Biological Journal of the Linnean Society, 2019, **126**, 178–202. With 4 figures.

Phylogeography of the New Zealand whelks *Cominella maculosa* and *C. virgata* (Gastropoda: Neogastropoda: Buccinoidea: Buccinidae)

KERRY WALTON[1,2,*], BRUCE A. MARSHALL[2], NICOLE E. PHILLIPS[1], ALEXANDER J.F. VERRY[1,3] and PETER A. RITCHIE[1]

[1]*School of Biological Sciences, Victoria University of Wellington, Wellington, New Zealand*
[2]*Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand*
[3]*Department of Zoology, University of Otago, Dunedin, New Zealand*

Received 4 August 2018; revised 4 October 2018; accepted for publication 4 October 2018

Cominella maculosa and *C. virgata* are common whelk species that inhabit rocky shores around much of the North Island of New Zealand, the northern South Island and, for *C. maculosa*, the Chatham Islands. This study used DNA sequences from the mitochondrial gene *CO1* to examine the phylogeographical structure of populations of both species in areas that have not previously been sampled. Collections of both species were made from sites in the Cook Strait region, *C. maculosa* from the Chatham Islands and *C. virgata* from the northern North Island. Both species were found to have a considerable degree of genetic differentiation, but genetic diversity and phylogeographical patterns differed greatly between regions. South Island populations of *C. virgata* may have originated, or been supplemented, by human-mediated translocations. Phylogenetic analyses were conducted using the mitochondrial genes *CO1* and 16S rRNA, and the nuclear gene 18S rRNA. The northern subspecies *C. virgata brookesi* did not form a monophyletic lineage and is synonymized with *C. virgata.* A lectotype is designated for *Buccinum lineolatum* Quoy & Gaimard, 1833, of which *C. virgata* is a replacement name.

ADDITIONAL KEYWORDS: Chatham Islands – Cook Strait – lectotype – Mollusca –taxonomy.

The genus *Cominella* Gray, 1850 comprises about 25 extant species, each endemic either to Australia, Norfolk Island or New Zealand (Donald *et al.*, 2015). *Cominella* (*s.s.*) *maculosa* (Martyn, 1784) and *C.* (*Cominula*) *virgata* H. Adams & A. Adams, 1853–1854 are common, sympatric, often syntopic, carnivorous (Ansell, 2000; Stewart & Creese, 2004; Morley *et al.*, 2006) whelk species. They are usually found in association with hard substrata (Morton & Miller, 1968) and range from the intertidal zone to 16 m and 11 m depth, respectively. *Cominella maculosa* occurs around the entire North Island, the northern South Island and the Chatham Islands (Fig. 1C). *Cominella virgata* is absent from the Chatham Islands (Marston, 1996, 1998; Walton, 2017) and has a disjunct distribution comprising two discrete regional populations (see Fig. 2C), one in the northern and north-eastern North Island and the other in the Cook Strait region (see Discussion). Both species show direct development (Carrasco & Phillips, 2012; Carrasco *et al.*, 2012). Their abundance and similar distributions, habitats and behaviours make them ideal subjects for comparative phylogeographical analyses (Fleming *et al.*, 2018).

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 substrata other than rock, such as crabs (Graham, 1941), algae and other snails (Walton, 2017: fig. 1.5a, c). Development takes several months (van der Sman, 2007). Although *Cominella* species do not normally associate with substrata with high rafting potential (Donald *et al.*, 2015; Dohner *et al.*, 2018), such as algae and driftwood, *C. maculosa* and *C. virgata* are often abundant near such

