylogeographic structure is widely discussed (Avise 1992; Burton 1998; Waltari *et al.* 2007) and presumably relates to differences between species and haplotype occupancy times. Haplotypes are usually shorter-lived than species, depending on the markers and species studied. This discrepancy allows different influences and dispersal barriers to emerge, resulting in differing patterns of species and haplotype distributions.

The amount of genetic variation that accumulates and the rates of change differ relative to population size, the degree of admixture between populations, and the DNA marker chosen. Accordingly, selecting a sample design and DNA markers with an appropriate degree of resolution is important for successfully addressing a proposed question (Sunnucks 2000: Hills *et al.* 2011). The various DNA marker types differ in their degree of resolution,

which is a product of the number of loci sampled, mutation rate, mode of inheritance (single- or bi-parental), and the amount of recombination that occurs. A range of molecular methods are currently available, which differ in their requirements for development time, resources, and sample quality.

Allozyme electrophoresis, although often cheap and easy to develop, offers relatively low levels of resolution and statistical confidence (Mueller and Wolfenbarger 1999). DNA microsatellites remain a common method but can be time consuming to develop for each study taxon (Gardner *et al.* 2010). With ever decreasing cost and increasing efficiency, DNA sequence-based analyses are very popular with contemporary phylogeographic studies (Teske *et al.* 2011).

Unlike nuclear DNA, mitochondrial DNA (mtDNA) does not undergo recombination and is maternally inherited in most animal groups, making it more likely to preserve the genetic patterns of a population's demographic history. However , most common mtDNA markers have less power to detect recent admixture and mtDNA can be subject to very rare interspecies exchanges (Shaw 2002; Leaché and McGuire 2006). The best approach is to use sequences from both mitochondrial and nuclear DNA sources. New genome-wide DNA sequence techniques offer a high degree of resolution and a more comprehensive dataset for less effort. Single-nucleotide polymorphisms (SNPs) and massively parallel DNA sequencing are becoming increasingly popular, but for now, the cost and development time remains prohibitive for small projects.

The body of studies relating to the distribution of genes and species is rapidly growing. This enables researchers to gain a clearer understanding of the influence of geography, abiotic and biotic factors, and morphological or behavioural characteristics on the ability or probability of individuals to survive in or disperse across an area. This knowledge helps to inform planning of Marine Protected Areas (MPAs) (Palumbi 2003; Laurel and Bradbury 2006; Rocha *et al*. 2007; Bell 2008; Arrieta *et al.* 2010; Baco *et al.* 2016), management of ecosystem resources, endangered species or those

commercially exploited (Carvalho and Hauser 1994; Jennings *et al*. 1999; Ward 2000; Manel *et al*. 2003; Palumbi 2003; Claudet and Pelletier 2004) and make predictions on the influence of changes to the environment in the future (Palumbi 2003; Baco *et al.* 2016).

New Zealand physical geography

New Zealand is an archipelago in the South Pacific roughly 2000 km south-east of Australia (Close *et al*. 1978; Fig. 1.2). The emergent landmass lies on the largely submerged continent Zealandia (Chapple *et al*. 2009; Mortimer *et al*. 2017; Fig. 1.2) with the two largest islands, constituting 'the mainland', spanning approximately 13° of latitude (Sponer and Roy 2002; Will *et al.* 2015). New Zealand has the fifth largest exclusive economic zone (EEZ) in the world (Chiswell *et al.* 2015), encompassing more than 30° of latitude and over 700 islands (Gordon *et al*. 2010). Bisecting New Zealand is a plate boundary between the Pacific and Indo-Australian plates (Weissel *et al*. 1977; Fig. 1.2) and tectonic forces have significantly shaped the geography (Weissel *et al*. 1977; Hoernle *et al*. 2006; Trewick *et al*. 2007; Landis *et al*. 2008; Giribet and Boyer 2010) and biology (Heads 1998; Trewick and Wallis 2001) of the region.

Parts of Zealandia have been subjected to repeated tectonic uplift and/or subsidence (Trewick *et al*. 2007; Landis *et al*. 2008; Chapple *et al*. 2009), notably resulting in a period of considerable marine transgression during the Oligocene (Campbell and Landis 2003; Waters and Craw 2006; Trewick *et al*. 2007; Landis *et al*. 2008; Bunce *et al*. 2009). More recently, drastic changes in eustatic sea-levels during Pliocene and Pleistocene glacial cycles have led to the episodic emergence and closure of numerous marine straits (Lewis *et al*. 1994; Beu 2004; Stevens and Hogg 2004; Carter 2005; Bunce *et al.* 2009; Chapple *et al*. 2009; Fig. 1.3).

Figure 1.2. Bathymetric map of New Zealand. Red dashed line shows plate boundary, grey dashed line shows outline of Zealandia, inset shows New Zealand in relation to Australia. Image: Alexander Karnstedt 2008.

During the Pliocene and Early Pleistocene, must of the area currently forming the southern North Island was partially inundated, resulting in the formation of numerous islands and straits (Lewis *et al.* 1994; Stevens and Hogg 2004; Bunce *et al.* 2009; Fig. 1.3). Cook Strait first appeared c.450 ka BP (Lewis *et al.* 1994). Further north, the narrow and low-lying Auckland Isthmus has also been bisected repeatedly by straits in the Pliocene (Beu 2004; Stevens and Hogg 2004; Fig. 1.3) and possibly the Pleistocene (Beu 2004) but the location and timing of such events is poorly constrained (B.W. Hayward pers. comm. 2016; Chapter 3).
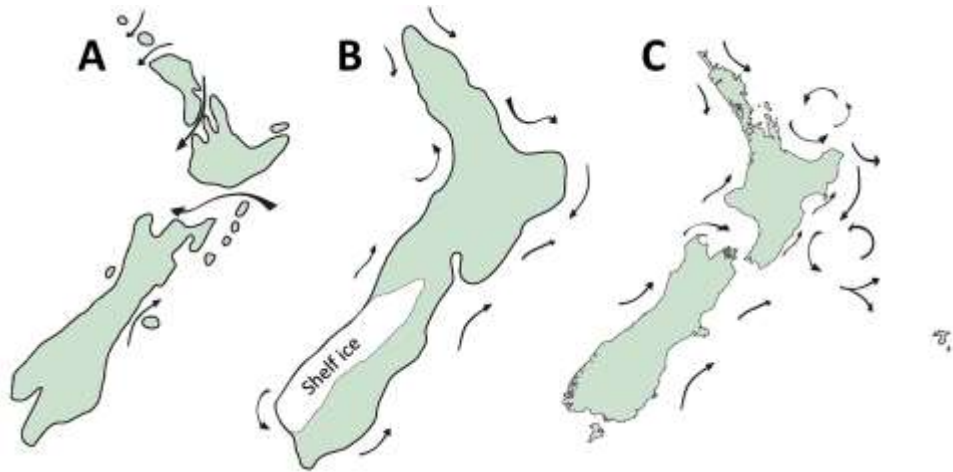
Figure 1.3. New Zealand's changing coastlines and predominant surface currents (arrows). **A**) Pliocene (6–2 Ma BP). **B**) Last Glacial Maximum (c.17 ka BP). **C**) Present day. Adapted from Stevens and Hogg (2004).
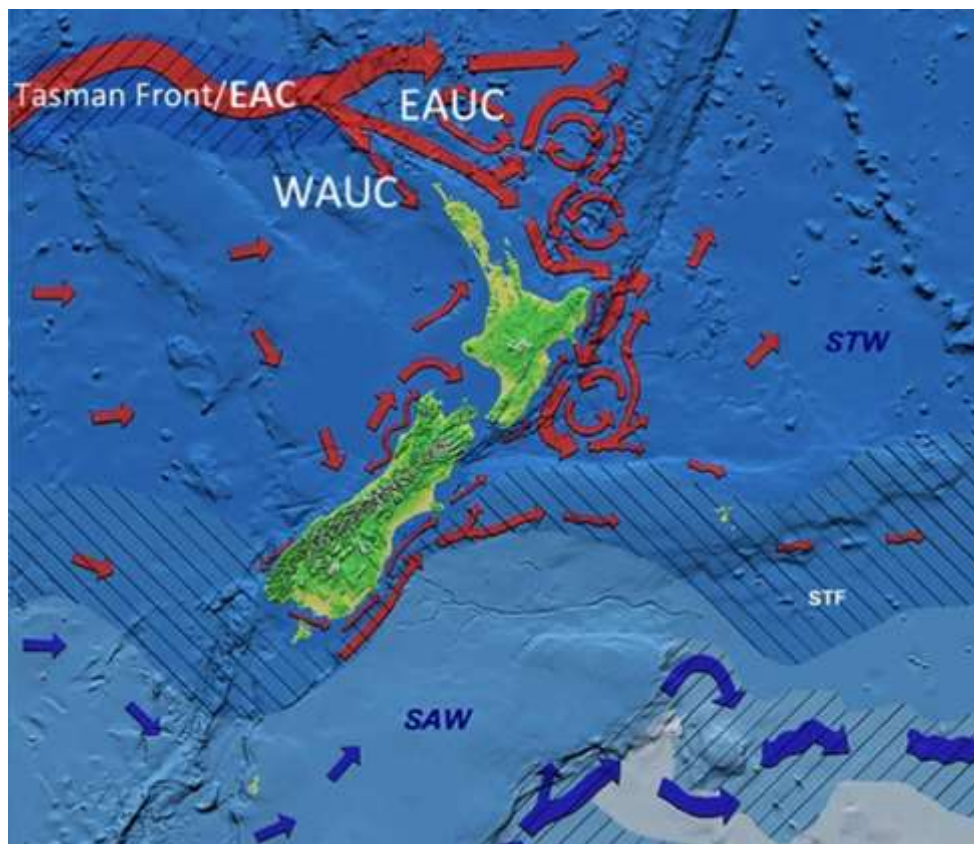
Figure 1.4. New Zealand ocean circulation. EAC: East Australian Current. WAUC: West Auckland Current. EAUC: East Auckland Current. STW: sub-tropical water. SAW: sub-antarctic water. STF: Sub-tropical Front. Red and blue arrows depict the movement of sub-tropical and sub-antarctic water respectively. Adapted from Carter *et al*. (1998).

New Zealand lies on a boundary between sub-tropical and sub-antarctic water, demarcated by the Sub-tropical Front (Fig. 1.4), which runs along the southern coast of the South Island, along the Chatham Rise and past the Chatham Islands (Heath 1981; Butler *et al*. 1992) where it results in a productive (Bradford 1983) marine fauna.

The East Australian Current transports sub-tropical water south along the Queensland coast before heading eastwards across the Tasman Sea, where it becomes known as the Tasman Front. Near north-western New Zealand, the Tasman Front bifurcates to form the West Auckland and East Auckland currents (Godfrey *et al.* 1980; Chiswell *et al.* 1997; Ridgway and Dunn 2003; Fig. 1.4). Between these major current systems run a myriad of smaller current networks, deep-water currents, eddies and gyres (Bowman *et al*. 1983). Those nearest the coasts and fine scale movements are currently poorly understood.

A dynamic geological history, considerable geographic and temporal isolation from other land-masses and complex oceanography (Bradford-Grieve *et al*. 1991; Ross *et al*. 2009) have resulted in striking endemism in the contemporary flora and fauna of New Zealand. While few taxonomic groups present in New Zealand prove to have a vicariant Gondawanan origin (Waters and Craw 2006; Waters 2008; Giribet and Boyer 2010), trans-Tasman or other cross-border dispersal events are likely to be very rare in many terrestrial or coastal marine groups. Accordingly, there is a high rate of endemism in New Zealand species, which primarily result from local radiations. The unique biota and diversity of climatic and habitat extremes in a relatively small area makes New Zealand an excellent location to study biogeography and phylogeography (Giribet and Boyer 2010).

Phylogeography of New Zealand's marine fauna

The phylogeography of New Zealand's marine fauna has been reviewed by Ross *et al.* (2009), Gardner *et al.* (2010) and Hannan *et al.* (2016), citing

between them over 60 studies, and several have been published subsequent to 2010 (Hannan *et al.* 2016 reviewed soft-sediment taxa only). A relatively large number of studies are available from New Zealand compared with other regions around the world (Hardy *et al.* 2011; Teske *et al.* 2011), however, when divided up into markers used, geographic coverage, phyla, life history strategies or habitat type, few studies are directly comparable.

Studies using different markers often present contrasting patterns of connectivity, perhaps reflecting marker sensitivity, geographic coverage or sample sizes. Examples include the paua *Haliotis iris* Gmelin, 1791 (Frusin 1982; Smith and McVeagh 2006; Will and Gemmell 2008; Will *et al.* 2011; Will *et al.* 2015), mussel *Perna canaliculus* (Gmelin, 1791) (Smith 1988; Gardner *et al.* 1996; Apte and Gardner 2001, 2002; Apte *et al.* 2003; Star *et al.* 2003; Wei *et al.* 2013a, b) and crayfish *Jasus edwardsii* (Hutton, 1875) (Smith *et al.* 1980; Ovenden *et al.* 1992; Morgan *et al.* 2013; Thomas and Bell 2013). These examples also demonstrate a bias in the literature favouring commercially exploited species, in part driven by funding availability. Additionally, there is a bias against smaller, obscure or less charismatic taxa and groups. Few phylogeographic studies feature, for example, species smaller than 10 mm. Phylogeographic principles and biases appear congruent globally.

Studies often do not cite historical records from museum collections and midden sites or distribution information beyond their sampling coverage. Such information would help to establish natural distributions or potential for human influence on a species' distribution or genetic structure. Potential human mediated translocation events or range shifts are also seldom discussed in detail and smaller signatures of translocation may be dismissed as artefacts, natural or indeterminate in origin.

Maritime biosecurity efforts tend to focus on vessels crossing international borders rather than domestic movements. Exotic species are being detected at a greater rate than ever before, both in New Zealand and globally (Bax *et al.* 2003), probably reflecting a combination of increasing shipping volumes, biosecurity search effort and changing climatic conditions. The extent of

human mediated translocation events through different vectors is most studied in invasive species (Bax *et al.* 2003; Ruiz and Carlton 2003) while the effects of domestic vessel movements on native species remain to be established and may be more difficult to observe.

The New Zealand marine region has a number of regions frequently associated with phylogeographic breaks. Several north/south breaks have been reported in the Cook Strait region for a variety of taxa (Apte and Gardner 2002; Apte *et al*. 2003; Star *et al*. 2003; Waters and Roy 2004; Ayers and Waters 2005; Goldstien 2005; Goldstien *et al*. 2006; Veale and Lavery 2011; Wei *et al*. 2013a, b), although the precise location, nature and causes of these breaks are unclear (Ross *et al.* 2009) and may differ between species. East/west breaks are also commonly but less frequently reported (Schnabel *et al.* 2000; Stevens and Hogg 2004; Knox *et al.* 2011; Veale and Lavery 2011) but are not readily associated with a single region or attributable to any one cause. Most studies have too few sample sites to narrow down break localities, and sampling sites differ between studies, hampering direct comparison. Breaks are often associated with or superimposed against proposed biogeographic provinces (Shears *et al.* 2008) but the degree of correlation is often low (Ross *et al.* 2012; Veale and Lavery 2012). Interpretations frequently focus on the single line of explanation deemed to be the most probable for each detected pattern. Speculation regarding the causes of phylogeographic patterns can direct further research but should be approached with caution. Often results will simply provide more questions than answers.

Related species with similar life-history strategies frequently have differing patterns of phylogeographic structure (Goldstien 2005; Goldstien *et al.* 2006; Stevens and Hogg 2004; Knox *et al.* 2011). Multiple studies featuring different species and markers are needed to determine if repeating patterns are due to common causes or to infer or deconstruct causality with greater confidence (Ross *et al.* 2009).

Genus *Cominella* Gray, 1850

The large and widespread neogastropod superfamily Buccinoidea comprises a diverse group of families, genera and species (Bouchet and Rocroi 2005; Kosyan and Kantor 2007). Despite several anatomical and molecular reviews, taxonomic relationships within Buccinoidea remain contentious (Ponder 1973; Harasewych 1998; Harasewych and Kantor 1999; Kantor 2003; Kosyan and Kantor 2004, 2007; Hayashi 2005), due, in part, to often extremely variable shell morphologies (Walton and Marshall in prep.).

The familial placement of *Cominella* Gray, 1850 is unclear. The genus has previously been referred to its own family, Cominellidae Gray, 1857 (e.g. Powell 1929, 1937, 1946; Dell 1956; Marwick 1965; Morton and Miller 1968), however *Cominella* is here maintained in Buccinidae Rafinesque, 1815 in the interest of continuity pending more conclusive molecular and anatomical analyses of the superfamily. The type species is *C. maculosa* (Martyn, 1784) (=*Buccinum testudineum* Bruguière, 1789: ICZN opinion 479, 1957).

Within *Cominella*, five extant subgenera are recognised (Donald *et al.* 2015) comprising roughly 25 extant species, several of which are awaiting description (Walton and Marshall in prep.). All *Cominella* species are endemic either to Australia, Norfolk Island or New Zealand, and all extant subgenera are endemic to New Zealand except *Josepha* Tenison-Woods, 1879, which only contains the species from Australia and Norfolk Island (Donald *et al.* 2015). The presently available DNA sequences support the reciprocal monophyly of each subgenus (Donald *et al.* 2015; Chapter 2) although many of the rare or deep-water forms and species have yet to be collected alive in the molecular age.

Most *Cominella* species have highly variable shell morphologies both within and between populations, confounding specific determination or subgeneric placement in the absence of large samples and/or molecular data (Walton and

Marshall in prep.). High diversity and a tendency for character convergence make the relationships of many fossil taxa difficult to discern and non-molecular subgeneric diagnoses (e.g. Marshall *et al.* 2016) near-impossible. The interpretation of fossils in relation to the living fauna is further complicated when it is unclear if a fossil is a direct ancestor or extinct sister lineage (Magallón 2004; Rydin *et al.* 2004). Roughly half of extant *Cominella* species inhabit rocky coasts, a habitat with low fossilisation potential (Schopf 1978; Hayes *et al.* 1993), and the fossil record is likely biased towards soft-sediment dwelling species (Schopf 1978).

A fossil at the Museum of New Zealand Te Papa Tongarewa (NMNZ) from Sparrow Bluff (Kaimatira) along the Whanganui River and dating from the Late Pleistocene c.1 Ma BP (M.017786) is clearly of a species closely related to *C. virgata* but may not be a direct ancestor (pers. obs.). Marwick (1965) described and figured a Waitotaran fossil as *C. virgata* H. Adams & A. Adams, 1853 although the figured specimen is does not appear to be conspecific. It differs from *C. virgata* in having much stronger and more numerous spiral threads, narrower and more persistent axial costae and less evenly rounded teleoconch whorls. This was the source of the record in Beu and Maxwell (1990) and was subsequently used as a calibration node for the molecular clock of Donald *et al.* (2015). The ancestral state reconstruction of Donald *et al.* (2015) found slight support (probability = c.55%) for a New Zealand origin of the genus subsequent to the divergence of New Zealand and Australia c.82 Ma BP (Kamp 1986). This suggestion was unexpected as *Cominella* species are thought to have a generally poor dispersal ability (Donald *et al.* 2015) and a New Zealand post-vicariance origin would have required a historic long-distance dispersal event counter to most regional oceanic circulation patterns (Donald *et al.* 2015; Fig. 1.4).

Australia has fewer *Cominella* species and several require revision. *C. lineolata* (Lamarck, 1816) is one such species, introduced as *Buccinum lineolatum* Lamarck, 1816, a name which has priority over the taxon of the same name of Quoy and Gaimard (1833), for which *C. virgata* H. Adams & A. Adams, 1853 is a replacement name (Chapter 2). One of Lamarck's daughters

annotated his collection in their personal copy of Lamarck (1822), now at the Muséum d'Histoire Naturelle de la Ville de Genève, Geneva, Switzerland (MHNG) (Beu and Cernorhorsky 1986). The annotations note two specimens of *C. lineolata*, each measuring 15 lines (E. Tardy pers. comm. 2017), equating to specimens approximately 33.84 mm in length converting from the French line. Two specimens (MHNG-MOLL-96341) are known at MHNG from the Delessert collection, which includes the Lamarck collection, but their provenance, and so type status, is uncertain (E. Tardy pers. comm. 2017). As these exactly match the annotations, they are very likely to be syntypes.

C. glandiformis (Reeve, 1847) from New Zealand occurs around the North, South, Stewart and Chatham Islands, exclusively in sheltered muddy intertidal habitats (Morton and Miller 1968), and forms a clade sister to that of all sampled congeners in some phylogenies (Donald *et al*. 2015). It has an extremely patchy distribution due to high habitat specificity, relatively little genetic divergence between widely separate populations (Donald *et al*. 2015) and the smallest protoconch (0.80–0.85 mm versus ≥1.05 mm) of any extant *Cominella* species. Accordingly, it seems plausible that *C. glandiformis* has or has recently had a pelagic larval stage. Gastropods with lecithotrophic larval development generally have relatively small protoconchs (Kano 2006). However, Morley (2013) did not mention swimming or free-floating hatchlings in laboratory observations of *C. glandiformis* egg masses and hatchlings, although observations were not made daily and hatchling emergence was not observed.

The transition between some larval development types may not be a slow or infrequent process as previously considered (McEdward and Janies 1997; McHugh and Rouse 1998; McEdward and Miner 2001; Collin 2004), and a change from lecithotrophy to entirely benthic direct development may simply reflect a change in the buoyancy of juveniles with no swimming ability *sensu stricto*. Newly emerged *Cominella maculosa* (Martyn, 1784) hatchlings have been observed to float on still water in laboratory conditions but would sink when disturbed (Dohner 2016).

Figure 1.5. *Cominella* species with egg masses. **A**) *C. maculosa*, Owenga, Chatham Islands. This rock had just been upturned. Note communal egg-laying and eggs attached to living snails. Image: Pat Lakeman 2013. **B**) *C. adspersa*, Marfells Beach, Marlborough. **C**) *C. virgata*, Oriental Bay, Wellington.

Most *Cominella* species have relatively large and heavy paucispiral protoconchs, usually indicative of direct development (Walton and Marshall in prep.). It is likely that all extant species presently deposit leathery egg capsules onto hard substrates and have direct benthic development (Donald *et al.* 2015).