*Corresponding author. E-mail: walton.kerry@gmail.com

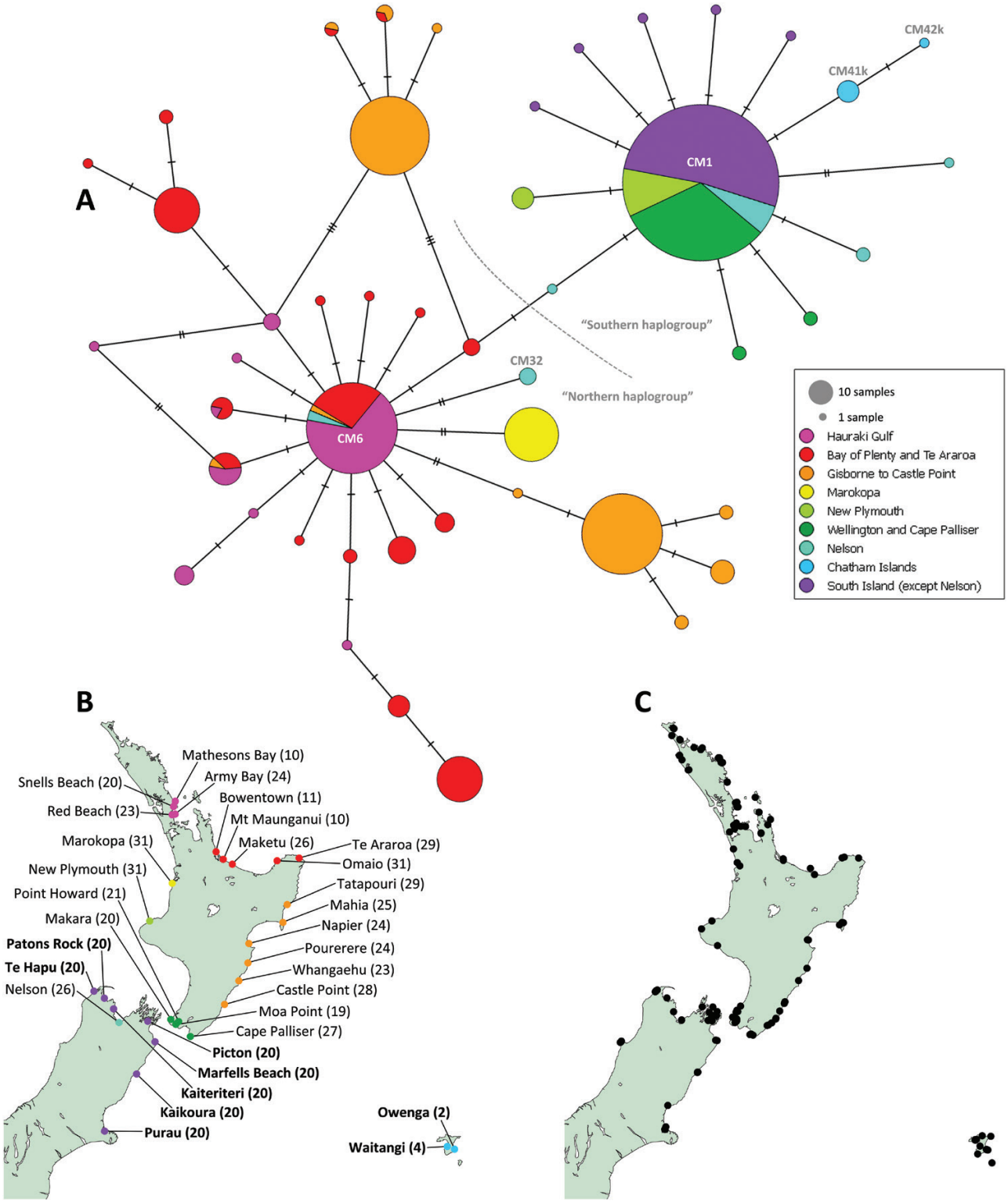

Figure 1. Distribution and sampling data for *Cominella maculosa*. A, CO1 median joining haplotype network map; "northern" and "southern" haplogroups indicated in grey. Hatch-marks represent one mutational step. Black circles represent hypothetical un-sampled haplotypes. Numbers prefixed "CM" indicate haplotypes specifically mentioned in Discussion. B, Sample sizes (numbers) and sites (circles coloured according to region, refer to key). Bold text indicates samples originating from this study; others comprise the dataset of Fleming *et al*. (2018). C, Distribution records (black circles) of *C. maculosa* held by NMNZ.