The number of individuals in each egg capsule differs between species. In *C. virgata*, only one hatchling is thought to emerge from each egg capsule whereas about eight emerge from those of *C. maculosa* (Carrasco *et al.* 2012) after several months of development (van der Sman 2007). Neither *C. maculosa* nor *C. virgata* is thought to produce nurse eggs (Carrasco *et al.* 2012). *C. glandiformis* differs in having six to seven embryos in each egg capsule with some possibly serving as nurse eggs (Pilkington 1974). The frequency of laying and the number and distribution of egg capsules deposited by each female is unclear as they host communal broods (Carrasco and Phillips 2012; Fig. 1.5). In lab studies, individual female *C. maculosa* have been documented depositing up to 82 egg capsules (average = 28) per year (van der Sman 2007; van der Sman *et al.* 2009).

Eggs of *C. glandiformis* have been observed on wood (Morley 2013), shell (Pilkington 1974) and seagrass, whereas those of *C. adspersa* (Bruguière, 1789), *C. maculosa* and *C. virgata* (Fig. 1.5) are normally cemented to the underside of rocks (Carrasco and Phillips 2012; Carrasco *et al.* 2012) but are sometimes attached to other snails (Fig. 1.5), crabs (Graham 1941) and potential rafting materials like algae, pumice and driftwood. Detached eggs of *C. adspersa* have been observed floating in calm water (Dohner 2016) and those of *C. glandiformis* attached to floating driftwood (Morley 2013). Even though they seldom associate with such materials, *Cominella* species frequently occur in high abundance and in close proximity to potential rafting material so occasional rafting events are likely (Donald *et al.* 2015). Rafting events may partially explain some of the patterns of phylogeographic structure in *C. maculosa* and *C. virgata* (Dohner 2016; Fleming *et al.* in review) as well as the occurrence of some species on outlying islands such as the Chatham Islands.

Aims and general approach

Phylogeographic and phylogenetic studies often report differing patterns of connectivity and diversity between even closely related species (Stevens and Hogg 2004; Goldstien 2005; Goldstien *et al.* 2006; Knox *et al.* 2011). Multiple approaches that include a range of molecular markers and taxa are required to identify common patterns of population structure (Ross *et al.* 2009; Teske *et al.* 2011) and to improve the general understanding about the processes that influence of gene-flow and barriers to dispersal for coastal New Zealand organisms (Ross *et al.* 2009; Gardner *et al.* 2010).

C. maculosa and *C. virgata* frequently occur in high abundance on New Zealand coasts and are ecologically significant components of many inshore marine environments (Morton and Miller 1968). They are sympatrically occurring and easy to collect, making them well suited for phylogeographic study (Fleming *et al.* in review). Neither species is currently of commercial interest or of conservation concern, although observed patterns of genetic connectivity might be helpful for inferring patterns for other species, especially those that are rare or range-restricted and cannot practically be sampled in similar quantity, or those commercially harvested such as *Penion sulcatus* (Lamarck, 1816) and *Austrofusus glans* (Röding, 1798).

Fleming *et al.* (in review) presented a phylogeographic study using DNA sequences of the mitochondrial gene cytochrome c oxidase subunit 1 (CO1) from *C. maculosa* and *C. virgata* from the North Island south of Cape Rodney, and Nelson in the South Island (Fig. 1.6). Both species occur north of Cape Rodney, but populations of *C. virgata* in the northern North Island are especially morphologically diverse (pers. obs.). This diversity led Powell (1952) to distinguish some northern populations as the subspecies *C. virgata brookesi* Powell, 1952 (type locality: Karikari Peninsula). Even more divergent forms from the west coast of Northland were unknown to or not listed by Powell (1952), and shells of the various forms, including *C. virgata virgata* and *C. virgata brookesi*, appear to intergrade. However, it has been

unclear if northern populations of *C. virgata* warrant subspecific distinction, and if so, where the boundaries between subspecies lie.

A concatenated three-gene phylogeny presented by Donald *et al.* (2015) proposed two major clades within *C. virgata* that the authors interpreted as corresponding to *C. virgata virgata* and *C. virgata brookesi*. That interpreted as *C. virgata brookesi* comprised samples from <30 km away from its type locality and shell vouchers at NMNZ, corresponding to some of these sequences, closely resemble the holotype of *C. virgata brookesi*, held at the Auckland War Memorial Museum. However, this clade included a sequence from the Bay of Islands, which is the type locality of *C. virgata virgata* (designated by Powell 1952), and another from Taupiri Bay. Both of these voucher specimens are of the typical *C. virgata virgata* shell-form.

Several studies have identified a phylogeographic break in the northern South Island for a range of taxa (Waters and Roy 2004; Ayers and Waters 2005; Goldstien *et al.* 2006; Ross *et al.* 2009). Fleming *et al.* (in review) reported the presence in Nelson of *C. maculosa* and *C. virgata* haplotypes that were also found in the Hauraki Gulf but that were not known from the lower North Island. This result could suggest a possible genetic break occurring across the Cook Strait and/or translocation events.

This present thesis research expands the geographic coverage of the Fleming *et al.* (in review) CO1 dataset (Fig. 1.6) utilising an extension of their methodologies and DNA markers (Chapter 2). Seven and three additional South Island populations were sampled for *C. maculosa* and *C. virgata* respectively (Fig. 1.6), encompassing most of their ranges around the South Island (Chapter 2). The inclusion of these additional South Island populations into a combined dataset is used to establish if South Island populations are naturally occurring, to test for evidence of phylogenetic breaks or gene-flow across Cook Strait, and allow comparison of the expanded dataset with other studies with a focus on the Cook Strait region. Although few samples of *C. maculosa* were available from the Chatham Islands (Fig. 1.6), these were

included to check for local cryptic diversity, mainland regional affiliation and to approximate the occupancy time of Chatham Islands populations.

Populations of *C. virgata* from Northland were included in the expanded CO1 dataset allowing these to be compared with the other North Island populations sampled by Fleming *et al.* (in review). The expanded *C. virgata* dataset is used to examine phylogeographic structure in populations from north of Cape Rodney, and establish if the geographically structured morphological diversity in this region was reflected in the diversity of the CO1 sequences. In addition, several phylogenies are presented using CO1 sequences as well as two additional DNA markers; the mitochondrial gene 16S rRNA and the nuclear gene 18S rRNA. Published sequences from Donald *et al.* (2015) were retrieved from GenBank (www.ncbi.nlm.nih.gov/genbank/). These phylogenies were used to test for reciprocal monophyly in samples representing the various forms and purported subspecies, with a view to review the support for the continued maintenance of distinct subspecies.

Specific research questions

- What are the patterns of phylogeographic structure of *C. maculosa* and *C. virgata* populations around the South Island and how do they compare with those of the North Island?
- How does the population genetic diversity in the Chatham Island populations of *C. maculosa* relate to mainland populations?
- How do patterns of phylogeographic structure present in the Northland population of *C. virgata* compare with those from other North Island localities?
- Do any forms of *C. virgata* warrant subspecific recognition based on a population-level sample of genetic data?
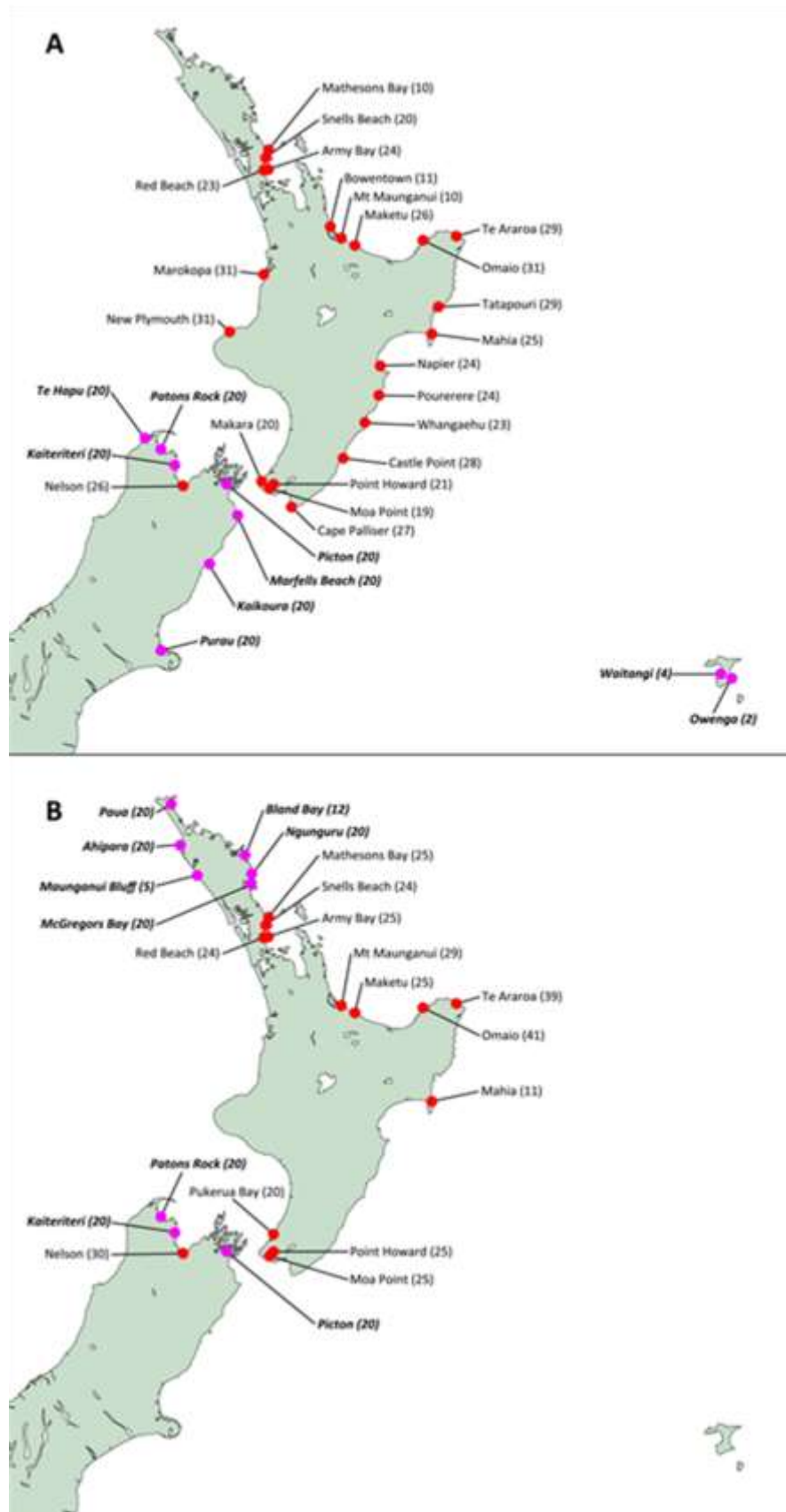
Figure 1.6. Maps showing sample sizes (numbers) and sites. Red dots and bold and italicised location names correspond to sites originating from this study; others comprise the dataset of Fleming *et al.* (in review). **A**) *C. maculosa*. **B**) *C. virgata.*

Chapter 2: Phylogeography of *Cominella* (*Cominella*) *maculosa* (Martyn, 1784) and *C.* (*Cominula*) *virgata* H. Adams & A. Adams, 1853 (Gastropoda: Neogastropoda: Buccinidae) in New Zealand

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Abstract

Cominella maculosa and *C. virgata* are common whelk species that inhabit rocky shores throughout much of the North Island, the northern South Island, and, for *C. maculosa*, the Chatham Islands. This study used DNA sequences from the mitochondrial gene cytochrome c oxidase subunit 1 (CO1) to expand an earlier unpublished dataset and examine the phylogeographic structure of populations of both species in the Cook Strait region, of *C. maculosa* in the Chatham Islands, and *C. virgata* in the northern North Island. Both species are found to have a considerable degree of phylogeographic structure. South Island populations of *C. virgata* may have originated from human-mediated translocations. Phylogenetic analyses were also conducted using the mitochondrial genes CO1 and 16SrRNA, and the nuclear gene 18S rRNA. The purported northern subspecies *C. virgata brookesi* does not form a monophyletic lineage and is synonymised with *C. virgata.* A lectotype is designated for *Buccinum lineolatum* Quoy & Gaimard, 1833, of which *Cominella virgata* is a replacement name.

Keywords: Mollusca; Buccinoidea; genetics; systematics; taxonomy; lectotype; Cook Strait; Chatham Islands

Introduction

Cominella Gray, 1850 is a genus comprising about 25 extant species, each endemic either to Australia, Norfolk Island or New Zealand (Donald *et al.* 2015). *Cominella* (*Cominella*) *maculosa* (Martyn, 1784) and *C.* (*Cominula*) *virgata* H. Adams & A. Adams, 1853 are common, sympatric, often syntopic, carnivorous (Ansell 2000; Stewart and Creese 2004; Morley *et al.* 2006) whelks. They are usually found in association with hard substrates (Morton and Miller 1968) and range from the intertidal zone to 16 and 11 m respectively. *C. maculosa* occurs throughout the North Island, the northern South Island, and the Chatham Islands (Fig. 2.1A). *C. virgata* is absent at the Chatham Islands (Marston 1996, 1998) and has a disjunct distribution comprising two population centres, one in the northern and north-eastern North Island, and the other in the Cook Strait region (Fig. 2.2A). Both species have direct development (Carrasco and Phillips 2012; Carrasco *et al.* 2012) and their abundance, similar distributions, habitats and behaviours make them ideal subjects for phylogeographic analyses in conjunction (Fleming *et al.* in review).

Species with direct development generally have poor dispersal ability, which makes them more likely to have genetically structured populations than species with a pelagic larval phase (Thorson 1950; Mileikovsky 1971). The egg capsules of *C. maculosa* and *C. virgata* are frequently cemented to substrates other than rock, such as crabs (Graham 1941), algae and other snails (Dohner 2016; Chapter 1). Development takes several months (van der Sman 2007). Detached egg masses of *C. adspersa* (Bruguière, 1789) have been observed floating in calm water (Dohner 2016) and those of *C. glandiformis* (Reeve, 1847) attached to floating driftwood (Morley 2013). Although *Cominella* species do not normally associate with substrates with high rafting potential (Donald *et al.* 2015), such as algae and driftwood, *C. maculosa* and *C. virgata* occur in high abundance near such materials and sporadic rafting events are likely, especially as egg capsules (Donald *et al.* 2015). Infrequent

rafting events could explain some of the patterns of gene-flow in *C. maculosa* and *C. virgata* (Dohner 2016).

Juveniles and egg capsules of both species are sometimes found on the brown alga *Carpophyllum maschalocarpum* Turner (Greville, 1830), which occurs sympatrically throughout their distributions. Detached fronds from *C. maschalocarpum* form rafts capable of traversing Cook Strait and the Chatham Rise (Buchanan and Zuccarello 2012). The alga *Durvillaea antarctica* (Chamisso) Hariot, 1892 occurs throughout the South Island and sporadically around the southern North Island. It is significantly sturdier, larger and more buoyant, and accordingly, has even greater rafting potential (Collins *et al.* 2010; Nikula *et al.* 2010; Fraser *et al.* 2011; Nikula *et al.* 2011a, b) than *C. maschalocarpum*. *D. antarctica* has been implicated as a vector for gene-flow of several marine invertebrate species in southern New Zealand (Fraser *et al.* 2011; Nikula *et al.* 2011a, b).

Human activity can also result in the translocation of species through several vectors. Whilst shells of both *C. maculosa* and *C. virgata* have been found in low abundance in midden sites (Willan 1974; Hayward *et al.* 1978; Hayward 1982; Foster 1986), it is unlikely that either species formed a significant food source for Māori or was deliberately translocated. Although *Cominella* species dislodge easily, they could become established and be transported on heavily fouled hulls. Perhaps a more common vector for *Cominella* species relates to dry-ballast. Rocks were widely used as ballast in New Zealand as recently as the early 1900's (Moore and Kenny 1986; Hewitt *et al.* 2009) and many taxa, including commercially important and pest species, have been introduced or spread as bio-foul attached to or among ballast rocks (Carlton 1999; Bax *et al.* 2003; Carlton 2011). These types of human-mediated translocations are presumably most common in port areas.

Another means of unintentional human mediated dispersal may be via transport of craypots, which *Cominella* species regularly enter, attracted by the bait (Ansell 2000; Stewart and Creese 2004). *C. maculosa* and *C. virgata* can survive out of water for several days if they remain cool and moist. With many

vessels running lines of craypots tens of kilometres apart, it is conceivable adult snails are regularly transported considerable distances, increasing the effective dispersal ability and rate for the species, although how significant this effect may be remains unclear.

Geographic context

Cook Strait bisects central New Zealand and features intricate submarine canyons and ocean circulation patterns (Bowman *et al.* 1983; Proctor and Carter 1989; Lewis *et al.* 1994). Complex and temporally variable geography and currents in the Cook Strait region have led to many differing patterns of phylogeographic structure in a range of marine invertebrates with various life history strategies (Stevens and Hogg 2004; Waters and Roy 2004; Ayers and Waters 2005; Goldstien *et al.* 2006; Knox *et al.* 2011; Veale and Lavery 2011; Veale and Lavery 2012). Many species exhibit a phylogeographic break in the Cook Strait region (Waters and Roy 2004; Ayers and Waters 2005; Goldstien *et al.* 2006), often to the south of Cape Campbell, although the location and causes of these breaks are often unclear (Ross *et al.* 2009).

During some Pleistocene glacial maxima, a land-bridge connecting Whanganui and Golden Bay closed Cook Strait (Fleming 1979; Proctor and Carter 1989; Lewis *et al.* 1994). For many marine species, the formation of continuous land between the North and South Islands would have severed gene-flow between the western and eastern coasts of central New Zealand. However, for terrestrial or coastal species with little or no long-distance over-water dispersal ability, this closure would have facilitated gene-flow between the North and South Islands (Fleming 1979; Liggins *et al.* 2008; O'Neill *et al.* 2008).

Between the onset of the Last (Otiran) Glacial Maximum (LGM) roughly 25 ka BP (Sandiford *et al.* 2002), and its more gradual end about 7 ka BP (Lambeck *et al.* 2002), eustatic sea-levels dropped as much as 120–130 m lower than at present (Fleming *et al.* 1998; Lambeck *et al.* 2002). A lack of fossil or molecular evidence for the exchange of several terrestrial vertebrates

across a land-bridge during this time (Worthy and Holdaway 1994, 2002; Liggins *et al.* 2008; O'Neill *et al.* 2008) should not be interpreted as evidence for the lack of a land-bridge (Liggins *et al.* 2008; O'Neill *et al.* 2008). Such a land-bridge is likely to have been comprised mostly of low-lying coastal dunes and may have been short-lived or not conducive to the passage of larger terrestrial species (Greaves *et al.* 2008; O'Neill *et al.* 2008) such as moa. Several terrestrial species with presumed low dispersal ability do indeed show evidence of post-Pliocene genetic connectivity between the North and South Islands (O'Neill *et al.* 2008; Trewick *et al.* 2011), although their means of dispersal are unclear.

The shallowest possible connection between the North and South Islands, following Farewell Rise, has a maximum depth presently of 94 m (Lewis *et al.* 1994). However, little is known of the rates of uplift and subsidence in the vicinity of Farewell Rise, or rates of sedimentation from the Whanganui catchment or via west-wind drift from the north-western South Island (Lewis *et al.* 1994). Nevertheless there is no evidence that a land-bridge was not present as recently as 17–15 ka BP (Proctor and Carter 1989; Lewis *et al.* 1994).

The Chatham Islands lie roughly 700 km east of the New Zealand mainland and straddle the Subtropical Convergence, which directs relatively warm temperate water and cool sub-antarctic water eastwards along the Chatham Rise (Chiswell 1994). This confluence results in a productive local marine fauna (Bradford 1983), comprising species with both eastern North Island and eastern South Island affinities (Finlay 1928; Dell 1960; Craw 1988, 1989; Marshall and Walton 2015).

Despite the Chatham Islands having been isolated from the mainland for at least 70 Ma (Campbell *et al.* 1993; Emberson 1995; Trewick 2000) and by several hundred kilometres of ocean deeper than 200 m, the region has few endemic coastal marine invertebrates (Young 1929; Beu 2012). Dell (1960) recorded 49 locally endemic species of marine molluscs from depths shallower than 20 m, but subsequent work (e.g. Ponder 1965a, b, 1972; Marshall 1993,

1995, 1998a, b, 2003; Reisser *et al*. 2012; Marshall and Walton 2015; Walton and Marshall in prep.) suggests that no more than 10 named mollusc species or subspecies are truly unique to the Chatham Islands. The Chatham Islands were fully submerged upon splitting from the mainland, emerging as recently as the early Pliocene (Campbell 1998; Stevens and Hogg 2004), thus the terrestrial and coastal marine faunas comprise predominantly recent arrivals dispersed from the mainland (Trewick 2000).

Study background and aims

Fleming *et al*. (in review) reported DNA sequence data from the mitochondrial gene cytochrome c oxidase subunit 1 (CO1) from populations of *C. maculosa* and *C. virgata* from south of Cape Rodney in the North Island, and Nelson in the northern South Island (Figs. 2.1B, 2.2B). Fleming *et al*. (in review) found both species to have a considerable amount of phylogeographic structure while Nelson populations appeared distinct from those in Wellington. The present contribution includes populations of both species from the northern South Island, *C. virgata* from north of Cape Rodney, and *C. maculosa* from the Chatham Islands. Although only a few Chatham Islands samples of *C. maculosa* were available, these were included to check for cryptic diversity, mainland regional affiliation and to approximate the occupancy time of the Chatham Islands populations. The combined dataset now covers much of the distribution of these two species (Figs. 2.1C, 2.2C), enabling wider geographic comparison between populations, as well as comparison with studies of other species with an emphasis on the Cook Strait region. Phylogeographic patterns often differ widely between species, even for congeners with similar characteristics (Goldstien 2005; Goldstien *et al.* 2006; Knox *et al.* 2011). Increasing the breadth of species, sample sites and markers examined in the literature will improve understanding of the processes structuring populations (Ross *et al.* 2009; Gardner *et al.* 2010).

C. virgata has pronounced variation in shell morphology between populations in the northern North Island, but less variation further south (Fig. 2.7A–G). Powell (1952) distinguished populations from the east coast north of the Bay

of Islands as a subspecies, *C. virgata brookesi* Powell, 1952 (holotype: Fig. 2.7E), based on colour pattern (see below), either ignoring or unaware of diverse populations on the west coast of Northland (Fig. 2.7F, G). Shells of the various forms, including *C. virgata brookesi* and the nominal subspecies, appear to intergrade, leading to confusion regarding the name to apply to each population or if the continued maintenance of subspecies is justified.

Materials and methods

Sampling and specimen handling

Over 1,000 specimens of *C. virgata* were examined in 230 lots at the Museum of New Zealand Te Papa Tongarewa (NMNZ) (Fig. 2.2C). Samples were collected by searching the intertidal zone on the turn of the low tide. Where *C. maculosa* or *C. virgata* were difficult to find or seemingly absent, mussels were broken and scattered in pools in an attempt to attract them. Samples for molecular analyses were stored in 98% ethanol and vouchers deposited at NMNZ (Table 2.1). Photoshop CS6 (Adobe) was used for image clear-cutting and plate assembly.

DNA preparation, sequencing and alignment

Approximately 1 mm^3 of foot tissue was digested at 56°C for 2 hours in 600 µL of extraction solution comprising 10 mM Tris pH 8.0, 10 mM EDTA, 50 mM NaCl, 0.2% sodium dodecyl sulphate, and 1 µg/µl proteinase-K. The digested tissue was purified using phenol-chloroform extraction (Sambrook *et al.* 1989), precipitated with 2.5 volumes of 100% ethanol and 3 mM sodium acetate pH 5.2. The precipitates were then pelleted by centrifugation, washed with 70% ethanol, dried, and re-suspended in TE buffer (10 mM Tris pH 8.0, 1 mM EDTA). DNA yields were quantified using a NanoDrop 1000 spectrophotometer.

Portions of the mitochondrial genes CO1 and 16S rRNA (16S) and the nuclear gene 18S rRNA (18S) were amplified by PCR using the primers LCO1490 and HCO2198 (Folmer *et al*. 1994; CO1), 16Sar and 16Sbr (Simon *et al*. 1994; 16S), 18S-5 (Winnepenninckx *et al*. 1998; 18S) and 18S1100R (Williams *et al*. 2004; 18S). Each 10 µl PCR solution contained 67 mM Tri-HCl pH 8.8, 16 mM $(NH_4)_2SO_4$, 3 mM of $MgCl_2$, 0.6 mg/mL of BSA, 0.1 µM each forward and reverse primer, 0.4 mM dNTPs, 0.05 U/µL of taq polymerase (Biostor), and 50 ng/µL of DNA template. Thermal cycling conditions for CO1 and 16S were: 180 s at 95°C followed by 40 cycles of 95°C for 35 s, 50°C for 35 s and 72°C for 45 s. A final extension followed of 72°C for 10 minutes. The 18S thermal cycling conditions followed Donald *et al*. (2015).

The resultant PCR products were electrophoresed on an agarose gel, stained with ethidium bromide and visualised using UV light. Amplified PCR products were purified using ExoSAP-IT (Amersham Parmacia Biotech) and their DNA sequence determined using a 3730xl Genetic Analyser (Applied Biosystems) at Macrogen Inc. (Seoul, South Korea).

Previously published DNA sequences originating from Donald *et al.* (2015) were sourced from Genbank (Table 2.2). CO1 sequences were trimmed to 610 bp for population genetic analyses to match the Fleming *et al*. (in review) dataset. For phylogenies, the CO1, 16S and 18S sequences were trimmed to 528, 457 and 711 bp respectively to match available sequences on Genbank. All DNA sequences were aligned using the Geneious (version 8.0.5) (Biomatters Ltd.) alignment option (Kearse *et al*. 2012).

Phylogenetic trees

Maximum likelihood trees were generated using the PhyML (version 2.2.0) (Guindon and Gascuel 2003; Guindon *et al.* 2010) plug-in in Geneious with 500 bootstrap replications. Bayesian trees were generated using the MrBAYES (version 3.2.6) (Huelsenback and Ronquist 2001) plug-in in Geneious with 1,100,000 MCMC replications, of which 100,000 were

discarded as burn-in. Phylogenetic trees were edited in FigTree (version 1.4.3) (Rambaut and Drummond 2012) and formatted using Photoshop.

Statistical analyses

Diversity indices (Table 2.1) were calculated using DnaSP (Version 5.10) (Librado and Rozas 2009) and included the number of segregating sites (S), nucleotide diversity (π), haplotype diversity (H_D) and the average number of nucleotide substitutions between sequences (k). Tajima's *D* (Tajima 1989) and Fu's F_S (Fu 1997) neutrality test statistics, Harpending's raggedness statistic (*rg*) (Harpending *et al*. 1993; Harpending 1994), sum of squared deviations (SSD), tau (τ), θ_0 and θ_1 (supplementary Tables 1, 2) were calculated in Arlequin (Version 3.5.2.2) (Excoffier and Lischer 2010) for each sample location.

Median joining haplotype networks were made in PopART (version 1.7; http://popart.otago.ac.nz/) and coloured according to sample locations that were clustered *a priori* on the basis of region and unique haplotypes (Figs. 2.1A, B, 2.2A, B, 2.3). Rarefaction analyses (Fig. 2.4A, B) performed in Analytic Rarefaction (version 1.3; Holland, 2003) were used to approximate the proportion of the total (true) haplotype diversity that was detected with the present samples.

Pairwise genetic differences between sample locations, using the fixation index Φ_{ST}, were calculated by both haplotype frequencies and pairwise genetic differences (supplementary Tables 3–6) in Arlequin using 10,000 permutations, to assay the degree of gene-flow between locations. Populations were assigned *a priori* to regional groups (Tables 2.3, 2.4) for analyses of the molecular variance (AMOVA). AMOVAs were performed using Arlequin, using both haplotype frequencies and pairwise genetic differences, to estimate the variance components and Φ_{ST} values within and between regions (Tables 2.3, 2.4). The high proportion of private haplotypes in both the *C. maculosa* and *C. virgata* datasets may have led to many *a priori* combinations yielding

statistically significant results. Significance was determined using 10,000 permutations.

Abbreviations used in the text

AM – Auckland War Memorial Museum, Auckland, New Zealand; BP – before present; GNS – Institute of Geological and Nuclear Sciences, Lower Hutt, New Zealand; MHNG – Muséum d'Histoire Naturelle de la Ville de Genève, Geneva, Switzerland; MNHN – Muséum National d'Histoire Naturelle, Paris, France; NHMUK – The Natural History Museum, London, England; NMNZ – Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand; TMAG – Tasmanian Museum and Art Gallery, Hobart, Australia; VUW – Victoria University of Wellington, New Zealand. Unless specified, material examined is at NMNZ (six-digit registration numbers prefixed 'M.').

Results

This study added 126 CO1 sequences of *C. maculosa* from eight new sample localities to the Fleming *et al*. (in review) dataset giving a total of 658 sequences from 30 localities (Table 2.1) for analyses. These featured 47 haplotypes, of which 33 were private to one locality, and 43 segregating sites (Table 2.1). For *C. virgata*, 156 CO1 sequences and nine new sample sites were added, giving a total of 497 sequences from 22 localities (Table 2.1). Present were 41 haplotypes, of which 31 were private to one locality, and 45 segregating sites (Table 2.1).

In *C. maculosa*, 23% of sequences from Nelson fall into a haplogroup predominantly comprising sequences from Hauraki Gulf and Bay of Plenty samples. All other sequences from populations in the South Island, from Cape Palliser to New Plymouth in the southern North Island, and the Chatham Islands, form a private ''southern'' haplogroup comprised of several haplotypes

one or two mutational steps divergent from a predominant central haplotype
(Fig. 2.1A). Samples from the Chatham Islands form a private sub-group to
this "southern" haplogroup. This sub-group comprises one haplotype (n=5) a
single mutational step divergent from the predominant central haplotype of the
"southern" haplogroup, and a second haplotype (n=1) an additional mutational
step divergent (Fig. 2.1A).

Both haplotypes present in the South Island in *C. virgata* are also present in
the North Island. One is represented in the South Island by one sequence from
Nelson and in the North Island by one sequence from the Hauraki Gulf and
many sequences from Wellington (Fig. 2.2A). The second haplotype present
in the South Island, represented by 89 of the 90 sequences, also occurs at a
high frequency in the Hauraki Gulf. This haplotype forms the centre of a
recently expanded ('star-shaped') haplogroup (Fig. 2.2A) that has greater
diversity in- and probably originated from- the north-eastern North Island (see
below).

Populations of *C. virgata* from the lower North Island form two distinct
haplogroups (Fig. 2.2A). One comprises two private haplotypes. The other
features a single haplotype, represented by many sequences from Wellington
and a single sequence from both the Hauraki Gulf and Nelson (Fig. 2.2A).

Comparatively few samples (n=5) were available from Maunganui Bluff
(Table 2.1). Samples of *C. virgata* from Maunganui Bluff and Ahipara form a
private haplogroup (Fig. 2.2A) that comprises a common shared haplotype and
another private to Ahipara. Five private haplotypes were present in samples
from Parengarenga Harbour, forming a private haplogroup (Fig. 2.2A). The
lack of shared haplotypes between many northern populations means that the
geographic scale of haplotype transitions cannot be discerned in the region.

Haplotype and nucleotide diversities, and the distributions of haplotypes
between populations that were sampled for this study, appear to be concordant
with those of populations from the Fleming *et al.* (in review) dataset. While
most haplogroups are private to a region or have regional affinities, most

regions have multiple haplogroups that often do not cluster together (Figs. 2.1A, 2.2A).

The 16S dataset was smaller and most DNA sequences were from north of Cape Rodney (Table 2.1). The 16S haplotype network map (Fig. 2.3A) suggests some north/south structure and there appears to be regional structure, although sample sizes were too low to draw conclusions (Fig. 2.3B). No sampled locality had more than two haplotypes or haplotypes more than one mutational step divergent (Fig. 2.3A).

18S is a more highly conserved gene and was uninformative for within species analyses

Table 2.1. Sample location data, summary statistics and haplotype lists. n= sample size; s=number of segregating sites; h_p=number of private haplotypes; h_n=number of haplotypes; h_d=haplotype diversity (standard deviation); π=nucleotide diversity (standard deviation); k=average number of nucleotide substitutions. Rows in bold denote samples originating from this study. The rest comprise the dataset of Fleming *et al.* (in review). Each haplotype is identified by a number, '6(20)', for example, would refer to 20 sequences of haplotype '6'. '*' denotes haplotypes private to that site; '#' denotes haplotypes private to one site.

Species (voucher)	Site code	Location	Co-ordinates	n	s	h_p	h_n	h_d (sd)	π (sd)	k	Haplotypes (n) '*' denotes private
C. maculosa	AMB	Mathesons Bay	36°18.00'S, 174°48.00'E	10	5	1	4	0.778 (0.091)	0.0030 (0.001)	1.800	3(3), 4(1)*, 5(2), 6(4)
C. maculosa	ASB	Snells Beach	36°25.00'S, 174°44.00'E	20	3	1	4	0.284 (0.128)	0.0006 (<0.001)	0.389	3(1), 5(1), 6(17), 11(1)*
C. maculosa	ARB	Red Beach	36°35.00'S, 174°42.00'E	23	4	2	4	0.320 (0.121)	0.0007 (<0.000)	0.427	5(2), 6(19), 9(1)*, 10(1)*
C. maculosa	AAB	Army Bay	36°35.00'S, 174°48.00'E	24	3	1	4	0.370 (0.117)	0.0006 (<0.000)	0.395	5(1), 6(19), 7(1), 8(3)*
C. maculosa	BBO	Bowentown	37°28.00'S, 175°59.00'E	11	6	0	4	0.491 (0.175)	0.0034 (0.001)	2.073	14(8), 20(1), 38(1), 39(1)
C. maculosa	BMM	Mount Maunganui	37°37.00'S, 176°10.00'E	10	5	3	5	0.756 (0.130)	0.0030 (0.001)	1.822	6(5), 14(1), 15(2)*, 16(1)*, 17(1)*
C. maculosa	BMA	Maketu	37°44.00'E, 176°27.00'E	26	5	2	6	0.717 (0.078)	0.0015 (<0.000)	0.914	5(6), 4(13), 18(4)*, 19(2), 20(2), 21(1)*
C. maculosa	BOM	Omaio	37°48.00'S, 177°37.00'E	31	8	4	7	0.774 (0.056)	0.0038 (<0.001)	2.288	6(5), 7(4), 14(13), 22(1)*, 23(5)*, 24(1)*, 25(2)*
C. maculosa	GTA	Te Araroa	37°37.00'S, 178°23.00'E	29	3	1	3	0.394 (0.094)	0.0018 (<0.001)	1.099	6(1), 19(6), 26(22)*
C. maculosa	GTT	Tatapouri	38°39.00'S, 178°08.00'E	29	4	0	2	0.069 (0.063)	0.0005 (<0.001)	0.276	5(1), 27(28)
C. maculosa	GMA	Mahia	39°05.00'S, 177°55.00'E	25	8	1	4	0.360 (0.117)	0.0023 (0.001)	1.427	6(1), 27(20), 28(2), 36(2)*

Table 2.1. Continued...

Species (voucher)	Site code	Location	Co-ordinates	n	s	h_p	h_n	h_d (sd)	π (sd)	k	Haplotypes (n) '*' denotes private
C. maculosa	HPA	Napier	39°28.00'S, 176°53.00'E	24	1	1	2	0.083 (0.075)	0.0001 (<0.001)	0.083	28(23), 37(1)*
C. maculosa (M.162486)	HPB	Pourerere Beach	40°07.00'S, 176°52.00'E	24	4	0	2	0.083 (0.075)	0.0006 (<0.001)	0.333	6(1), 28(23)
C. maculosa	HWB	Whangaehu Beach	40°24.00'S, 176°38.00'E	23	9	0	4	0.605 (0.079)	0.0063 (0.001)	3.850	27(13), 28(7), 38(1), 39(2)
C. maculosa	WCS	Castle Point	40°51.00'S, 176°14.00'E	28	9	3	5	0.717 (0.042)	0.0065 (0.001)	3.963	27(9), 28(11), 29(2)*, 30(6)*, 47k(1)*
C. maculosa	WCP	Cape Palliser	41°36.00'S, 175°17.00'E	27	1	1	2	0.142 (0.086)	0.0002 (<0.001)	0.142	1(25), 35(2)*
C. maculosa	WMA	Makara	41°13.00'S, 174°42.00'E	20	0	0	1	-	-	-	1(20)
C. maculosa	WPH	Point Howard	41°15.00'S, 174°54.00'E	21	0	0	1	-	-	-	1(21)
C. maculosa	WMP	Moa Point	41°20.00'S, 174°48.00'E	19	1	1	2	0.199 (0.112)	0.0003 (<0.001)	0.199	1(17), 2(2)*
C. maculosa	TMA	Marokopa	38°19.00'S, 174°42.00'E	31	0	1	1	-	-	-	13(31)*
C. maculosa	TNP	New Plymouth	39°03.00'S, 174°03.00'E	31	1	1	2	0.280 (0.090)	0.0005 (<0.001)	0.280	1(26), 12(5)*
***C. maculosa* (M.129798)**	**WCM**	**Te Hapu**	**40°36.92'S, 172°28.72'E**	**20**	**1**	**2**	**3**	**0.195 (0.115)**	**0.0003 (<0.001)**	**0.200**	**1(18), 45k(1)*, 46k(1)***
***C. maculosa* (M.302312)**	**PRM**	**Patons Rock**	**40°47.19′S, 172°45.94′E**	**20**	**0**	**0**	**1**	**-**	**-**	**-**	**1(20)**
***C. maculosa* (M.321239)**	**KTM**	**Kaiteriteri**	**41°02.10′S, 173°01.42′E**	**20**	**0**	**0**	**1**	**-**	**-**	**-**	**1(20)**
C. maculosa	NEL	Nelson	41°16.00'S, 173°15.00'E	26	8	4	6	0.609 (0.102)	0.0031 (0.001)	1.874	1(16), 5(1), 6(3), 31(2), 32(3), 33(1)

Table 2.1. Continued...

Species (voucher)	Site code	Location	Co-ordinates	n	s	h_p	h_n	h_d (sd)	π (sd)	k	Haplotypes (n) '*' denotes private
C. maculosa (M.316880)	PBM	**Picton**	**41°17.30′S, 174°00.47′E**	**20**	**1**	**1**	**2**	**0.100 (0.088)**	**0.0002 (<0.001)**	**0.100**	**1(19), 44k(1)***
C. maculosa (M.106630)	MBM	**Marfells Beach**	**41°43.33'S, 174°13.42'E**	**20**	**1**	**1**	**2**	**0.100 (0.088)**	**0.0002 (<0.001)**	**0.100**	**1(19), 43k(1)***
C. maculosa (M.108444)	KKM	**Kaikoura**	**42°24.76′S, 173°41.43′E**	**20**	**0**	**0**	**1**	**-**	**-**	**-**	**1(20)**
C. maculosa (M.114548)	CHM	**Purau Bay**	**43°38.22'S, 172°44.87'E**	**20**	**1**	**1**	**2**	**0.100 (0.088)**	**0.0002 (<0.001)**	**0.100**	**1(19), 40k(1)***
C. maculosa (M.315669)	CIW	**Waitangi**	**43°56.70'S, 176°33.80'W**	**4**	**1**	**1**	**2**	**0.500 (0.265)**	**0.0008 (<0.001)**	**0.500**	**41k(3), 42k(1)***
C. maculosa (M.315642)	CIO	**Owenga**	**44°01.70'S, 176°21.00'W**	**2**	**0**	**0**	**1**	**-**	**-**	**-**	**41k(2)**
C. maculosa	-	All sample locations	-	658	43	33[#]	47	0.801 (0.013)	0.0057 (<0.001)	3.469	1(260), 2(2)[#], 3(4), 4(1)[#], 5(11), 6(88), 7(5), 8(15)[#], 9(1)[#], 10(1)[#], 11(1)[#], 12(5)[#], 13(31)[#], 14(22), 15(2)[#], 16(1)[#], 17(1)[#], 18(4)[#], 19(8), 20(3), 21(1)[#], 22(1)[#], 23(5)[#], 24(1)[#], 25(2)[#], 26(22)[#], 27(69), 28(66), 29(2)[#], 30(6)[#], 31(2)[#], 32(3)[#], 33(1)[#], 34(1)[#], 35(2)[#], 36(2)[#], 37(1)[#], 38(3), 39(2), 40k(1)[#], 41k(5), 42k(2)[#], 43k(1)[#], 44k(1)[#], 45k(1)[#], 46k(1)[#], 47k(1)[#]
C. virgata (M.100905)	MAV	**Maunganui Bluff**	**35°46.08'S, 173°34.10'E**	**5**	**0**	**0**	**1**	**-**	**-**	**-**	**22(5)**
C. virgata (M.122735)	AHV	**Ahipara**	**35°10.50'S, 173°07.05'E**	**20**	**1**	**1**	**2**	**0.100 (0.088)**	**0.0002 (<0.001)**	**0.100**	**22(19), 23(1)***

Table 2.1. Continued...

Species (voucher)	Site code	Location	Co-ordinates	n	s	h_p	h_n	h_d (sd)	π (sd)	k	Haplotypes (n) '*' denotes private
C. virgata (M.166286)	**PAV**	**Paua**	**34°31.53'S, 172°57.00'E**	**20**	**5**	**5**	**5**	**0.600 (0.101)**	**0.0016 (<0.001)**	**0.974**	**24(12)*, 25(1)*, 26(1)*, 27(5)*, 28(1)***
C. virgata (M.100890)	**BBV**	**Bland Bay**	**35°21.03'S, 174°22.58'E**	**12**	**12**	**2**	**4**	**0.773 (0.069)**	**0.0094 (0.002)**	**5.742**	**4(4), 29(4)*, 30(3)*, 31(1)**
C. virgata (M.092949)	**NGV**	**Ngunguru**	**35°38.22'S, 174°31.83'E**	**20**	**16**	**5**	**8**	**0.747 (0.097)**	**0.0046 (0.002)**	**2.789**	**4(10), 31(1), 32(1), 33(2)*, 34(2)*, 35(1)*, 36(2)*, 37(1)***
C. virgata (M.105361)	**MGV**	**McGregors Bay**	**35°49.68'S, 174°30.97'E**	**17**	**17**	**4**	**5**	**0.772 (0.057)**	**0.0130 (0.001)**	**7.912**	**32(4), 38(6)*, 39(5)*, 40(1)*, 41(1)***
C. virgata	AMB	Mathesons Bay	36°18.00'S, 174°48.00'E	25	0	0	1	-	-	-	4(25)
C. virgata	ASB	Snells Beach	36°25.00'S, 174°44.00'E	24	4	4	5	0.312 (0.121)	0.0006 (<0.001)	0.333	4(20), 10(1)*, 11(1)*, 12(1)*, 13(1)*
C. virgata	ARB	Red Beach	36°35.00'S, 174°42.00'E	24	3	0	3	0.163 (0.099)	0.0005 (<0.001)	0.326	1(1), 4(22), 9(1)
C. virgata	AAB	Army Bay	36°35.00'S, 174°48.00'E	25	12	4	5	0.680 (0.067)	0.0083 (0.001)	5.067	4(12), 5(2)*, 6(8)*, 7(2)*, 8(1)*
C. virgata	BMM	Mount Maunganui	37°37.00'S, 176°10.00'E	29	5	0	2	0.192 (0.090)	0.0016 (0.001)	0.961	9(3), 14(26)
C. virgata	BMA	Maketu	37°44.00'E, 176°27.00'E	25	12	2	6	0.647 (0.073)	0.0049 (0.001)	2.993	4(1), 9(8), 14(13), 15(1)*, 16(1)*, 17(1)
C. virgata	BOM	Omaio	37°48.00'S, 177°37.00'E	41	3	1	3	0.096 (0.062)	0.0003 (<0.001)	0.193	14(1), 18(39)*, 19(1)
C. virgata	GTA	Te Araroa	37°37.00'S, 178°23.00'E	39	9	2	6	0.784 (0.032)	0.0067 (<0.001)	4.084	4(6), 14(13), 17(10), 19(7), 20(2)*, 21(1)*
C. virgata	GMA	Mahia	39°05.00'S, 177°55.00'E	11	0	0	1	-	-	-	19(11)

Table 2.1. Continued...