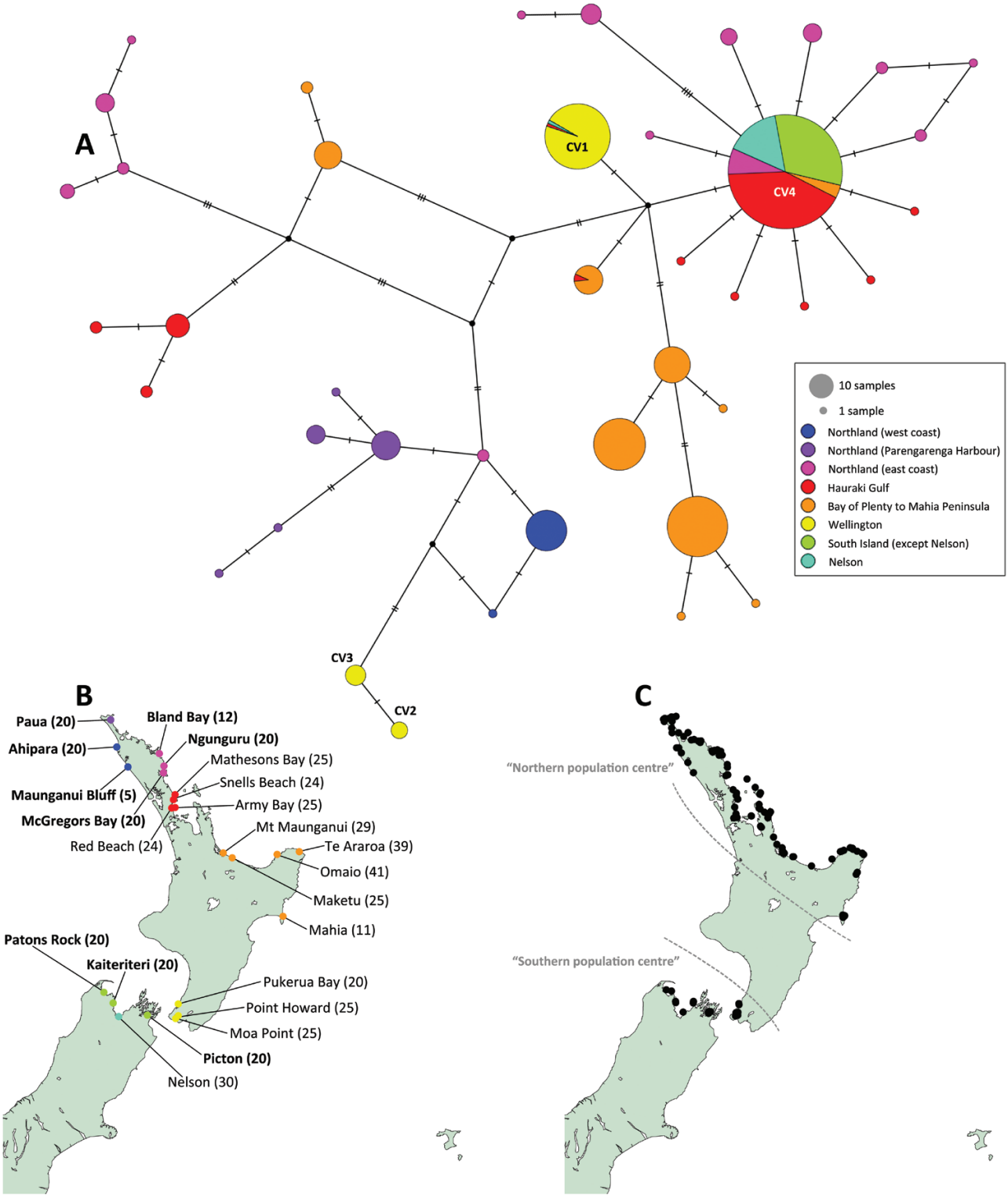

Figure 2. Distribution and sampling data for *Cominella virgata*. A, CO1 median joining haplotype network map. Hatchmarks represent one mutational step. Black circles represent hypothetical un-sampled haplotypes. Numbers prefixed "CV" indicate haplotypes specifically mentioned in Discussion. B, Sample sizes (numbers) and sites (circles coloured according to region, refer to key). Bold text indicates samples originating from this study; others comprise the dataset of Fleming *et al.* (2018). C, Distribution records of *C. virgata* at NMNZ; distribution disjunction ('population centres') indicated in grey.

materials. Juveniles and egg capsules of *C. maculosa* and *C. virgata* are sometimes found on the buoyant brown alga *Carpophyllum maschalocarpum* Turner (Greville, 1830), which occurs throughout their distributional ranges. Detached fronds from *Carpophyllum maschalocarpum* form rafts capable of traversing Cook Strait and the Chatham Rise (Buchanan & Zuccarello, 2012). The alga *Durvillaea antarctica* (Chamisso) Hariot, 1892 lives around the entire South Island, at the Three Kings, Stewart, Snares, Auckland and Campbell Islands and patchily around the southern North Island (Fraser *et al.*, 2009; Fraser *et al.* 2012b). *Durvillaea antarctica* is significantly sturdier, larger and more buoyant than *Carpophyllum maschalocarpum*, and consequently has even greater rafting potential (Collins *et al.*, 2010; Nikula *et al.*, 2010; Fraser *et al.*, 2011; Nikula *et al.*, 2011a, b). *Durvillaea antarctica* has been implicated as a vector for gene flow in several marine invertebrate taxa off southern New Zealand (Fraser *et al.*, 2011; Nikula *et al.*, 2011a, b). Furthermore, detached egg-masses of *Cominella adspersa* (Bruguière, 1789) have been observed floating in calm water (Dohner, 2016) and those of *Cominella glandiformis* (Reeve, 1847) attached to floating driftwood (Morley, 2013). Rafting events of intertidal *Cominella* species probably occur frequently, especially of egg capsules (Donald *et al.*, 2015), and presumably reflect predominant shallow-water ocean circulation patterns (reviewed by: Heath, 1985; Chiswell *et al.*, 2015). Few dispersers per generation are required to homogenize genetic diversity (Ovenden, 2013). Occasional rafting events probably explain several of the patterns of gene flow already reported for *C. maculosa* and *C. virgata* (Dohner, 2016; Walton, 2017; Dohner *et al.*, 2018; Fleming *et al.*, 2018).

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 middens (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 potentially establish and be transported on heavily fouled hulls (Walton, 2017). Coastal rocks were widely used as ballast in New Zealand as recently as the early 1900s (Moore & Kenny, 1986; Hewitt *et al.*, 2009) and many taxa, including commercially harvested and/or pest species, have been introduced or spread as biofoul attached to or among ballast rocks (Carlton, 1999, 2011; Bax *et al.*, 2003). Instances of human-mediated translocations are presumably most prevalent in ports (Carlton, 1999, 2011).

Another means of unintentional human-mediated dispersal may be via transportation of craypots, which *Cominella* species regularly enter, attracted by the bait (Ansell, 2000; Stewart & Creese, 2004). *Cominella maculosa* and *C. virgata* can survive out of water for several days if they remain cool and moist. With many fishing vessels running lines of craypots tens of kilometres apart, it is conceivable that *Cominella* species are regularly transported considerable distances, increasing the effective dispersal ability and rate for these and other species, although how significant this mechanism may be remains unknown.

In the northern North Island, populations of *C. virgata* have highly variable shell morphologies, with comparatively little variation occurring further south (Walton, 2017). Powell (1952) distinguished populations from the east coast north of the Bay of Islands as a subspecies, *C. virgata brookesi* Powell, 1952, based on colour pattern (see below), either ignoring or unaware of diverse populations on the west coast of Northland. *Cominella v. brookesi* and the nominal subspecies have intergrading colour patterns in Northland, leading to uncertainty as to the subspecific name to apply to particular populations or indeed as to the validity of continued maintenance of subspecies.