Species (voucher)	Site code	Location	Co-ordinates	n	s	h_p	h_n	h_d (sd)	π (sd)	k	Haplotypes (n) '*' denotes private
C. virgata	WPB	Pukerua Bay	41°01.00'S, 174°53.00'E	20	0	0	1	-	-	-	1(20)
C. virgata	WPH	Point Howard	41°15.00'S, 174°54.00'E	25	9	0	3	0.410 (0.111)	0.0053 (0.001)	3.260	1(19), 2(3), 3(3)
C. virgata	WMP	Moa Point	41°20.00'S, 174°48.00'E	25	10	0	3	0.290 (0.110)	0.0040 (0.002)	2.460	1(21), 2(1), 3(3)
***C. virgata* (M.114916)**	**PRV**	**Patons Rock**	**40°47.19′S, 172°45.94′E**	**20**	**0**	**0**	**1**	**-**	**-**	**-**	**4(20)**
***C. virgata* (321238)**	**KTV**	**Kaiteriteri**	**41°02.10′S, 173°01.42′E**	**20**	**0**	**0**	**1**	**-**	**-**	**-**	**4(20)**
C. virgata	NEL	Nelson	41°16.00'S, 173°15.00'E	30	2	0	2	0.067 (0.061)	0.0002 (<0.001)	0.133	1(1), 4(29)
***C. virgata* (M.316881)**	**PBV**	**Picton**	**41°17.30′S, 174°00.47′E**	**20**	**0**	**0**	**1**	**-**	**-**	**-**	**4(20)**
C. virgata	-	All sample locations	-	497	45	31[#]	41	0.817 (0.014)	0.0073 (<0.001)	4.476	1(62), 2(4), 3(6), 4(189), 5(2) [#], 6(8) [#], 7(2) [#], 8(1) [#], 9(12), 10(1) [#], 11(1) [#], 12(1) [#], 13(1) [#], 14(53), 15(1) [#], 16(1) [#], 17(11), 18(39) [#], 19(19), 20(2) [#], 21(1) [#], 22(24), 23(1) [#], 24(12) [#], 25(1) [#], 25(1) [#], 26(1) [#], 27(5) [#], 28(1) [#], 29(4) [#], 30(3) [#], 31(2), 32(5), 33(2) [#], 34(2) [#], 35(1) [#], 36(2) [#], 37(1) [#], 38(6) [#], 39(5) [#], 40(1) [#], 41(1) [#]

Table 2.2. Samples used in molecular analyses and GenBank accession numbers where available. Rows in bold denote samples originating from this study. The rest originated from Donald *et al*. (2015) via GenBank.

Species	ID	Registration	Location	Accession # (CO1)	Accession # (16S)	Accession # (18S)
Cominella acuminata Hutton, 1893	1	M.317682	Paratutae Island, Manukau Harbour	KP694160	-	-
C. acutinodosa (Reeve, 1846)	2	M.300749	Broome, Western Australia	KP694120	KP694068	KP694163
C. adspersa (Bruguière, 1789)	3	M.317714	Bucklands Beach, Hauraki Gulf	KP694149	KP694101	KP694196
C. adspersa (Bruguière, 1789)	4	M.300751	Karaka Bay, Hauraki Gulf	KP694161	KP694113	KP694205
C. adspersa (Bruguière, 1789)	5	M.300752	Mill Bay, Manukau Harbour	KP694144	KP694094	KP694190
C. adspersa (Bruguière, 1789)	**6**	**M.321242**	**Point Howard, Wellington**	**TBA**	**-**	**-**
C. adspersa (Bruguière, 1789)	**7**	**M.315639**	**Owenga, Chatham Islands**	**TBA**	**TBA**	**TBA**
C. alertae (Dell, 1956)	8	NIWA 30033	Chatham Rise	KP694141	KP694091	KP694187
C. alertae (Dell, 1956)	9	NIWA 30041	Chatham Rise	KP694142	KP694092	KP694188
C. alertae (Dell, 1956)	**10**	**M.284015**	**Off Chatham Islands**	**TBA**	**TBA**	**TBA**
C. glandiformis (Reeve, 1847)	11	M.317684	Farm Cove, Hauraki Gulf	KP694152	KP694104	KP694199
C. glandiformis (Reeve, 1847)	12	M.317685	Karaka Bay, Hauraki Gulf	KP694151	KP694103	KP694198
C. glandiformis (Reeve, 1847)	13	M.317686	Pukenui, Aupouri Peninsula	KP694154	KP694106	KP694201
C. glandiformis (Reeve, 1847)	14	M.317687	Otehei Bay, Bay of Islands	KP694155	KP694107	KP694202
C. glandiformis (Reeve, 1847)	15	M.317688	Ligar Bay, Golden Bay	KP694150	KP694102	KP694197
C. glandiformis (Reeve, 1847)	16	M.317689	Lower Portobello, Otago Harbour	KP694153	KP694105	KP694200
C. glandiformis (Reeve, 1847)	**17**	**M.321240**	**Kaiteriteri, Tasman Bay**	**TBA**	**-**	**-**
C. glandiformis (Reeve, 1847)	**18**	**M.321241**	**Pauatahanui Inlet, Wellington**	**TBA**	**-**	**-**
C. griseicalx Willan, 1978	19	M.134974	Great Island, Three Kings Islands	KP694129	KP694077	KP694173
C. lineolata (Lamarck, 1816)	20	M.309452	Bicheno, Tasmania	KP694130	KP694078	KP694174
C. lineolata (Lamarck, 1816)	21	M.300769	Pirates Bay, Tasmania	KP694133	KP694081	KP694177
C. lineolata (Lamarck, 1816)	22	M.317695	Stanley, Tasmania	KP694132	KP694080	KP694176
C. lineolata (Lamarck, 1816)	23	M.317696	Sulphur Creek, Tasmania	KP694131	KP694079	KP694175
C. maculosa (Martyn, 1784)	24	M.317699	Milford, Hauraki Gulf	KP694140	KP694090	KP694186
C. maculosa (Martyn, 1784)	25	M.317718	Kaikoura	KP694145	KP694096	KP694192
C. maculosa (Martyn, 1784)	26	M.317719	Kaikoura	KP694146	KP694097	KP694193
C. maculosa (Martyn, 1784)	**27**	**M.315669**	**Waitangi, Chatham Islands**	**TBA**	**TBA**	**TBA**
C. maculosa (Martyn, 1784)	**28**	**M.315642**	**Owenga, Chatham Islands**	**TBA**	**TBA**	**TBA**

Table 2.2. Continued…

Species	ID	Registration	Location	Accession # (CO1)	Accession # (16S)	Accession # (18S)
C. mirabilis canturiensis **(Dell, 1951)**	29	**M.284022**	**Chatham Rise**	**TBA**	**TBA**	**TBA**
C. mirabilis canturiensis **(Dell, 1951)**	30	**M.284022**	**Chatham Rise**	**TBA**	**TBA**	**TBA**
C. mirabilis canturiensis **(Dell, 1951)**	31	**M.284016**	**Off Chatham Islands**	**TBA**	**TBA**	**TBA**
C. nassoides **(Reeve, 1846)**	32	**M.319324**	**Veryan Bank, Chatham Rise**	**TBA**	**TBA**	**TBA**
C. nassoides **(Reeve, 1846)**	33	**M.305586**	**Off Auckland Islands**	**TBA**	**TBA**	**TBA**
C. nassoides **(Reeve, 1846)**	34	**M.305586**	**Off Auckland Islands**	**TBA**	**TBA**	**TBA**
C. nassoides **(Reeve, 1846)**	35	**M.315663**	**Owenga, Chatham Islands**	**TBA**	**TBA**	**TBA**
C. nassoides **(Reeve, 1846)**	36	**M.315900**	**Okawa Point, Chatham Islands**	**TBA**	**TBA**	**TBA**
C. nassoides **(Reeve, 1846)**	37	**M.302874**	**Off Kaikoura**	**TBA**	**TBA**	**TBA**
C. nassoides **(Reeve, 1846)**	38	**M.302877**	**Off Kaikoura**	**TBA**	**TBA**	**TBA**
C. nassoides **(Reeve, 1846)**	39	**M.305641**	**Off Stewart Island**	**TBA**	**TBA**	**TBA**
C. nassoides **(Reeve, 1846)**	40	**M.305583**	**Off Snares Islands**	**TBA**	**TBA**	**TBA**
C. nassoides **(Reeve, 1846)**	41	**M.305583**	**Off Snares Islands**	**TBA**	**TBA**	**TBA**
C. nassoides (Reeve, 1846)	42	M.300779	Off Snares Islands	KP694147	KP694098	KP694194
C. nassoides **(Reeve, 1846)**	43	**M.321152**	**Ulva Island, Stewart Island**	**TBA**	**TBA**	**TBA**
C. norfolkensis (Iredale, 1940)	44	M.317720	Cemetery Bay, Norfolk Island	KP694135	KP694085	KP694181
C. norfolkensis (Iredale, 1940)	45	M.317720	Cemetery Bay, Norfolk Island	KP694158	KP694111	KP694210
C. quoyana A. Adams, 1855	46	M.317702	Eastern Beach, Auckland	KP694121	KP694069	KP694164
C. regalis Willan, 1978	47	M.309472	Princes Island, Three Kings Islands	KP694128	KP694076	KP694172
C. tolagaensis Ponder, 1968	48	M.302859	Tolaga Bay	KP694126	KP694074	KP694169
C. virgata **H. Adams & A. Adams, 1853**	49	**M.100905**	**Maunganui Bluff**	**TBA**	**TBA**	**TBA**
C. virgata H. Adams & A. Adams, 1853	50	M.317704	Maunganui Bluff	KP694125	KP694073	KP694168
C. virgata H. Adams & A. Adams, 1853	51	M.317705	Tapeka Point, Bay of Islands	KP694123	KP694071	KP694166
C. virgata H. Adams & A. Adams, 1853	52	M.317703	Pukenui, Aupouri Peninsula	KP694124	KP694072	KP694167
C. virgata H. Adams & A. Adams, 1853	53	M.317707	Tata Beach, Golden Bay	KP694159	KP694116	KP694211
C. virgata H. Adams & A. Adams, 1853	54	M.317721	Pohara, Nelson	KP694127	KP694075	KP694171
C. virgata H. Adams & A. Adams, 1853	55	M.317708	Karaka Bay, Hauraki Gulf	KP694070	KP694165	KP694122
C. virgata **H. Adams & A. Adams, 1853**	56	**M.166286**	**Paua, Parengarenga Harbour**	**TBA**	**TBA**	**TBA**
C. virgata **H. Adams & A. Adams, 1853**	57	**M.166286**	**Paua, Parengarenga Harbour**	**TBA**	**TBA**	**TBA**
C. virgata **H. Adams & A. Adams, 1853**	58	**M.166286**	**Paua, Parengarenga Harbour**	**TBA**	**TBA**	**TBA**

Table 2.2. Continued…

Species	ID	Registration	Location	Accession # (CO1)	Accession # (16S)	Accession # (18S)
C. virgata **H. Adams & A. Adams, 1853**	**59**	**M.122735**	**Ahipara**	**TBA**	**TBA**	**TBA**
C. virgata **H. Adams & A. Adams, 1853**	**60**	**M.100890**	**Bland Bay**	**TBA**	**TBA**	**TBA**
C. virgata **H. Adams & A. Adams, 1853**	**61**	**M.100890**	**Bland Bay**	**TBA**	**TBA**	**TBA**
C. virgata **H. Adams & A. Adams, 1853**	**62**	**M.100890**	**Bland Bay**	**TBA**	**TBA**	**TBA**
C. virgata **H. Adams & A. Adams, 1853**	**63**	**M.105361**	**McGregors Bay, Whangarei**	**TBA**	**TBA**	**TBA**
C. virgata **H. Adams & A. Adams, 1853**	**64**	**M.105361**	**McGregors Bay, Whangarei**	**TBA**	**TBA**	**TBA**
C. virgata **H. Adams & A. Adams, 1853**	**65**	**M.105361**	**McGregors Bay, Whangarei**	**TBA**	**TBA**	**TBA**
C. virgata **H. Adams & A. Adams, 1853**	**66**	**M.105361**	**McGregors Bay, Whangarei**	**TBA**	**TBA**	**TBA**
C. virgata **H. Adams & A. Adams, 1853**	**67**	**M.092949**	**Whangaumu Bay, Ngunguru**	**TBA**	**TBA**	**TBA**
C. virgata **H. Adams & A. Adams, 1853**	**68**	**M.092949**	**Whangaumu Bay, Ngunguru**	**TBA**	**TBA**	**TBA**
Buccinulum pertinax (Martens, 1878)	69	M.300791	The Snares Islands	KP694134	KP694084	KP694180
B. vittatum (Quoy & Gaimard, 1833)	70	M.317713	Milford, Hauraki Gulf	KP694162	KP694109	KP694203
B. vittatum (Quoy & Gaimard, 1833)	71	M.317712	Warrington	KP694136	KP694086	KP694182
Pareuthria fuscata (Bruguière, 1789)	72	M.317715	Northwest Bay, Campbell Island	KP694138	KP694088	KP694184
P. fuscata (Bruguière, 1789)	73	M.317716	Beeman Point, Campbell Island	KP694139	KP694089	KP694185

Table 2.3. *Cominella maculosa* AMOVA *a priori* groups and results. df=degrees of freedom; 'var. comp.'=variance components; '%var.'=percentage variation; 'hapl. freq.'=measured by haplotype frequency; 'gen. diff.'= measured by pairwise genetic difference.

A priori groups		Among groups					Among populations within groups					Within populations				
		df	var. comp.	%var.	ϕ_{CT}	p-value	df	var. comp.	%var.	ϕ_{SC}	p-value	df	var. comp.	%var.	ϕ_{ST}	p-value
(Marokopa and Hauraki Gulf to Castle Pt)	hapl. freq.	1	0.2231	43.03	0.4303	<0.000	29	0.1508	29.09	0.5106	<0.000	627	0.1446	27.88	0.7212	<0.000
(New Plymouth, Wellington, South Is and Chatham Is)	gen. diff.	1	1.3851	56.34	0.5634	<0.000	29	0.6602	26.85	0.6150	<0.000	627	0.4133	16.81	0.8319	<0.000
(Marokopa) (Hauraki Gulf to Te Araroa) (Tatapouri to Castle Point)	hapl. freq.	5	0.2458	51.84	0.5184	<0.000	25	0.0839	17.68	0.3671	<0.000	627	0.1446	30.48	0.6952	<0.000
(New Plymouth, Wellington, South Is except Nelson) (Nelson) (Chatham Is)	gen. diff.	5	1.3244	62.16	0.6216	<0.000	25	0.3930	18.44	0.4874	<0.000	627	0.4133	19.40	0.8060	<0.000
(North Is) (South Is) (Chatham Is)	hapl. freq.	2	0.1312	27.10	0.2711	<0.000	28	0.2082	43.02	0.5902	<0.000	627	0.1446	29.87	0.7013	<0.000
	gen. diff.	2	0.7681	34.64	0.3464	<0.000	28	1.0361	46.73	0.7149	<0.000	627	0.4133	18.64	0.8137	<0.000

Table 2.4. *Cominella virgata* AMOVA *a priori* groups and results. df=degrees of freedom; 'var. comp.'=variance components; '%var.'=percentage variation; 'hapl. freq.'=measured by haplotype frequency; 'gen. diff.'= measured by pairwise genetic difference.