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

Phylogeographical patterns often vary widely between species, even among congeners with similar characteristics (Goldstien *et al.*, 2006; Knox *et al.*, 2011). Phylogeographical structure results from multiple synergistic factors that can limit or promote dispersal (Ross *et al.*, 2009), including direction and strength of ocean circulation, tolerance of changes in water temperature and chemistry, larval and adult behaviour, life-history strategies, habitat patchiness, chance and high-density blocking effects by resident individuals or species (Roughgarden *et al.*, 1985, 1988; Ross *et al.*, 2009; Waters, 2011; Pinsky & Fogarty, 2012; Waters *et al.*, 2013; Fleming *et al.*, 2018). It is difficult to delimit the effects of any given factor influencing phylogeographical structure. Increasing the breadth of species, sample sites and markers examined can improve the overall understanding of the processes

that structure populations (Ross *et al.*, 2009; Gardner *et al.*, 2010).

Study background and aims

Fleming *et al.* (2018) 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 from Nelson in the northern South Island (Figs 1B, 2B). Both species were found to have considerable regional structure, and Nelson populations appeared distinct from those in Wellington (Fleming *et al.*, 2018). The present contribution includes data from populations that have not previously been sampled for both species from several localities in the northern South Island to determine if South Island populations are naturally occurring and the effect of Cook Strait on gene flow. *Cominella virgata* were sampled from north of Cape Rodney to test the distribution or validity of maintenance of discrete subspecies. Although few samples were available, *C. maculosa* from the Chatham Islands were also included to test for cryptic diversity and mainland regional affiliation, and to approximate the age of the Chatham Islands population. The present dataset covers most of the distribution of these two species (Figs 1C, 2C), enabling a wider geographical comparison between populations, as well as comparison with studies of other species with an emphasis on the Cook Strait region.

MATERIAL AND METHODS

Sampling and specimen handling

Samples of *C. maculosa* and *C. virgata* (Table 1; Figs 1B, 2B) were collected by searching the intertidal zone at low tide. Where either species was difficult to find or seemingly absent, mussels were broken and scattered in pools in an attempt to attract whelks out of crevices or sediments. Samples for molecular analyses were preserved in 98% ethanol and stored at the Museum of New Zealand Te Papa Tongarewa (NMNZ) (Table 1). Over 1000 specimens of *C. virgata* were examined from 230 lots at NMNZ (Fig. 2C) to determine the geographical distribution and diversity of morphological forms. Photoshop CS6 (Adobe) was used for image clear-cutting and plate assembly. Place and region names mentioned in the text other than sample sites are shown in Supporting Information, Figure S1.

DNA preparation, sequencing and alignment

Approximately 1 mm^3 of foot tissue was digested at 56 °C for 2 h 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. 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 Tris-HCl pH 8.8, 16 mM $(NH_4)_2SO_4$, 3 mM $MgCl_2$, 0.6 mg/mL bvine srum albumin, 0.1 µM each of forward and reverse primer, 0.4 mM dNTPs, 0.05 U/µL taq polymerase (Biostor) and 50 ng/µL 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 min. 18S thermal cycling conditions followed Donald *et al.* (2015). Resultant PCR products were electrophoresed on agarose gels, stained with ethidium bromide and visualized using UV light. Amplified PCR products were purified using ExoSAP-IT (Amersham Pharmacia Biotech) and their DNA sequence was determined using a 3730xl Genetic Analyser (Applied Biosystems) at Macrogen Inc.

CO1 sequences were trimmed to 610 bp for population genetic analyses to match the Fleming *et al.* (2018) dataset. The DNA sequences reported by Donald *et al.* (2015) were sourced from GenBank (Table 2). For phylogenies, the *CO1*, 16S and 18S sequences were trimmed to 528, 457 and 711 bp, respectively, to match available sequences from GenBank. DNA sequences were aligned using the Geneious (v.8.0.5) (Biomatters Ltd) alignment option (Kearse *et al.*, 2012).

Phylogenetic trees and statistical analyses

16S and 18S sequences were included to resolve subgeneric placement and improve node confidence values in the phylogenies as per Donald *et al.* (2015) and not evaluated individually. Maximum likelihood trees were generated using the PhyML (v.2.2.0) (Guindon & Gascuel, 2003; Guindon *et al.*, 2010) plug-in within Geneious with 500 bootstrap replications. Bayesian trees were generated using the MrBAYES (v.3.2.6) (Huelsenbeck & Ronquist, 2001) plug-in within Geneious with 1 100 000 Markov chain Monte carlo replications, 100 000 of which were discarded as

Table 1. Sample locality data, summary statistics and haplotype information. N = sample size; s = number of segregating sites; h_p = number of private haplotypes; h_n = number of haplotypes; h_d = haplotype diversity (SD = standard deviation); π = nucleotide diversity (SD = standard deviation); k = average number of nucleotide substitutions. Bold text indicates samples originating from this study; others originated from Fleming *et al.* (2018). Each haplotype is identified by a number; '6(20)' for example would refer to 20 sequences of haplotype '6'. '*' denotes haplotypes only detected at one site.

Species (voucher)	Location	Coordinates	N	s	h_p	h_n	h_d (SD)	π (SD)	k	Haplotypes (N)
C. maculosa	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	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	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	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	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), 40(1)*, 41(1)*
C. maculosa	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	Maketu	37°44.00′E, 176°27.00′E	26	5	2	6	0.717 (0.078)	0.0015 (<0.000)	0.914	5(4), 6(13), 18(4)*, 19(2), 20(2), 21(1)*
C. maculosa	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	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	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	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)*
C. maculosa	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)	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	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	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	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	Makara	41°13.00′S, 174°42.00′E	20	0	0	1	–	–	–	1(20)

Table 1. Continued

Species (voucher)	Location	Coordinates	*N*	*s*	h_p	h_n	h_d (SD)	π (SD)	*k*	Haplotypes (*N*)
C. maculosa	Point Howard	41°15.00′S, 174°54.00′E	21	0	0	1	–	–	–	1(21)
C. maculosa	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	Marokopa	38°19.00′S, 174°42.00′E	31	0	1	1	–	–	–	13(31)*
C. maculosa	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)**	**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), 45(1)*, 46(1)***
C. maculosa **(M.302312)**	**Patons Rock**	**40°47.19′S, 172°45.94′E**	**20**	**0**	**0**	**1**	**–**	**–**	**–**	**1(20)**
C. maculosa **(M.321239)**	**Kaiteriteri**	**41°02.10′S, 173°01.42′E**	**20**	**0**	**0**	**1**	**–**	**–**	**–**	**1(20)**
C. maculosa	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), 6(3), 31(2)*, 32(3)*, 33(1)*, 34(1)*
C. maculosa **(M.316880)**	**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), 44(1)***
C. maculosa **(M.106630)**	**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), 43(1)***
C. maculosa **(M.108444)**	**Kaikoura**	**42°24.76′S, 173°41.43′E**	**20**	**0**	**0**	**1**	**–**	**–**	**–**	**1(20)**
C. maculosa **(M.114548)**	**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), 47(1)***
C. maculosa **(M.315669)**	**Waitangi**	**43°56.70′S, 176°33.80′W**	**4**	**1**	**1**	**2**	**0.500 (0.265)**	**0.0008 (<0.001)**	**0.500**	**48(3), 42(1)***
C. maculosa **(M.315642)**	**Owenga**	**44°01.70′S, 176°21.00′W**	**2**	**0**	**0**	**1**	**–**	**–**	**–**	**48(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(3)#, 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(70), 28(66), 29(2)#, 30(6)#, 31(2)#, 32(3)#, 33(1)#, 34(1)#, 35(2)#, 36(2)#, 37(1)#, 38(1)#, 39(2)#, 40(1)#, 41(1)#, 42(1)#, 43(1)#, 44(1)#, 45(1)#, 46(1)#, 47(1)#, 48(5)
C. virgata **(M.100905)**	**Maunganui Bluff**	**35°46.08′S, 173°34.10′E**	**5**	**0**	**0**	**1**	**–**	**–**	**–**	**22(5)**