A priori groups		Among groups					Among populations within groups					Within populations				
		df	var. comp.	%var.	ϕ_{CT}	p-value	df	var. comp.	%var.	ϕ_{SC}	p-value	df	var. comp.	%var.	ϕ_{ST}	p-value
(Ahipara, Maunganui Bluff) (Parengarenga Harbour) (Bland Bay to Whangarei) (Hauraki Gulf and South Is) (Bay of Plenty to Mahia) (Wellington)	hapl. freq.	5	0.2207	46.89	0.4689	<0.000	16	0.0933	19.82	0.3731	<0.000	475	0.1567	33.29	0.6671	<0.000
	gen. diff.	5	1.3758	52.60	0.5260	<0.000	16	0.3950	15.10	0.3186	<0.000	475	0.8449	32.30	0.6770	<0.000
(Ahipara, Maunganui Bluff) (Parengarenga Harbour) (Bland Bay to Whangarei) (Hauraki Gulf) (Bay of Plenty to Mahia) (Wellington) (South Is)	hapl. freq.	6	0.1964	43.59	0.4359	<0.000	15	0.0975	21.63	0.3834	<0.000	475	0.1567	34.78	0.6522	<0.000
	gen. diff.	6	1.2414	49.80	0.4980	<0.000	15	0.4062	16.30	0.3247	<0.000	475	0.8449	33.90	0.6610	<0.000
(north of Wellington) (Wellington and South Is)	hapl. freq.	1	0.0376	8.52	0.0852	0.050	20	0.2476	56.03	0.6124	<0.000	475	0.1567	35.46	0.6454	<0.000
	gen. diff.	1	0.1694	7.05	0.0706	0.082	20	1.3871	57.76	0.6215	<0.000	475	0.8449	35.18	0.6482	<0.000
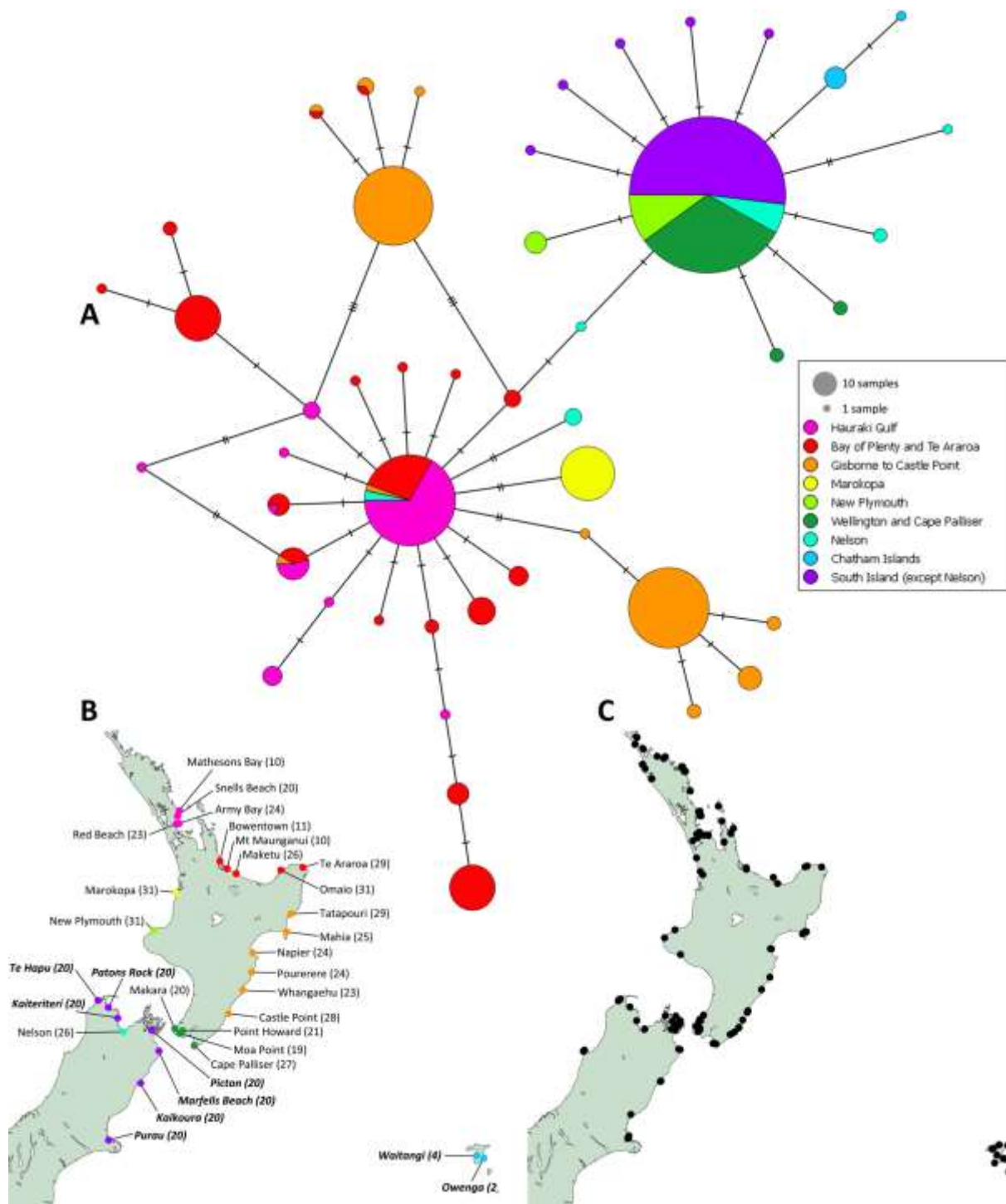
Figure 2.1. A) CO1 median joining haplotype network for *Cominella maculosa*. Hatch-marks represent one mutational step. **B)** Sample sizes (numbers) and sites (coloured circles). Colours correspond to the haplotype network regions (see key). Bold and italicized location names correspond to sites originating from this study. Others comprise the dataset of Fleming *et al*. (in review). **C)** Distribution records of *C. maculosa* held at NMNZ.
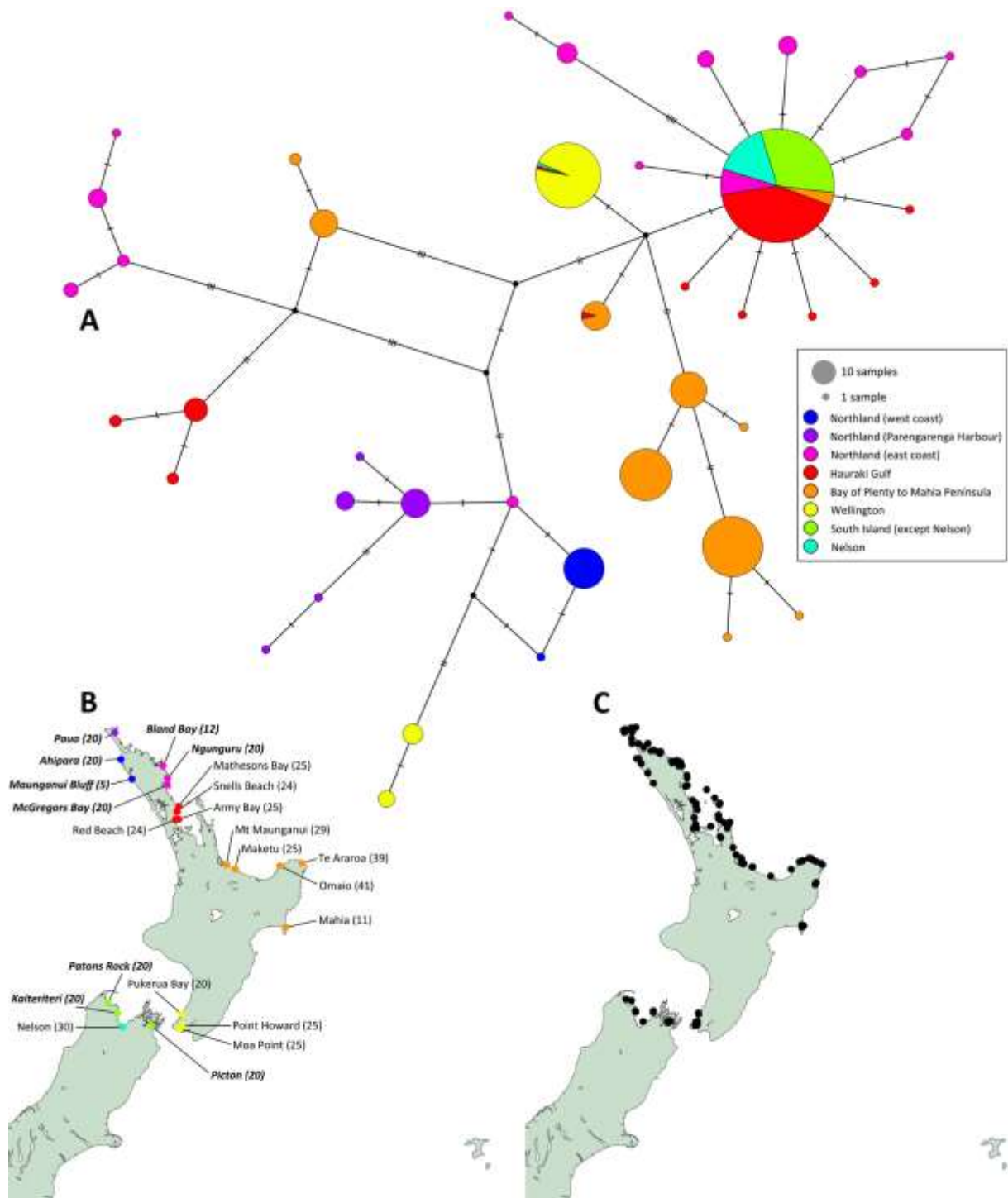
Figure 2.2. A) CO1 median joining haplotype network for *Cominella virgata*. Hatch-marks represent one mutational step. **B)** Sample sizes (numbers) and sites (coloured circles). Colours correspond to the haplotype network regions (see key). Bold and italicized location names correspond to sites originating from this study. Others comprise the dataset of Fleming *et al*. (in review). **C)** Distribution records of *C. virgata* held at NMNZ. Note the disjunct population centres.
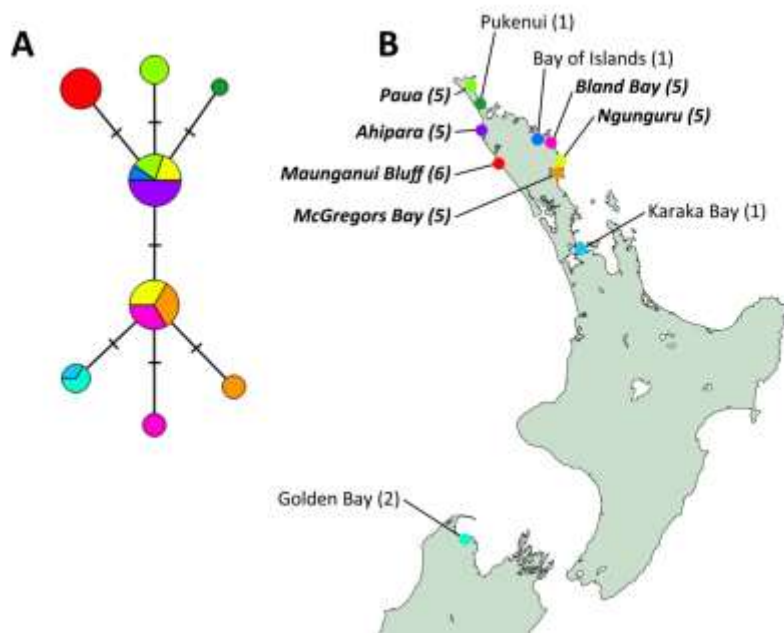
Figure 2.3. A) 16S median joining haplotype network for *Cominella virgata*. Hatch-marks represent one mutational step. **B)** Sample sizes (numbers) and sites (coloured circles). Colours correspond to the haplotype network regions (see key). Bold and italicized location names correspond to sites originating from this study. Others originated from Donald *et al.* (2015) via GenBank
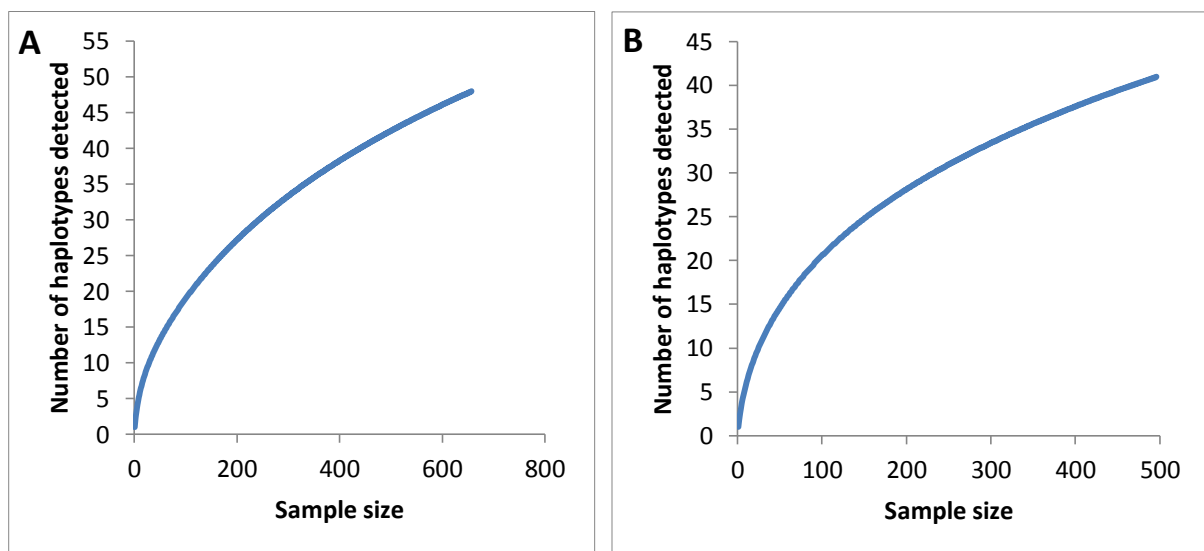
Figure 2.4. Rarefaction curves for CO1 haplotypes of **A)** *Cominella maculosa.* **B)** *C. virgata.*
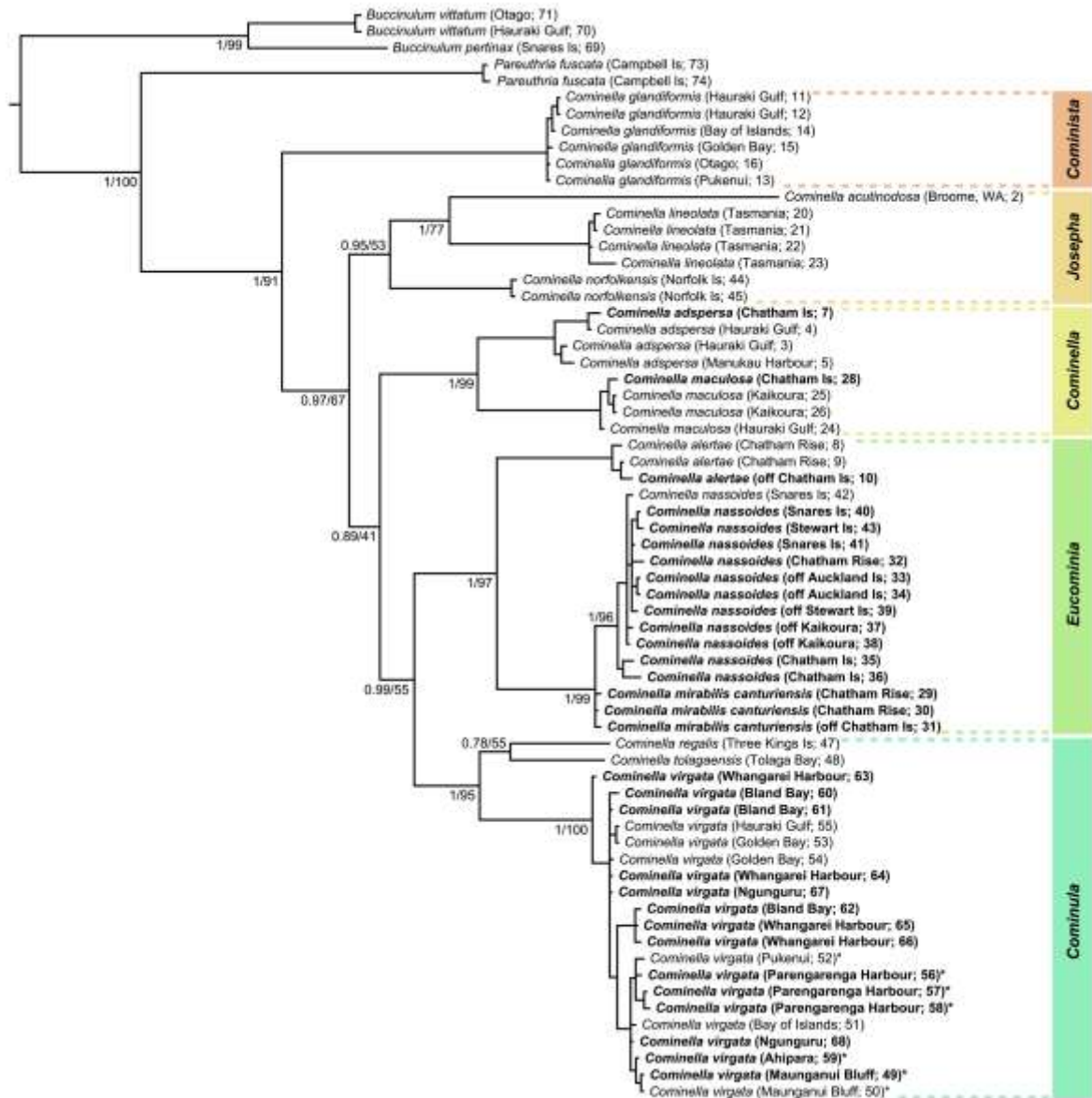
Figure 2.5. Bayesian phylogenetic tree of concatenated CO1 (528 bp), 16S (457 bp) and 18S (711 bp) gene sequences totalling 1,696 bp. Node labels correspond to Bayesian posterior probabilities (left) and maximum likelihood (ML) consensus bootstrap support percentage (right), the latter from a ML tree with very similar topologies (see appendix). Bold and italicized sequence labels correspond to sequences originating from this study. Others originated from Donald *et al*. (2015) via GenBank (Table 2.2). '*' denotes specimens of *C. virgata* of the '*brookesi*' shell form.
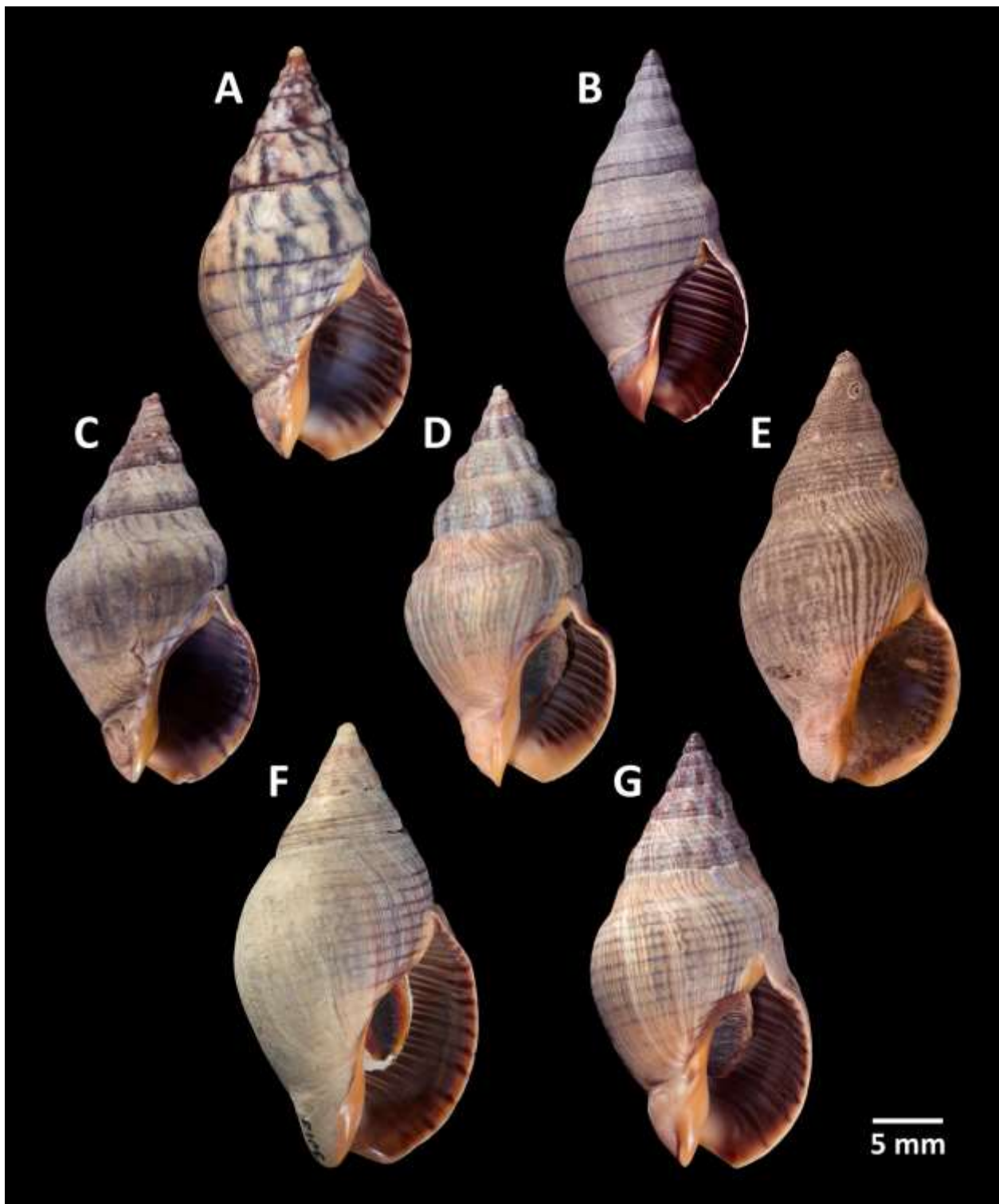
Figure 2.6. Type specimens and variations of *C. virgata* to scale. **A)** Pink Beach, Leigh, M.090919. **B)** Waihau Bay, Raukumara Peninsula, M.321237. **C)** Bay of Islands, lectotype (here designated) of both *Buccinum lineolatum* Quoy & Gaimard, 1833 and *C. virgata* H. Adams & A. Adams, 1853, MNHN-IM-2000-6968. **D)** Te Hapua, Parengarenga Harbour, M.278721. **E)** Whatuwhiwhi, Karikari Peninsula, holotype of *C. virgata brookesi* Powell, 1952, AM 71191. **F)** The Bluff, Ninety Mile Beach, M.278743. **G)** Reef Point, Ahipara, M.278752.

Discussion

Distribution of Cominella virgata

The distribution of *C. virgata* features two separate population centres, one situated in the Cook Strait region, and the other in the northern and north-eastern North Island (Fig. 2.2C). Beu (2012) noted similar distribution patterns for other mollusc taxa, including *Murexul octogonus* (Quoy & Gaimard, 1833) and *Roseaplagis rufozona* (A. Adams, 1853) (Marshall 1998), but what Beu (2012: 4) considered a "minor" pattern proves to be quite common throughout the Gastropoda and Bivalvia (B.A.M. pers. obs.). The causes of these north-eastern/south-western disjunctions remain to be established. While the ages of the disjunctions are also unclear, most or all are likely to predate the LGM as some of these taxa (including *M. octogonus* and *R. rufozona*) have fossil records in the Whanganui coastal sequence (Fleming 1953).

The present distribution gap between the two population centres for *C. virgata* on the west coast falls between Maunganui Bluff and Paekākāriki. This region includes seemingly favourable habitats interspersed between large tracts of unfavourable sandy beach habitat. On the east coast the distribution gap falls between Mahia Peninsula and Pencarrow Head. There is a long stretch of unfavourable sandy beach habitat to the west of Mahia in Hawkes Bay, followed by a long stretch of seemingly favourable habitats to the south between Napier and Pencarrow Head. The eastern and western gaps both seem unlikely to be sampling artefacts because extensive searches in seemingly suitable habitat yielded no *C. virgata* between Napier and Palliser Bay or near Hawera, New Plymouth, Raglan and Port Waikato (all localities where *C. maculosa* occurs). The species was notably omitted from published records of the west coast fauna of the central North Island (Morley *et al.* 1997; Hayward *et al.* 1999; Hayward *et al.* 2002), except for a 'dubious' record from off Ngā Motu in New Plymouth (Hayward and Morley 2002: 3).

Low CO1 diversity and a lack of private haplotypes in South Island populations of *C. virgata* suggest recent population size and/or range expansion. One of the two haplotypes present falls into a haplogroup primarily affiliated with Wellington, and is represented by a single sequence from Nelson (Fig. 2.2A), of indeterminate origin, but probably stemming from a translocated lineage. The most common South Island haplotype, comprising 89 of the 90 sequences, is shared with populations from the north-eastern North Island, but has not been sampled in geographically intermediate populations on the north-western North Island, at Mahia or around Wellington (Table 2.1; Fig. 2.2A). This haplotype forms the centre-point of a recently diversified ('star-shaped') haplogroup that features several haplotypes which are one mutational step divergent from the centre-point. All of these haplotypes are from the north-eastern North Island, suggesting that this haplogroup has had a longer presence in- and probably originated from- the north-eastern North Island. The South Island populations of *C. virgata* are therefore likely to have originated through unintentional human-mediated translocations, probably from both the north-eastern North Island as well as Wellington, accounting for both haplotypes present. Similarly, it is likely that populations of the fasciolariid *Taron dubius* (Hutton, 1878) in the northern South Island were also introduced from the north-eastern North Island, where it normally occurs.

By the mid 1960's, populations of *C. virgata* were established in the Marlborough Sounds (M.278694), Tasman Bay (M.023105) and Golden Bay (M.278701), encompassing much of their current range in the South Island. A lack of earlier records may reflect sampling effort. The timing of the proposed translocation events and the subsequent rate of range expansion in the South Island are unknown. The reason for failure to spread further south, where there is seemingly suitable habitat, remains to be established, but it may simply be a matter of time.

It is unclear from the presently available data if Wellington populations of *C. virgata* are naturally occurring or if these also originated from human-mediated translocations from the north-eastern North Island. The earliest records date from 1953 (M.005888), neither supporting nor contradicting either contention. However, had the Wellington populations originated through translocation events, several rare haplotypes otherwise undetected by the present sampling must have been translocated and become fixed due to genetic drift and/or founder effects. Three haplotypes are present in Wellington. Two of these form a private haplogroup. The third clusters on its own and occurs at the highest frequency of the three. In addition to sequences from Wellington, this third haplotype is represented by one sequence from the Hauraki Gulf and another from Nelson (Fig. 2.2A). Both of these sequences are potentially from translocated lineages as all three locations constitute major ports, in which case all three Wellington haplotypes might then be considered private. The presence of multiple private haplotypes supports the suggestion that Wellington populations are naturally-occurring.

Cook Strait populations of Cominella maculosa

C. maculosa and *C. virgata* have very different patterns of genetic structure in the Cook Strait region. *C. maculosa* has nine private South Island haplotypes and shares a high-frequency haplotype with populations from the southern North Island (Fig. 2.1A). A second haplotype is shared between the North and South islands. In the South Island, this haplotype only occurs in Nelson, and together with a haplotype that is private to Nelson (both represented by three out of the 26 sequences), it falls into a haplogroup otherwise unique to the northern North Island (Fig. 2.1A). All other haplotypes present in populations from and to the south of New Plymouth on the west coast and Cape Palliser on the east coast form a single 'southern' haplogroup.

'Southern' populations have far less diversity than populations from further north (Fig. 2.1A), potentially resulting from smaller population sizes, shorter regional occupancy times or a combination of the two. Lower diversity in southern regions may reflect southward range expansion by isotherm tracking

following the LGM (Fraser *et al.* 2012), which would be characterised by both population size expansion and founder events (Fraser *et al.* 2012; Waters *et al.* 2013) leading to low diversity. When a population became established at a site, the success of additional dispersers from other regions could have been limited by high-density blocking effects (Waters 2011; Waters *et al.* 2013). Combined with the poor dispersal ability of *C. maculosa*, blocking effects could maintain low levels of genetic diversity in southern populations. Isotherm tracking has been reported for several New Zealand molluscs, including *C. nassoides* (Reeve, 1846) (Walton and Marshall in prep.), the scallop *Zygochlamys delicatula* (Hutton, 1873) (Beu 1969; Beu and Maxwell 1990; Beu 1999), and the trochoid gastropod *Maurea blacki* (Powell, 1950) (Marshall 1995).