Table 1. Continued

Species (voucher)	Location	Coordinates	*N*	*s*	h_p	h_n	h_d (SD)	π (SD)	*k*	Haplotypes (*N*)
C. virgata **(M.122735)**	**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)***
C. virgata **(M.166286)**	**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)**	**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)**	**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)**	**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	Mathesons Bay	36°18.00′S, 174°48.00′E	25	0	0	1	–	–	–	4(25)
C. virgata	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	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	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	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	Maketu	37°44.00′S, 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	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	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	Mahia	39°05.00′S, 177°55.00′E	11	0	0	1	–	–	–	19(11)
C. virgata	Pukerua Bay	41°01.00′S, 174°53.00′E	20	0	0	1	–	–	–	1(20)
C. virgata	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	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)**	**Patons Rock**	**40°47.19′S, 172°45.94′E**	**20**	**0**	**0**	**1**	**–**	**–**	**–**	**4(20)**

Table 1. Continued

Species (voucher)	Location	Coordinates	*N*	*s*	h_p	h_n	h_d (SD)	π (SD)	*k*	Haplotypes (*N*)
C. virgata **(321238)**	**Kaiteriteri**	**41°02.10′S, 173°01.42′E**	**20**	**0**	**0**	**1**	–	–	–	**4(20)**
C. virgata	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)**	**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)#

burn-in. Phylogenetic trees were visualized and edited in FigTree (v.1.4.3) (Rambaut & Drummond, 2012) and formatted using Adobe Photoshop.

Diversity indices (Table 1) were calculated using DnaSP (v.5.10) (Librado & Rozas, 2009) and included the number of segregating sites, nucleotide diversity (π), haplotype diversity (h_d) and the average number of nucleotide substitutions between sequences. 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, tau, θ_0 and θ_1 (Tables S1 and S2) were calculated in Arlequin (v.3.5.2.2) (Excoffier & Lischer, 2010) for each sample location.

Median joining haplotype networks were made in PopART (v.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 1A, B, 2A, B, 3). Pairwise genetic differences between sample locations were calculated based on both haplotype frequencies and pairwise genetic differences using the fixation index Φ_{ST} (Tables S3–6) in Arlequin. The analyses were permuted 10 000 times to determine the level of significance.

Populations were assigned a priori to regional groups (Tables 3 and 4) for analyses of molecular variance (AMOVAs). A priori groups (listed in Tables 3 and 4) were selected by considering the haplotype network maps (Figs 1A, 2A) and grouping together sample sites that shared many haplotypes. For *C. maculosa*, the North, South and Chatham Islands were evaluated as discrete groups to test for the effect of island isolation. For *C. virgata*, rather than evaluating the North and South Islands as a priori groups, samples from the Wellington region were included with those from the South Island and contrasted with those from the north-eastern North Island; these represented the two widely separated regional populations (see Fig. 2C). AMOVAs were performed in Arlequin, using both haplotype frequencies and pairwise genetic differences, to estimate the variance components and Φ_{ST} values within and between regions (Tables 3 and 4). Significance was determined using 10 000 permutations.

Abbreviations used in the text

AM – Auckland War Memorial Museum, Auckland, 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, UK; NMNZ – Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand; VUW – Victoria University of Wellington, New Zealand. Unless specified otherwise,

Table 2. Samples used in phylogenetic analyses. Museum voucher- and Genbank accession numbers are given when available. Bold text indicates samples originating from this study; others originated from Donald *et al*. (2015).