Phylogeographic breaks have been identified in the Cook Strait region for a range of taxa, although break locations are poorly constrained and may vary considerably between species (Ross *et al.* 2009; Gardner *et al.* 2010). Few species have a North Island/South Island break like *C. virgata*. More commonly, the 'northern group' includes populations from the northern South Island (Apte and Gardner 2002; Apte *et al.* 2003; Star *et al.* 2003; Waters and Roy 2004; Ayers and Waters 2005; Goldstien *et al.* 2006; Veale and Lavery 2011; Wei *et al.* 2013a, b). Some breaks have been recorded or implied near or to the south of Te Hapu (Waters and Roy 2004; Ayers and Waters 2005; Wei *et al.* 2013a, b), which is the southernmost site sampled for *C. maculosa* (Table 2.1). However, there are no apparent geographic features to the south of Te Hapu that are likely to cause a phylogeographic disjunction in *C. maculosa* and it seems unlikely that such a break exists if the low genetic diversity in southern populations is due to recent southern population size and range expansion.

Refugia during glacial maxima were probably located well to the north of Wellington as water temperatures are likely to have been too low for *C. maculosa* or *C. virgata*. Different refugia populations could have founded the various southern lineages in Wellington and the South Island of *C. virgata*. In *C. maculosa*, the phylogeographic break between Marokopa and New

Plymouth (Fleming *et al.* in prep.; Fig. 2.1A) and relative homogeneity of populations to the south, suggests a possible refugium in the vicinity of New Plymouth. The causes of a phylogeographic break in *C. maculosa* between Castle Point and Cape Palliser (Fleming *et al.* in prep.; Fig. 2.1A) are unclear but it seems unlikely that they reflect prevailing conditions in Cook Strait. This break may be due to the confluence of two lineages spreading southwards along the west and east coasts during the period of warming following the LGM. The patterns of a phylogenetic break that can be detected using mtDNA can take considerable time to disestablish through admixture, so the historic causes of a break might not reflect contemporary geography or ocean conditions.

As eustatic sea-levels rose subsequent to the LGM, the coastline along the south-western North Island would have advanced tens of kilometres inland from the near the edge of the continental shelf to its present location. The rate of introgression is unclear. Without continuous suitable habitat during this transition and on a relatively fine geographic scale, many populations of rocky-shore species with poor dispersal ability may have become isolated or extirpated during this period.

As with *C. maculosa* and *C. virgata*, amphipod species of the genus *Paracorophium* Stebbing, 1899 (Stevens and Hogg 2004; Knox *et al.* 2011), and some limpets of the genus *Cellana* H. Adams, 1869 (Goldstien 2005; Goldstien *et al.* 2006), congeners with similar life history strategies can exhibit differing patterns of genetic structure. Phylogeographic breaks in the Cook Strait region are likely to have several and differing causes. These may include aspects of the complex and dynamic local geography and ocean circulation patterns, and differences in larval duration and behaviour in the water column. The Cook Strait region extends far to the west of the Narrows, which are often incorrectly treated as the entirety of Cook Strait (Lewis *et al.* 1994). To loosely term 'the Cook Strait break' is, thus, misleading (Goldstien *et al.* 2006; Ross *et al.* 2009). Without multiple studies of different taxa and markers, deducing historical causes from patterns in genetic structure remains conjecture at best.

Throughout its distribution, the shell of *C. virgata* has a sculpture of commarginal axial costae, strongest at the edge of the subsutural concavity, and becoming evanescent near the abapical third of the base and often obsolete on later teleoconch whorls. Unusually, *C. virgata* inhabits mudflats in Parengarenga and Houhora Harbours. Specimens from these localities have larger and more persistent axial costae and a broader shoulder slope (Fig. 2.7D) than specimens from adjacent open coasts and the rest of New Zealand, perhaps local adaptations to reduce sinking in mud (Thayer 1975).

Specimens from and north of Maunganui Bluff on the west coast, and north of the Bay of Islands on the east coast (Fig. 2.7D–G), generally have more numerous (>8) and crowded spiral chords, as well as a colour pattern of crowded, narrow, flexuous, axial flammules, rather than the broad and highly irregular lines or blotches characteristic of southern populations (Fig. 2.7A–C). Powell (1952) distinguished *C. virgata brookesi* Powell, 1952 (type locality: Whatuwhiwhi, Karikari Peninsula) on this basis, listing Te Hapua, Whangaroa Harbour and Aurere as other localities, either ignoring or unaware of yet more divergent forms on the west coast of Northland (Fig. 2.7F, G).

Apart from the presence of narrow axial colour bands, the holotype of *C. virgata brookesi* (Fig. 2.7E) is indistinguishable from *C. virgata virgata* (type locality: the Bay of Islands), from and south of the Bay of Islands. Morley *et al.* (2006: 17) identified *C. virgata* from Mahia Peninsula as being "f. [*forma*] *brookesi*" although all specimens from Mahia Peninsula at NMNZ are the nominal form.

The phylogenies reported by Donald *et al.* (2015) showed two clades within *C. virgata*. Donald *et al.* (2015) interpreted the northern clade, comprised of specimens from Pukenui (c.25 km from Whatuwhiwhi), Maunganui Bluff, the Bay of Islands and Taupiri Bay, as conforming to the subspecies *C. virgata brookesi.* The southern clade was comprised of specimens from Waitemata Harbour and Golden Bay and was treated as *C. virgata virgata* (Donald *et al.*

2015). The shell voucher specimens from the Bay of Islands (M.317705) and Taupiri Bay (M.317706), although damaged during soft-tissue extraction, are typical *C. virgata virgata*. That from the Bay of Islands is arguably a topotype, although "the Bay of Islands" is a broad locality descriptor.

The expanded phylogeny (Fig. 2.6) did recover the same two clades within *C. virgata* reported by Donald *et al.* (2015) however these were obscured by numerous additional clades. None appear to warrant any formal taxonomic distinction. Neither the Northland forms nor typical *C. virgata* formed monophyletic clades (Fig. 2.7).

Considering the CO1 data (Fig. 2.2), DNA sequences from populations on the western and northern coasts of Northland clustered together and had numerous private haplotypes, but did not fall into significantly distinct haplogroups relative to other haplotypes and regions. In addition, the various shell forms of *C. virgata* from throughout its distribution, including the holotype of *C. virgata brookesi* and lectotype of *C. virgata virgata* (see below), fluidly intergrade, thus, continued recognition of separate subspecies is unjustified. As interpreted here, the *brookesi* form describes specimens with more than eight spiral threads and crowded narrow axial flammules. It is known only from north of the Bay of Islands but typical shell forms and intermediates occur sympatrically throughout much of this distribution although in low relative abundance.

Taxonomic remarks on Cominella virgata.

***Cominella* (*Cominula*) *virgata* H. Adams & A. Adams, 1853**
Fig. 2.7A–H.
Buccinum lineolatum Quoy & Gaimard, 1833: 419; pl. 30, figs. 14–16. Not *B. lineolatum* Lamarck, 1816 (homonym).
Cominella virgata H. Adams & A. Adams, 1853: 110; pl. 11, fig. 6 (not 6a, b). Undeclared replacement name for *B. lineolatum* Quoy & Gaimard, 1833.
Cominella virgata brookesi Powell, 1952: 181, p. 35, fig. 7. **New synonymy**.

Type material:

Buccinum lineolatum (Quoy & Gaimard; not Lamarck) and *Cominella virgata*:
lectotype (here selected) MNHN IM-2000-6968 and paralectotypes (3,
MNHN), Bay of Islands, New Zealand.

Cominella virgata brookesi: holotype AM 71191, Whatuwhiwhi, Rangiawhia
(Karikari) Peninsula, Mangonui County, D. Forsyth.

Quoy and Gaimard (1833) introduced *Buccinum lineolatum* for specimens
from the Bay of Islands, their illustrations and description matching the New
Zealand species *C. virgata*. All four syntypes (MNHN) are typical *C. virgata*,
one of which (Fig. 2.7C) is here designated the lectotype to ensure proper and
consistent future usage. Quoy and Gaimard's name is invalid due to
homonymy with the prior *B. lineolatum* of Lamarck (1816), a common
Cominella species from southern Australia (Wilson 1994; probable syntypes at
MHNG, Chapter 1).

H. Adams and A. Adams (1853) introduced *C. virgata* in conjunction with a
list of *Cominella* species "*virgata*, H. and A. Adams (*lineolata*, Quoy and
Gaim.)", referring to an illustration that is clearly a reproduction of one of
Quoy and Gaimard's (1833, pl. 30, fig. 15) original colour illustrations of the
New Zealand species. Although not specifically stated, *C. virgata* was
evidently intended as a replacement name for Quoy and Gaimard's (1833) and
so shares the same type material. No specimens were included in the H. and A.
Adams collection now at NHMUK (A. Salvador pers. comm. 2017).

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Author contributions

KW organised and participated in the collection of specimens, completed all lab-work, analyses, and wrote the manuscript. BAM assisted with specimen curation and taxonomic convention as well as providing comments on the interpretation and manuscript. NEP and PAR provided the Fleming *et al*. (in review) dataset and commented on the manuscript and project design. AJFV assisted with computer programs and statistics.

Chapter 3: General conclusion and closing remarks

Research questions overview

Whilst South Island populations of *Cominella maculosa* are undoubtedly naturally occurring, it seems highly likely that those of *C. virgata* were founded by human-mediated translocation events from the north-eastern North Island. It is unclear if populations of *C. virgata* from Wellington are naturally occurring. Haplotypes are present in Wellington that are rare or absent in other regions. However, *C. virgata* has a curious distribution disjunction and does not occur for hundreds of kilometres along either the western or eastern coasts of the North Island immediately to the north of Wellington.

In *C. maculosa* phylogeographic breaks are reported in the North Island between Marokopa and New Plymouth on the west coast and between Castle Point and Cape Palliser on the east coast. The causes of either of these breaks remain to be established. It seems unlikely that they reflect prevailing conditions in the Cook Strait or that they have much to do with the Cook Strait at all. The west coast break may be due to a refugium during the LGM at or to the north of New Plymouth. The east coast break may result from the confluence of two lineages range-expanding southwards down the western and eastern coasts of the North Island. Populations between these breaks to the south form a single 'southern' haplogroup with relatively low diversity.

The South Island populations of *C. maculosa* sampled in this study differ from the Nelson population sampled by Fleming *et al.* (in review) in having fewer haplotypes and less haplotype diversity. The only South Island samples to include haplotypes not of the 'southern' haplogroup for *C. maculosa* were from Nelson. In contrast, all South Island sites for *C. virgata* have the same fixed haplotype with the exception of one individual sampled from Nelson by Fleming *et al.* (in review) that had a haplotype that is most common in Wellington. This individual may be from a translocated lineage.

Chatham Islands samples of *C. maculosa* had two haplotypes that formed a separate sub-group to the 'southern' haplogroup. This result suggests that Chatham Islands populations are moderately isolated from those on the mainland but may have been founded from 'southern' populations relatively recently.

The purported northern subspecies *C. virgata brookesi* does not form a monophyletic lineage and is synonymised with *C. virgata.* Northland populations of *C. virgata* have very high CO1 diversity, paralleling their high morphological diversity, but forms are not so divergent as to warrant taxonomic recognition. Few haplotypes are shared between northern populations and additional sample sites would be needed to establish the geographic scale of haplotype transitions in this region. When high northern diversity is contrasted with the low diversity in southern populations of *C. maculosa* using the same methods and DNA marker, this illustrates the effect of occupancy time and/or population size on genetic diversity.

Future research

The results presented in this study have highlighted several potential directions for further research. Validity of the various proposed subspecies of *C. nassoides* (Reeve, 1846) is currently being reviewed by Walton and Marshall (in prep.) and the phylogeny presented here (Chapter 2) suggests relatively little genetic difference between individuals from widely separate localities. Low levels of regional structuring are also observed for *C. glandiformis* (Reeve, 1847) (Chapter 2, Fig. 2.5). Observations of its larval development under differing conditions would be valuable to help establish whether or not it has lecithotrophic larvae.

The patterns of phylogeographic structure detected in the present study are concordant with those of other littoral marine species studied that have direct

development (Kojima *et al.* 2004; Keeney *et al.* 2009; Keeney *et al.* 2013; Sánchez *et al.* 2013). Only a few species with direct development have been the subject of phylogeographic study in New Zealand (Keeney *et al.* 2009; Keeney *et al.* 2013; Dohner 2016; Fleming *et al.* in prep.) and *C. adspersa* (Bruguière, 1789) and species of *Haustrum* Perry, 1811 would be suitable candidates for building a more comprehensive picture of the general population genetic patterns. Littoral marine species are often predisposed to inadvertent human-mediated translocation. The genetic evidence for recent human-mediated translocation can be difficult to interpret and in some cases it could appear as just a complicated piece of the phylogeographic pattern.

The possible causes and ages of the 'north-eastern/south-western' pattern of distribution disjunctions presented in Chapter 2 for various mollusc taxa are worthy of future examination. The present molecular results do not provide much insight as to how this pattern may have arisen for *C. virgata*, but the causes may differ between species. Moreover, the susceptibility of *C. virgata* to translocation convolutes the interpretation of molecular results. Sub-littoral species such as *M. octogonus* (Quoy & Gaimard, 1833) and *R. rufozona* (A. Adams, 1853) are less likely to come into contact with potential rafting material or be translocated as bio-foul attached to hulls or within ballast. Accordingly, these species would be well suited to investigate these questions. In addition, both *M. octogonus* and *R. rufozona* occupy a range of habitat types and may accordingly be less susceptible to extirpation with changing coastlines during the transitions between glacial cycles.

The influence of changing water temperatures during glacial cycles on the formation and maintenance of these distribution patterns and disjunctions remains to be established. It is unclear if some or all species that have a similar disjunct distribution pattern once had continuous populations along the western and/or eastern coasts of the North Island. An interesting consideration is the presence of a marine strait bisecting the Auckland Isthmus in times of higher eustatic sea-levels during some glacial minima. A marine corridor between the west and east coasts would have allowed for the dispersal of some marine species and this corridor could have had a strong influence on

distribution patterns. Beu (2004: 119) implies the most recent occurrence of a strait through the Auckland Isthmus may have been during the previous interglacial in the Late Pleistocene, by suggesting that the strait was closed by an eruption in the Portage Volcano Complex c.25 ka BP (Sandiford *et al*. 2002; Beu 2004). This eruption would have coincided with the onset of the LGM (Sandiford *et al*. 2002) when eustatic sea-levels would have begun to lower considerably.

A Late Pleistocene strait in Auckland would have been located near Otahuhu, the narrowest point of the Auckland Isthmus at less than two kilometres wide, and/or along the "Clevedon Strait", c.14 km to the south. Both locations currently have as little as 30 m of elevation separating the western and eastern coasts. The vicinity of the Auckland Isthmus has been subject to considerable uplift post-Miocene (Claessens *et al*. 2009; Kenny *et al*. 2012) but seemingly little in the past 1 Ma (Alloway *et al*. 2004; Marra *et al*. 2006). The timing, location and rate of uplift and/or subsidence in the immediate vicinity of possible straits is unclear, therefore, it is likewise unclear during which glacial minima straits were present (B.W. Hayward pers. comm. 2016).

Straits through the Auckland Isthmus are likely to have been present during the Pliocene, when eustatic sea-levels were up to 30 m higher than present (Dwyer and Chandler 2009; Naish and Wilson 2009). There may have also been a strait present during the Early Pleistocene (B.W. Hayward pers. comm. 2016), however, there is little or no evidence for the presence of a strait within the past 1 Ma (B.W. Hayward pers. comm. 2016), when eustatic sea-levels during glacial minima were, at most, 10 m higher (Naish and Wilson 2009). The approximately three hours and 1.5 m tidal difference between the western and eastern coasts of Auckland would have led to very strong currents passing through any strait and scoured a large channel. Had there been a strait through the Auckland Isthmus within the past 1 Ma, it is expected that there would have been considerable amounts of erosion through the Kidnappers and Waitemata group basement formations; much more so than has been observed (B.W. Hayward pers. comm. 2016).

There is little or no evidence for Pleistocene gene-flow across the Auckland Isthmus from marine species. Conversely, there is some evidence of long-term isolation between populations on either side of the Auckland Isthmus in many species, such as the anemone *Actinia tenebrosa* Farquhar, 1898 (Veale and Lavery 2012) and cockle *Austrovenus stutchburyi* (Ross *et al*. 2012). While the relationships between populations of amphipods in genus *Paracorophium* (Stevens and Hogg 2004; Knox *et al*. 2011) could result from some historic dispersal through the Auckland Isthmus via a strait, it has been suggested that estuarine amphipods may also be translocated by wading birds (Schnabel *et al*. 2000).

Accurately dating or inferring directionality of gene-flow requires a large dataset. A future DNA-based approach comprising multiple species and higher resolution genome-wide markers could potentially help to establish the presence and constrain the timing of marine straits through the Auckland Isthmus during the Pliocene and Pleistocene.

Continued contributions improving our depth of knowledge about New Zealand's coastal marine fauna will hopefully make our understanding of reality a little less 'frequently inaccurate'.

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Appendix
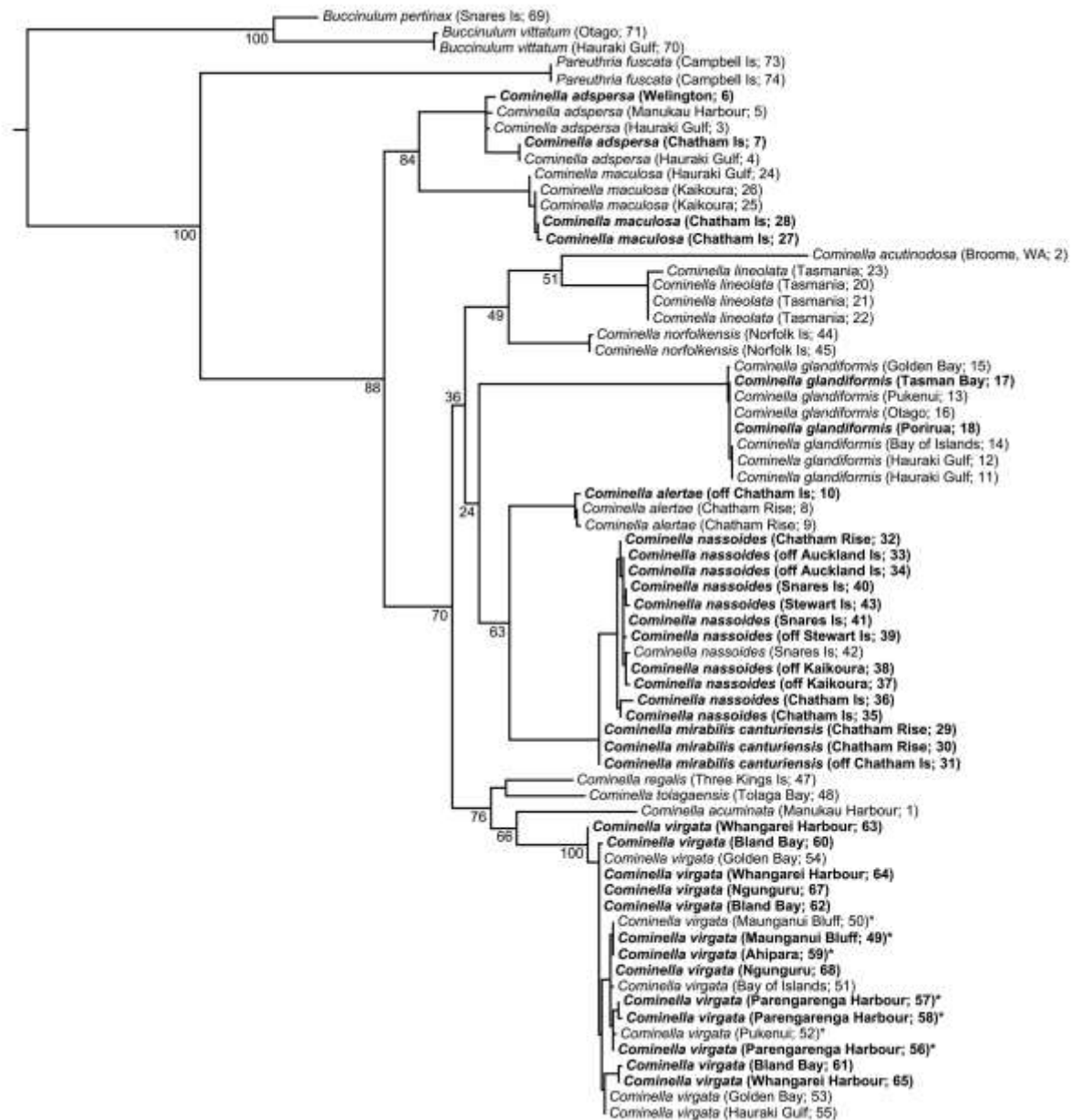
Supplementary Figure 1. Maximum likelihood phylogenetic tree of CO1 (528 bp) gene sequences. Node labels correspond to consensus bootstrap support percentage. Bold and italicized sequence labels correspond to sequences originating from this study. Others originated from Donald *et al*. (2015) via GenBank (Table 2.2). '*' denotes specimens of *Cominella virgata* of the '*brookesi*' shell form.
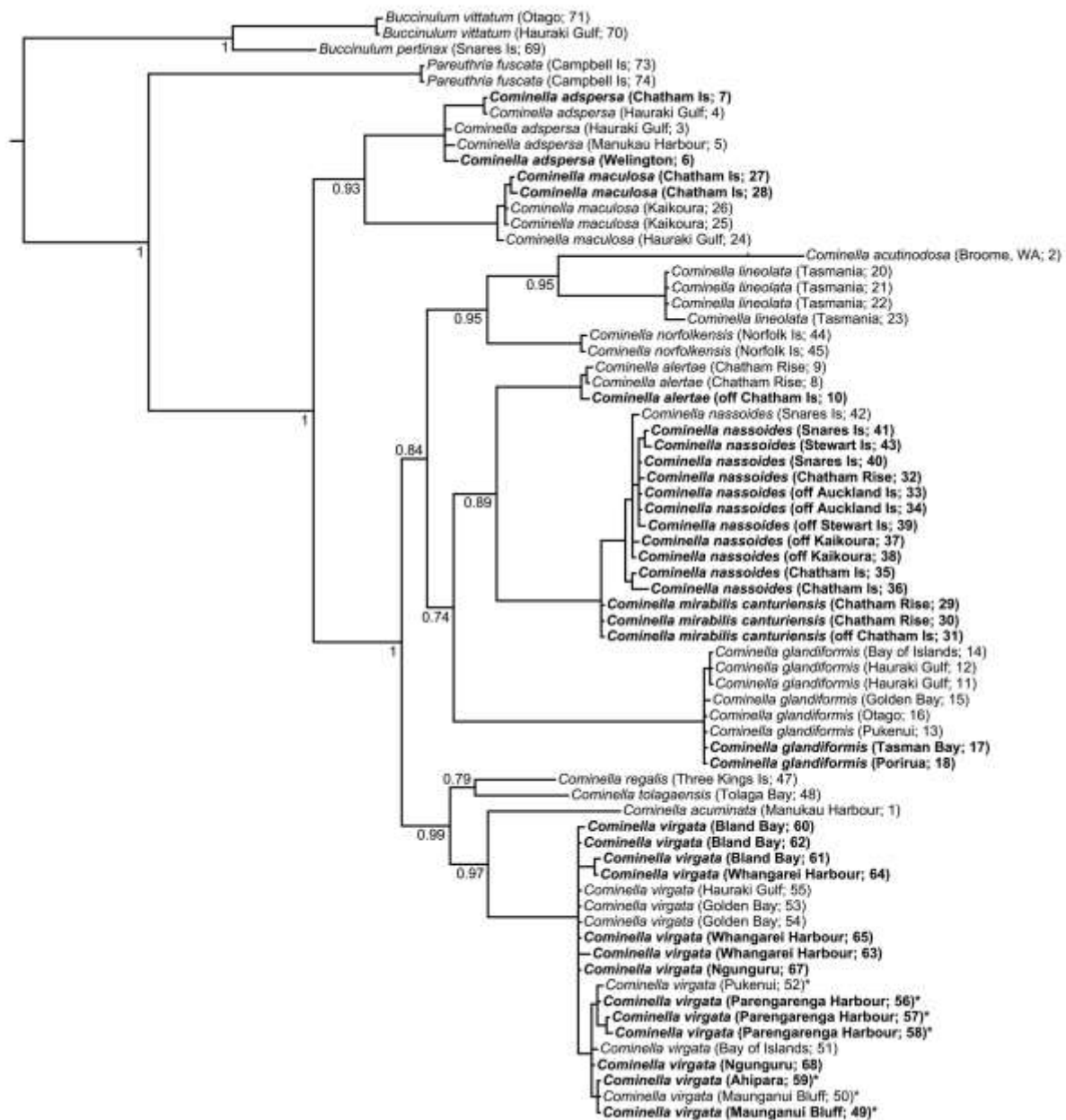
Supplementary Figure 2. Bayesian phylogenetic tree of CO1 (528 bp) gene sequences. Node labels correspond to posterior probability. Bold and italicized sequence labels correspond to sequences originating from this study. Others originated from Donald *et al*. (2015) via GenBank (Table 2.2). '*' denotes specimens of *Cominella virgata* of the '*brookesi*' shell form.
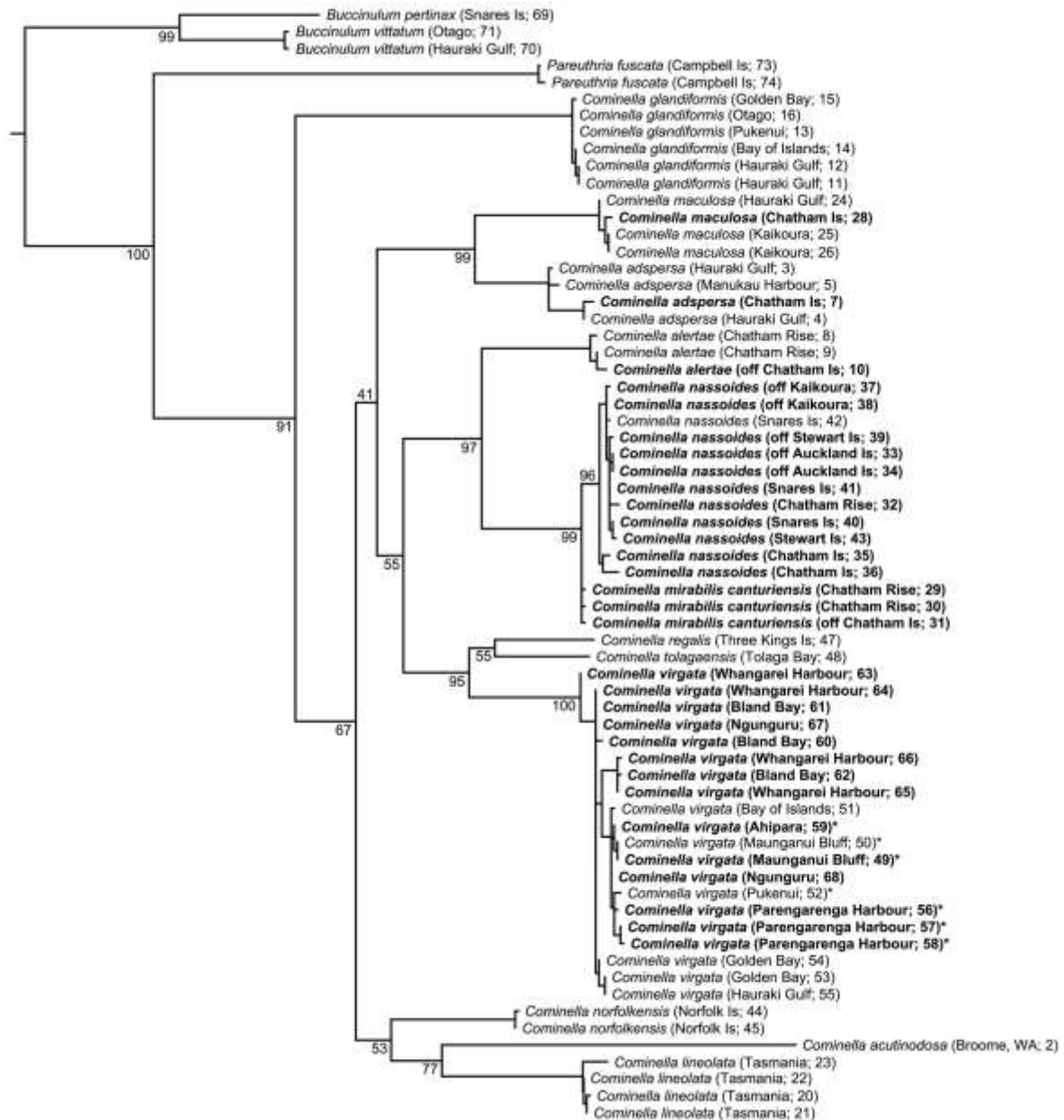
Supplementary Figure 3. Maximum likelihood tree of concatenated CO1 (528 bp), 16S (457 bp) and 18S (711 bp) gene sequences totalling 1,696 bp in length. Node labels correspond to consensus bootstrap support percentage. Bold and italicized sequence labels correspond to sequences originating from this study. Others originated from Donald *et al*. (2015) via GenBank (Table 2.2). '*' denotes specimens of *Cominella virgata* of the '*brookesi*' shell form.

Supplementary Table 1. *Cominella maculosa* additional statistics and neutrality tests.

Sampling Site	Tajima's D (p-value)	Fu's F-statistic (p-value)	SSD (p-value)	Rag (p-value)	Tau (95% CI)	Θ_0 (95% CI)	Θ_1 (95% CI)
BBO	-0.539(0.319)	0.851(0.693)	0.348(<0.000)	0.437(0.900)	0.00(0.00-0.582)	0.00(0.00-0.004)	99999(99869-99999)
WCP	-0.728(0.254)	-0.349(0.152)	<0.000(0.300)	0.532(0.650)	0.217(0.184-0.797)	0.00(0.00-0.037)	0.369(0.00-99999)
CHM	-1.164(0.155)	-0.879(0.064)	<0.000(0.350)	0.65(0.75)	3.00(0.559-22.016)	0.00(0.00-0.00)	0.118(0.00-99999)
CIO	-	-	-	-	-	-	-
CIW	-0.612(0.377)	0.172(0.353)	0.022(0.800)	0.250(0.900)	0.764(0.00-1.807)	0.00(0.000-0.004)	99999(349-99999)
KKM	-	-	-	-	-	-	-
KTM	-	-	-	-	-	-	-
MBM	-1.164(0.136)	-0.879(0.097)	<0.000(0.300)	0.65(0.75)	3.00(0.309-3.00)	0.00(0.00-0.030)	0.118(0.00-0.521)
PBM	-1.164(0.056)	-0.879(0.089)	<0.000(0.500)	0.650(0.700)	3.00(0.309-3.00)	0.00(0.00-0.030)	0.118(0.00-99999)
PRM	0(1)	0(-)	-	-	-	-	-
WCM	-1.513(0.056)	-14.863(0.011)	0.001(0.350)	0.413(0.75)	3.00(0.689-3.00)	0.00(0.00-0.060)	0.255(0.000-99999)
WPH	-	-	-	-	-	-	-
WMA	-	-	-	-	-	-	-
AAB	-1.279(0.077)	-1.936(0.034)	0.004(0.45)	0.184(0.300)	0.477(0.123-1.258)	0.00(0.00-0.016)	99999(14.684-99999)
ARB	-1.679(0.02)	-1.795(0.039)	<0.000(0.750)	0.232(0.500)	3.00(0.00-128.00)	0.00(0.00-1.020)	0.479(0.00-99999)
ASB	-1.441(0.071)	-2.135(0.009)	0.002(0.300)	0.299(0.750)	3.00(0.550-3.500)	0.00(0.00-0.217)	0.400(0.00-99999)
TNP	0.180(0.750)	0.637(0.461)	0.254(0.200)	0.273(0.150)	2.982(0.00-87.982)	0.900(0.00-7.140)	3.600(0.52-99999)
TMA	-	-	-	-	-	-	-
BMM	0.124(0.592)	-0.815(0.200)	0.043(0.45)	0.133(0.500)	3.047(0.00-4.266)	0.00(0.00-0.192)	4.883(2.299-99999)
BMA	-0.857(0.217)	-2.124(0.069)	0.026(0.050)	0.199(<0.000)	1.156(0.338-2.363)	0.002(0.00-0.156)	99999(1.931-99999)
BOM	0.430(0.726)	0.032(0.518)	0.031(0.100)	0.110(0.200)	3.55(0.00-10.625)	0.00(0.00-1.825)	5.723(0.414-99999)
GTA	1.041(0.856)	1.838(0.855)	0.135(0.050)	0.530(0.150)	4.086(0.00-128.00)	0.002(0.00-1.040)	0.667(0.00-99999)
GTT	-1.889(0.003)	0.587(0.424)	0.007(0.050)	0.876(0.900)	3.00(0.816-3.00)	0.00(0.00-0.00)	0.038(0.00-99999)
WCS	2.253(0.991)	3.929(0.944)	0.102(0.200)	0.123(0.100)	8.826(0.00-97.826)	0.002(0.00-14.538)	5.823(4.74-99999)
NEL	-0.334(0.416)	-0.019(0.515)	0.452(<0.000)	0.119(1.00)	0.00(0.00-0.314)	0.00(0.00-0.016)	99999(99869-99999)
WMP	-0.562(0.238)	-0.055(0.237)	0.332(0.200)	0.402(0.100)	2.930(0.00-87.93)	0.900(0.00-4.500)	3.600(2.731-99999)
AMB	0.074(0.571)	0.361(0.559)	0.023(0.400)	0.086(0.600)	2.293(0.689-4.051)	0.002(0.00-1.446)	7.020(2.313-99999)
GMA	-1.037(0.185)	1.132(0.761)	0.033(0.050)	0.314(0.700)	3.00(0.344-3.500)	0.00(0.00-0.217)	0.460(0.00-99999)
GPA	-1.159(0.151)	-1.028(0.077)	<0.000(0.100)	0.701(0.850)	2.992(0.621-2.992)	0.056(0.00-0.816)	0.113(0.00-99999)
GPB	-1.884(0.004)	0.795(0.479)	0.010(0.050)	0.854(0.950)	3.00(3.00-3.00)	0.00(0.00-0.00)	0.046(0.00-0.425)
GWB	1.918(0.978)	4.688(0.971)	0.194(0.050)	0.299(<0.000)	8.424(0.00-63.424)	0.002(0.00-5.409)	3.153(2.374-99999)

Supplementary Table 2. *Cominella virgata* additional statistics and neutrality tests.

Sampling Site	Tajima's D (p-value)	Fu's F-statistic (p-value)	SSD (p-value)	Rag (p-value)	Tau (95% CI)	Θ_0 (95% CI)	Θ_1 (95% CI)
AHV	-1.164 (0.164)	-0.879 (0.084)	<0.00 (0.15)	0.65 (0.85)	3.00 (0.45-3.00)	0.00 (0.00-0.005)	0.118 (0.00-99999)
BBV	1.870 (0.979)	4.187 (0.965)	0.14 (<0.00)	0.16 (0.30)	12.22 (0.50-65.21)	0.00 (0.00- 1.15)	3.91 (0.79-99999)
KTV	-	-	-	-	-	-	-
MAV	-	-	-	-	-	-	-
MGV	2.236 (0.993)	5.629 (0.987)	0.10 (0.05)	0.19 (<0.00)	15.75 (0.64-87.42)	0.00 (0.00-14.57)	14.38 (7.61-99999)
NGV	-1.418 (0.081)	-1.083 (0.300)	0.04 (0.45)	0.08 (0.55)	9.84 (0.34-95.84)	0.00 (0.0-1.49)	2.27 (0.32-99999)
PAV	-0.946 (0.187)	-1.183 (0.163)	0.01 (0.40)	0.09 (0.55)	0.88 (0.17-1.59)	0.00 (0.0-0.05)	99999 (4.26-99999)
PBV	-	-	-	-	-	-	-
PRV	-	-	-	-	-	-	-
WPB	-	-	-	-	-	-	-
WPH	1.193 (0.899)	5.917 (0.980)	0.12 (0.15)	0.89 (0.40)	3.00 (0.00-3.50)	0.00 (0.00-0.23)	0.46 (0.00-99999)
WMP	0.104 (0.586)	4.489 (0.970)	0.08 (<0.00)	0.56 (0.75)	3.00 (0.49-3.50)	0.00 (0.00-0.22)	0.24 (0.00-99999)
AMB	-	-	-	-	-	-	-
AAB	2.019 (0.983)	4.873 (0.965)	0.17 (0.10)	0.20 (<0.00)	10.61 (0.00-63.61)	0.00 (0.00-3.08)	5.44 (4.35-99999)
ARB	-1.494 (0.076)	-0.878 (0.167)	0.04 (0.15)	0.75 (0.50)	3.00 (0.00-3.00)	0.00 (0.00-0.00)	0.13 (0.00-99999)
ASB	-1.884 (0.004)*	-3.974 (<0.000)*	<0.00 (0.65)	0.23 (0.65)	0.67 (0.00-0.70)	0.00 (0.00-0.02)	99999 (12.98-99999)
BMM	-0.676 (0.287)	3.211 (0.916)	0.05 (0.05)	0.73 (0.65)	3.00 (0.45-3.50)	0.00 (0.00-0.91)	0.13 (0.00-99999)
BMA	-0.197 (0.503)	1.368 (0.749)	0.16 (0.10)	0.32 (0.05)	6.42 (0.00-12.56)	0.00 (0.00-0.097)	3.80 (2.06-99999)
BOM	-1.571 (0.019)*	-1.532 (0.025)	<0.00 (0.15)	0.74 (0.80)	3.00 (0.96-3.00)	0.00 (0.00-0.00)	0.08 (0.00-99999)
GTA	2.178 (0.982)	3.790 (0.940)	0.06 (0.00)	0.15 (<0.00)	7.59 (4.16-12.97)	0.00 (0.00-2.51)	8.90 (6.44-108.90)
NEL	-1.50738 (0.052)	-0.39563 (0.176)	<0.00 (<0.00)	0.88 (0.90)	3.00 (3.00-3.00)	0.00 (0.00-0.00)	0.04 (0.00-0.13)
GMP	-	-	-	-	-	-	-

Supplementary Table 3. *Cominella maculosa* sample site pairwise differences calculated using genetic distance (below) and associated p-values (above).

	BBO	WCP	CHM	CIO	CIW	KKM	KTM	MBM	PBM	PRM	WCM	WPH	WMA	AAB	ARB	ASB	TNP	TMA	BMM	BMA	BOM
BBO		<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.01	<0.01	0.01
WCP	0.85		0.33	0.01	<0.01	0.47	0.56	0.32	0.34	0.46	0.20	0.60	0.48	<0.01	<0.01	<0.01	0.02	<0.01	<0.01	<0.01	<0.01
CHM	0.83	0.02		0.02	<0,01	0.99	0.99	0.99	0.99	0.99	0.99	0.45	0.99	<0.01	<0.01	<0.01	0.14	<0.01	<0.01	<0.01	<0.01
CIO	0.70	0.88	0.91		0.99	<0.01	<0.01	<0.01	<0.01	0.01	0.02	<0.01	<0.01	0.01	<0,01	0.01	<0,01	0.02	0.01	<0.01	<0.01
CIW	0.73	0.85	0.87	0.00		<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.01	<0.01	<0.01
KKM	0.85	0.02	0.00	1.00	0.94		0.99	0.99	0.99	0.99	0.99	0.99	0.99	<0.01	<0.01	<0.01	0.16	<0.01	<0.01	<0.01	<0.01
KTM	0.85	0.02	0.00	1.00	0.94	0.00		0.99	0.99	0.99	0.50	0.99	0.99	<0.01	<0.01	<0.01	0.18	<0.01	<0.01	<0.01	<0.01
MBM	0.83	0.02	0.00	0.91	0.87	0.00	0.00		0.99	0.99	0.99	0.53	0.99	<0.01	<0.01	<0.01	0.06	<0.01	<0.01	<0.01	<0.01
PBM	0.83	0.02	0.00	0.91	0.87	0.00	0.00	0.00		0.99	0.99	0.44	0.99	<0.01	<0.01	<0.01	0.11	<0.01	<0.01	<0.01	<0.01
PRM	0.85	0.02	0.00	1.00	0.94	0.00	0.00	0.00	0.00		0.99	0.99	0.99	<0.01	<0.01	<0.01	0.10	<0.01	<0.01	<0.01	<0.01
WCM	0.82	0.02	0.00	0.83	0.81	0.00	0.00	0.00	0.00	0.00		0.23	0.99	<0.01	<0.01	<0.01	0.05	<0.01	<0.01	<0.01	<0.01
WPH	0.85	0.03	0.00	1.00	0.94	0.00	0.00	0.00	0.00	0.00	0.00		0.99	<0.01	<0.01	<0.01	0.04	<0.01	<0.01	<0.01	<0.01
WMA	0.85	0.02	0.00	1.00	0.94	0.00	0.00	0.00	0.00	0.00	0.00	0.00		<0.01	<0.01	<0.01	0.14	<0.01	<0.01	<0.01	<0.01
AAB	0.58	0.92	0.92	0.91	0.91	0.93	0.93	0.92	0.92	0.93	0.91	0.93	0.93		0.26	0.10	<0.01	<0.01	<0.01	0.02	<0.01
ARB	0.61	0.92	0.92	0.91	0.90	0.93	0.93	0.92	0.91	0.93	0.90	0.93	0.93	0.02		0.48	<0.01	<0.01	0.01	0.14	<0.01
ASB	0.60	0.92	0.92	0.91	0.91	0.94	0.93	0.92	0.92	0.94	0.91	0.94	0.94	0.03	0.00		<0.01	<0.01	<0.01	0.08	<0.01
TNP	0.84	0.10	0.09	0.78	0.78	0.10	0.10	0.09	0.09	0.10	0.08	0.10	0.10	0.90	0.90	0.90		<0.01	<0.01	<0.01	<0.01
TMA	0.87	0.99	0.99	1.00	0.99	1.00	1.00	0.99	0.99	1.00	0.98	1.00	1.00	0.92	0.92	0.93	0.97		<0.01	<0.01	<0.01
BMM	0.17	0.85	0.84	0.70	0.74	0.85	0.85	0.84	0.83	0.85	0.82	0.86	0.85	0.23	0.29	0.28	0.84	0.85		<0.01	0.35
BMA	0.54	0.85	0.84	0.81	0.82	0.85	0.85	0.84	0.83	0.85	0.83	0.85	0.85	0.06	0.03	0.04	0.84	0.83	0.24		<0.01
BOM	0.17	0.73	0.70	0.64	0.67	0.71	0.71	0.70	0.70	0.71	0.70	0.71	0.71	0.18	0.21	0.21	0.73	0.68	0.02	0.22	
GTA	0.66	0.87	0.86	0.82	0.83	0.86	0.86	0.86	0.86	0.86	0.85	0.87	0.86	0.60	0.58	0.59	0.86	0.86	0.54	0.54	0.40
GTT	0.85	0.96	0.97	0.96	0.96	0.97	0.97	0.97	0.97	0.97	0.96	0.97	0.97	0.89	0.89	0.90	0.95	0.97	0.83	0.83	0.36
WCS	0.34	0.65	0.62	0.48	0.53	0.62	0.62	0.62	0.62	0.62	0.62	0.63	0.62	0.40	0.41	0.40	0.66	0.66	0.31	0.40	0.34
NEL	0.58	0.16	0.13	0.29	0.37	0.14	0.14	0.13	0.12	0.14	0.13	0.14	0.14	0.60	0.59	0.58	0.17	0.81	0.52	0.54	0.51
WMP	0.82	0.05	0.04	0.84	0.81	0.06	0.06	0.04	0.04	0.06	-0.03	0.06	0.06	0.91	0.90	0.91	0.10	0.99	0.82	0.82	0.69
AMB	0.42	0.85	0.83	0.70	0.74	0.85	0.85	0.83	0.83	0.85	0.82	0.85	0.85	0.20	0.19	0.13	0.84	0.84	0.18	0.13	0.20
GMA	0.68	0.87	0.86	0.81	0.82	0.87	0.87	0.86	0.86	0.87	0.85	0.87	0.87	0.72	0.71	0.71	0.86	0.87	0.63	0.67	0.56
GPA	0.78	0.98	0.98	0.99	0.98	0.99	0.99	0.98	0.98	0.99	0.97	0.99	0.99	0.94	0.94	0.95	0.96	0.99	0.86	0.88	0.73
GPB	0.72	0.95	0.95	0.95	0.94	0.96	0.96	0.95	0.95	0.96	0.95	0.96	0.96	0.90	0.91	0.91	0.94	0.98	0.81	0.85	0.70
GWB	0.33	0.67	0.64	0.51	0.56	0.65	0.65	0.64	0.63	0.65	0.64	0.65	0.65	0.43	0.43	0.42	0.68	0.69	0.32	0.42	0.34

Supplementary Table 3 continued…

	GTA	GTT	WCS	NEL	WMP	AMB	GMA	GPA	GPB	GWB
BBO	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
WCP	<0.01	<0.01	<0.01	<0.01	0.20	<0.01	<0.01	<0.01	<0.01	<0.01
CHM	<0.01	<0.01	<0.01	0.01	0.24	<0.01	<0.01	<0.01	<0.01	<0.01
CIO	<0.01	<0.01	<0.01	0.05	0.03	0.04	0.01	<0.01	<0.01	<0.01
CIW	<0.01	<0.01	<0.01	0.02	<0.01	0.01	<0.01	<0.01	<0.01	<0.01
KKM	<0.01	<0.01	<0.01	0.01	0.24	<0.01	<0.01	<0.01	<0.01	<0.01
KTM	<0.01	<0.01	<0.01	<0.01	0.24	<0.01	<0.01	<0.01	<0.01	<0.01
MBM	<0.01	<0.01	<0.01	<0.01	0.28	<0.01	<0.01	<0.01	<0.01	<0.01
PBM	<0.01	<0.01	<0.01	<0.01	0.27	<0.01	<0.01	<0.01	<0.01	<0.01
PRM	<0.01	<0.01	<0.01	0.02	0.17	<0.01	<0.01	<0.01	<0.01	<0.01
WCM	<0.01	<0.01	<0.01	0.01	0.19	<0.01	<0.01	<0.01	<0.01	<0.01
WPH	<0.01	<0.01	<0.01	<0.01	0.20	<0.01	<0.01	<0.01	<0.01	<0.01
WMA	<0.01	<0.01	<0.01	0.01	0.26	<0.01	<0.01	<0.01	<0.01	<0.01
AAB	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
ARB	<0.01	<0.01	<0.01	<0.01	<0.01	0.01	<0.01	<0.01	<0.01	<0.01
ASB	<0.01	<0.01	<0.01	<0.01	<0.01	0.06	<0.01	<0.01	<0.01	<0.01
TNP	<0.01	<0.01	<0.01	<0.01	0.02	<0.01	<0.01	<0.01	<0.01	<0.01
TMA	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
BMM	<0.01	<0.01	<0.01	<0.01	<0.01	0.01	<0.01	<0.01	<0.01	0.01
BMA	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
BOM	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
GTA		<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
GTT	0.78		<0.01	<0.01	<0.01	<0.01	0.14	<0.01	<0.01	<0.01
WCS	0.44	0.33		<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.61
NEL	0.66	0.81	0.48		0.02	<0.01	<0.01	<0.01	<0.01	<0.01
WMP	0.85	0.96	0.61	0.13		<0.01	<0.01	<0.01	<0.01	<0.01
AMB	0.52	0.82	0.33	0.51	0.82		<0.01	<0.01	<0.01	<0.01
GMA	0.63	0.03	0.18	0.70	0.85	0.62		<0.01	<0.01	0.07
GPA	0.89	0.97	0.54	0.80	0.98	0.88	0.88		0.99	<0.01
GPB	0.87	0.96	0.50	0.77	0.95	0.83	0.86	0.00		<0.01
GWB	0.46	0.39	0.00	0.49	0.63	0.34	0.22	0.53	0.49	

Supplementary Table 4. *Cominella maculosa* sample site pairwise differences calculated using haplotype frequencies (below) and associated p-values (above).

	BBO	WCP	CHM	CIO	CIW	KKM	KTM	MBM	PBM	PRM	WCM	WPH	WMA	AAB	ARB	ASB	TNP	TMA	BMM	BMA	BOM
BBO		<0.01	<0.01	0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.05
WCP	0.74		0.50	<0.01	<0.01	0.59	0.51	0.46	0.41	0.56	0.61	0.52	0.51	<0.01	<0.01	<0.01	0.10	<0.01	<0.01	<0.01	<0.01
CHM	0.75	0.00		<0.01	<0.01	0.99	0.99	0.99	0.99	0.99	0.99	0.51	0.99	<0.01	<0.01	<0.01	0.13	<0.01	<0.01	<0.01	<0.01
CIO	0.59	0.87	0.91		0.99	<0.01	<0.01	<0.01	0.02	<0.01	<0.01	<0.01	0.01	<0,01	0.02	<0.01	<0.01	0.01	0.02	<0.01	<0.01
CIW	0.51	0.80	0.83	0.00		<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.02	<0.01	<0.01
KKM	0.82	0.02	0.00	1.00	0.92		0.99	0.99	0.99	0.99	0.58	0.99	0.99	<0.01	<0.01	<0.01	0.15	<0.01	<0.01	<0.01	<0.01
KTM	0.82	0.02	0.00	1.00	0.92	0.00		0.99	0.99	0.99	0.50	0.99	0.99	<0.01	<0.01	<0.01	0.11	<0.01	<0.01	<0.01	<0.01
MBM	0.75	0.00	0.00	0.91	0.83	0.00	0.00		0.99	0.99	0.99	0.47	0.99	<0.01	<0.01	<0.01	0.14	<0.01	<0.01	<0.01	<0.01
PBM	0.75	0.00	0.00	0.91	0.83	0.00	0.00	0.00		0.99	0.99	0.41	0.99	<0.01	<0.01	<0.01	0.17	<0.01	<0.01	<0.01	<0.01
PRM	0.82	0.02	0.00	1.00	0.92	0.00	0.00	0.00	0.00		0.54	0.99	0.99	<0.01	<0.01	<0.01	0.14	<0.01	<0.01	<0.01	<0.01
WCM	0.69	0.00	0.00	0.82	0.74	0.03	0.03	0.00	0.00	0.03		0.21	0.44	<0.01	<0.01	<0.01	0.12	<0.01	<0.01	<0.01	<0.01
WPH	0.82	0.03	0.00	1.00	0.92	0.00	0.00	0.00	0.00	0.00	0.03		0.99	<0.01	<0.01	<0.01	0.05	<0.01	<0.01	<0.01	<0.01
WMA	0.82	0.02	0.00	1.00	0.92	0.00	0.00	0.00	0.00	0.00	0.03	0.00		<0.01	<0.01	<0.01	0.12	<0.01	<0.01	<0.01	<0.01
AAB	0.59	0.75	0.76	0.67	0.60	0.80	0.80	0.76	0.76	0.80	0.71	0.80	0.80		0.47	0.42	<0.01	<0.01	0.05	0.03	<0.01
ARB	0.62	0.77	0.78	0.71	0.64	0.83	0.83	0.78	0.78	0.83	0.74	0.83	0.83	0.00		0.99	<0.01	<0.01	0.02	<0.01	<0.01
ASB	0.63	0.80	0.81	0.75	0.67	0.86	0.86	0.81	0.81	0.86	0.76	0.86	0.86	0.00	0.00		<0.01	<0.01	0.01	0.03	<0.01
TNP	0.65	0.05	0.05	0.75	0.68	0.10	0.10	0.05	0.05	0.10	0.03	0.10	0.10	0.68	0.70	0.72		<0,01	<0.01	<0.01	<0.01
TMA	0.86	0.93	0.96	1.00	0.95	1.00	1.00	0.96	0.96	1.00	0.92	1.00	1.00	0.84	0.86	0.89	0.86		<0.01	<0.01	<0.01
BMM	0.33	0.66	0.65	0.40	0.34	0.73	0.73	0.65	0.65	0.73	0.59	0.73	0.73	0.10	0.12	0.13	0.56	0.79		0.27	<0.01
BMA	0.37	0.57	0.57	0.41	0.35	0.61	0.61	0.57	0.57	0.61	0.52	0.62	0.61	0.09	0.09	0.11	0.51	0.66	0.02		<0.01
BOM	0.07	0.53	0.52	0.36	0.31	0.56	0.56	0.52	0.52	0.56	0.48	0.57	0.56	0.33	0.35	0.36	0.47	0.61	0.13	0.19	
GTA	0.57	0.73	0.73	0.65	0.58	0.77	0.77	0.73	0.73	0.77	0.69	0.78	0.77	0.61	0.63	0.64	0.66	0.81	0.47	0.43	0.41
GTT	0.80	0.90	0.92	0.93	0.87	0.96	0.96	0.92	0.92	0.96	0.88	0.96	0.96	0.79	0.82	0.84	0.82	0.97	0.72	0.62	0.57
WCS	0.36	0.56	0.55	0.39	0.33	0.59	0.59	0.55	0.55	0.59	0.51	0.60	0.59	0.44	0.46	0.47	0.50	0.64	0.25	0.27	0.24
NEL	0.44	0.13	0.13	0.48	0.42	0.18	0.18	0.13	0.13	0.18	0.09	0.19	0.18	0.46	0.48	0.49	0.09	0.72	0.29	0.30	0.29
WMP	0.69	0.01	0.00	0.82	0.74	0.06	0.06	0.00	0.00	0.06	0.00	0.06	0.06	0.71	0.74	0.76	0.04	0.92	0.58	0.52	0.48
AMB	0.37	0.65	0.65	0.39	0.32	0.72	0.72	0.65	0.65	0.72	0.58	0.72	0.72	0.19	0.20	0.21	0.55	0.78	0.04	0.03	0.17
GMA	0.59	0.75	0.76	0.68	0.61	0.80	0.80	0.76	0.76	0.80	0.72	0.81	0.80	0.62	0.65	0.66	0.68	0.84	0.48	0.45	0.42
GPA	0.78	0.89	0.91	0.92	0.85	0.95	0.95	0.91	0.91	0.95	0.87	0.96	0.95	0.77	0.80	0.82	0.81	0.96	0.69	0.59	0.54
GPB	0.78	0.89	0.91	0.92	0.85	0.95	0.95	0.91	0.91	0.95	0.87	0.96	0.95	0.77	0.79	0.82	0.81	0.96	0.68	0.58	0.54
GWB	0.43	0.64	0.64	0.49	0.42	0.68	0.68	0.64	0.64	0.68	0.59	0.69	0.68	0.51	0.54	0.55	0.57	0.73	0.33	0.34	0.30

Supplementary Table 4 continued…

	GTA	GTT	WCS	NEL	WMP	AMB	GMA	GPA	GPB	GWB
BBO	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
WCP	<0.01	<0.01	<0.01	0.01	0.44	<0.01	<0.01	<0.01	<0.01	<0.01
CHM	<0.01	<0.01	<0.01	<0.01	0.38	<0.01	<0.01	<0.01	<0.01	<0.01
CIO	<0.01	<0.01	<0.01	<0.01	0.01	0.02	0.01	<0.01	0.01	<0.01
CIW	<0.01	<0.01	<0.01	<0.01	<0,01	<0.01	<0.01	<0.01	<0.01	0.01
KKM	<0.01	<0.01	<0.01	0.01	0.26	<0.01	<0.01	<0.01	<0.01	<0.01
KTM	<0.01	<0.01	<0.01	<0.01	0.29	<0.01	<0.01	<0.01	<0.01	<0.01
MBM	<0.01	<0.01	<0.01	<0.01	0.31	<0.01	<0.01	<0.01	<0.01	<0.01
PBM	<0.01	<0.01	<0.01	<0.01	0.37	<0.01	<0.01	<0.01	<0.01	<0.01
PRM	<0.01	<0.01	<0.01	<0.01	0.26	<0.01	<0.01	<0.01	<0.01	<0.01
WCM	<0.01	<0.01	<0.01	0.01	0.45	<0.01	<0.01	<0.01	<0.01	<0.01
WPH	<0.01	<0.01	<0.01	<0.01	0.19	<0.01	<0.01	<0.01	<0.01	<0.01
WMA	<0.01	<0.01	<0.01	<0.01	0.28	<0.01	<0.01	<0.01	<0.01	<0.01
AAB	<0.01	<0.01	<0.01	<0.01	<0.01	0.03	<0.01	<0.01	<0.01	<0.01
ARB	<0.01	<0.01	<0.01	<0.01	<0.01	<0,01	<0.01	<0.01	<0.01	<0.01
ASB	<0.01	<0.01	<0.01	<0.01	<0.01	0.04	<0.01	<0.01	<0.01	<0.01
TNP	<0.01	<0.01	<0.01	0.01	0.19	<0.01	<0.01	<0.01	<0.01	<0.01
TMA	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
BMM	<0.01	<0.01	<0.01	<0.01	<0.01	0.17	<0.01	<0.01	<0.01	<0.01
BMA	<0.01	<0.01	<0.01	<0.01	<0.01	0.13	<0.01	<0.01	<0.01	<0.01
BOM	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
GTA		<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
GTT	0.77		<0.01	<0.01	<0.01	<0.01	0.05	<0.01	<0.01	<0.01
WCS	0.44	0.45		<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.05
NEL	0.50	0.67	0.33		0.01	<0.01	<0.01	<0.01	<0.01	<0.01
WMP	0.69	0.88	0.50	0.09		<0.01	<0.01	<0.01	<0.01	<0.01
AMB	0.46	0.71	0.25	0.29	0.57		<0.01	<0.01	<0.01	<0.01
GMA	0.62	0.06	0.25	0.51	0.71	0.47		<0.01	<0.01	0.07
GPA	0.75	0.92	0.33	0.65	0.87	0.68	0.76		0.99	<0.01
GPB	0.75	0.92	0.33	0.64	0.87	0.67	0.76	0.00		<0.01
GWB	0.51	0.28	0.06	0.39	0.59	0.32	0.08	0.52	0.52	

Supplementary Table 5. *Cominella virgata* sample site pairwise differences calculated using genetic distance (below) and associated p-values (above).

	AHV	BBV	KTV	MAV	MGV	NGV	PAV	PBV	PRV	WPB	WPH	WMP	AMB	AAB	ARB	ASB	BMM	BMA	BOM	GTA	NEL	MP
AHV		<0.01	<0.01	0.99	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
BBV	0.72		<0.01	<0.01	0.10	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.05	<0.01	0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
KTV	0.99	0.35		<0.01	<0.01	0.02	<0.01	0.99	0.99	<0.01	<0.01	<0.01	0.99	<0.01	0.43	0.99	<0.01	<0.01	<0.01	<0.01	0.99	<0.01
MAV	0.00	0.54	1.00		<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
MGV	0.63	0.08	0.35	0.47		<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
NGV	0.79	0.13	0.07	0.70	0.21		<0.01	0.01	0.02	<0.01	<0.01	<0.01	<0.01	<0.01	0.04	<0.01	<0.01	<0.01	<0.01	<0.01	0.01	<0.01
PAV	0.79	0.67	0.94	0.71	0.60	0.00		<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
PBV	0.99	0.35	0.00	1.00	0.35	0.07	0.93		0.99	<0.01	<0.01	<0.01	0.99	<0.01	0.42	0.99	<0.01	<0.01	<0.01	<0.01	0.99	<0.01
PRV	0.99	0.35	0.00	0.99	0.35	0.07	0.94	0.00		<0.01	<0.01	<0.01	0.99	<0.01	0.49	0.99	<0.01	<0.01	<0.01	<0.01	0.99	<0.01
WPB	0.99	0.46	1.00	1.00	0.41	0.55	0.94	1.00	1.00		0.02	0.21	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
WPH	0.72	0.24	0.51	0.62	0.29	0.31	0.68	0.51	0.51	0.18		0.74	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
WMP	0.79	0.28	0.57	0.71	0.31	0.34	0.75	0.57	0.57	0.10	0.00		<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
AMB	0.99	0.39	0.00	1.00	0.39	0.09	0.94	0.00	0.00	1.00	0.54	0.60		<0.01	0.42	0.04	<0.01	<0.01	<0.01	<0.01	0.28	<0.01
AAB	0.59	0.13	0.41	0.46	0.20	0.25	0.61	0.41	0.41	0.51	0.36	0.39	0.44		<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
ARB	0.97	0.34	0.01	0.96	0.36	0.06	0.92	0.01	0.01	0.91	0.48	0.53	0.02	0.41		0.42	<0.01	<0.01	<0.01	<0.01	0.75	<0.01
ASB	0.97	0.35	0.00	0.96	0.37	0.07	0.92	0.00	0.00	0.92	0.51	0.56	0.00	0.42	0.01		<0.01	<0.01	<0.01	<0.01	0.28	<0.01
BMM	0.94	0.64	0.88	0.92	0.58	0.70	0.91	0.88	0.88	0.88	0.67	0.71	0.89	0.61	0.86	0.86		0.03	<0.01	<0.01	<0.01	<0.01
BMA	0.81	0.38	0.59	0.74	0.39	0.43	0.78	0.59	0.59	0.60	0.44	0.47	0.62	0.41	0.57	0.59	0.14		<0.01	<0.01	<0.01	<0.01
BOM	0.98	0.76	0.97	0.98	0.69	0.78	0.95	0.97	0.97	0.97	0.74	0.78	0.97	0.71	0.94	0.94	0.83	0.62		<0.01	<0.01	<0.01
GTA	0.69	0.24	0.44	0.61	0.30	0.32	0.67	0.44	0.44	0.47	0.37	0.38	0.46	0.25	0.43	0.44	0.26	0.51	0.51		<0.01	<0.01
NEL	0.98	0.41	0.00	0.98	0.41	0.09	0.94	0.00	0.00	0.96	0.54	0.59	0.00	0.45	0.00	0.00	0.88	0.96	0.96	0.47		<0.01
MP	0.99	0.53	1.00	1.00	0.47	0.60	0.93	1.00	1.00	1.00	0.55	0.62	0.46	0.52	0.93	0.93	0.69	0.85	0.85	0.27	0.97	

Supplementary Table 6. *Cominella virgata* sample site pairwise differences calculated using haplotype frequencies (below) and associated p-values (above).

	AHV	BBV	KTV	MAV	MGV	NGV	PAV	PBV	PRV	WPB	WPH	WMP	AMB	AAB	ARB	ASB	BMM	BMA	BOM	GTA	NEL	MP
AHV		<0.01	<0.01	0.99	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
BBV	0.62		<0.01	<0.01	<0.01	0.05	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.02	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
KTV	0.95	0.51		<0.01	<0.01	<0.01	<0.01	0.99	0.99	<0.01	<0.01	<0.01	0.99	<0.01	0.58	0.13	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
MAV	0.00	0.50	1.00		<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
MGV	0.58	0.23	0.64	0.47		<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
NGV	0.58	0.08	0.25	0.48	0.23		<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.02	<0.01	0.04	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
PAV	0.65	0.32	0.70	0.57	0.32	0.33		<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.01	<0.01
PBV	0.95	0.51	0.00	1.00	0.64	0.25	0.70		0.99	<0.01	<0.01	<0.01	0.99	<0.01	0.54	0.14	<0.01	<0.01	<0.01	<0.01	0.99	<0.01
PRV	0.95	0.51	0.00	1.00	0.64	0.25	0.70	0.00		<0.01	<0.01	<0.01	0.99	<0.01	0.51	0.12	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
WPB	0.95	0.69	1.00	1.00	0.64	0.63	0.70	1.00	1.00		0.03	0.18	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.07	<0.01
WPH	0.73	0.44	0.78	0.68	0.43	0.43	0.50	0.78	0.78	0.13		0.86	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
WMP	0.80	0.52	0.84	0.77	0.50	0.50	0.57	0.84	0.84	0.08	0.00		<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
AMB	0.96	0.55	0.00	1.00	0.67	0.67	0.73	0.00	0.00	1.00	0.80	0.86		<0.01	0.16	0.02	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
AAB	0.59	0.14	0.32	0.51	0.28	0.28	0.36	0.32	0.32	0.63	0.46	0.52	0.35		<0.01	0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
ARB	0.87	0.40	0.01	0.87	0.57	0.57	0.63	0.01	0.01	0.91	0.70	0.76	0.02	0.24		0.63	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
ASB	0.79	0.29	0.05	0.76	0.48	0.48	0.55	0.05	0.05	0.83	0.64	0.70	0.07	0.17	0.00		<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
BMM	0.85	0.60	0.89	0.84	0.57	0.57	0.63	0.89	0.89	0.89	0.70	0.76	0.90	0.58	0.82	0.75		<0.01	<0.01	<0.01	<0.01	<0.01
BMA	0.61	0.29	0.64	0.53	0.30	0.30	0.38	0.64	0.64	0.65	0.47	0.53	0.66	0.32	0.57	0.50	0.17		<0.01	<0.01	<0.01	<0.01
BOM	0.90	0.71	0.94	0.92	0.67	0.67	0.72	0.94	0.94	0.94	0.78	0.83	0.94	0.66	0.88	0.82	0.869	0.67		<0.01	0.99	<0.01
GTA	0.50	0.18	0.46	0.43	0.22	0.22	0.30	0.46	0.46	0.53	0.39	0.44	0.48	0.21	0.41	0.35	0.28	0.11	0.56		0.99	<0.01
NEL	0.92	0.94	0.71	0.26	0.51	0.65	0.04	0.00	0.03	0.00	0.87	0.92	0.65	0.47	0.95	0.77	0.96	0.83	0.00	0.00		<0.01
MP	0.94	0.60	1.00	1.00	0.56	0.56	0.64	1.00	1.00	1.00	0.73	0.81	1.00	0.57	0.89	0.79	0.86	0.59	0.92	0.39	1.00	