Species	ID	Registration	Location	Accession number (*CO1*)	Accession number (16S)	Accession number (18S)
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)**	**7**	**M.315639**	**Owenga, Chatham Islands**	**MH918557**	**MH918576**	**MH918607**
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**	**MH918559**	**MH918577**	**MH918608**
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. 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)**	**28**	**M.315642**	**Owenga, Chatham Islands**	**MH891650**	**MH918578**	**MH918609**
C. mirabilis canturiensis **(Dell, 1951)**	**29**	**M.284022**	**Chatham Rise**	**MH918562**	**MH918579**	**MH918610**
C. mirabilis canturiensis **(Dell, 1951)**	**30**	**M.284022**	**Chatham Rise**	**MH918563**	**MH918580**	**MH918611**
C. mirabilis canturiensis **(Dell, 1951)**	**31**	**M.284016**	**Off Chatham Islands**	**MH918564**	**MH918581**	**MH918612**
C. nassoides **(Reeve, 1846)**	**32**	**M.319324**	**Veryan Bank, Chatham Rise**	**MH918565**	**MH918582**	**MH918613**
C. nassoides **(Reeve, 1846)**	**33**	**M.305586**	**Off Auckland Islands**	**MH918569**	**MH918583**	**MH918614**

Table 2. Continued

Species	ID	Registration	Location	Accession number (*CO1*)	Accession number (16S)	Accession number (18S)
C. nassoides **(Reeve, 1846)**	**34**	**M.305586**	**Off Auckland Islands**	**MH918570**	**MH918584**	**MH918615**
C. nassoides **(Reeve, 1846)**	**35**	**M.315663**	**Owenga, Chatham Islands**	**MH918571**	**MH918585**	**MH918616**
C. nassoides **(Reeve, 1846)**	**36**	**M.315900**	**Okawa Point, Chatham Islands**	**MH918572**	**MH918586**	**MH918617**
C. nassoides **(Reeve, 1846)**	**37**	**M.302874**	**Off Kaikoura**	**MH918573**	**MH918587**	**MH918618**
C. nassoides **(Reeve, 1846)**	**38**	**M.302877**	**Off Kaikoura**	**MH918574**	**MH918588**	**MH918619**
C. nassoides **(Reeve, 1846)**	**39**	**M.305641**	**Off Stewart Island**	**MH918575**	**MH918589**	**MH918620**
C. nassoides **(Reeve, 1846)**	**40**	**M.305583**	**Off Snares Islands**	**MH918566**	**MH918590**	**MH918621**
C. nassoides **(Reeve, 1846)**	**41**	**M.305583**	**Off Snares Islands**	**MH918567**	**MH918591**	**MH918622**
C. nassoides (Reeve, 1846)	42	M.300779	Off Snares Islands	KP694147	KP694098	KP694194
C. nassoides **(Reeve, 1846)**	**43**	**M.321152**	**Ulva Island, Stewart Island**	**MH918568**	**MH918592**	**MH918623**
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**	**MH891624**	**MH918593**	**MH918624**
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**	**MH891626**	**MH918594**	**MH918625**
C. virgata **H. Adams & A. Adams, 1853**	**57**	**M.166286**	**Paua, Parengarenga Harbour**	**MH891627**	**MH918595**	**MH918626**
C. virgata **H. Adams & A. Adams, 1853**	**58**	**M.166286**	**Paua, Parengarenga Harbour**	**MH891628**	**MH918596**	**MH918627**
C. virgata **H. Adams & A. Adams, 1853**	**59**	**M.122735**	**Ahipara**	**MH891624**	**MH918606**	**MH918637**
C. virgata **H. Adams & A. Adams, 1853**	**60**	**M.100890**	**Bland Bay**	**MH891631**	**MH918601**	**MH918632**
C. virgata **H. Adams & A. Adams, 1853**	**61**	**M.100890**	**Bland Bay**	**MF161373**	**MH918602**	**MH918633**
C. virgata **H. Adams & A. Adams, 1853**	**62**	**M.100890**	**Bland Bay**	**MH891632**	**MH918603**	**MH918634**

Table 2. Continued

Species	ID	Registration	Location	Accession number (*CO1*)	Accession number (16S)	Accession number (18S)
***C. virgata* H. Adams & A. Adams, 1853**	**63**	**M.105361**	**McGregors Bay, Whangarei**	**MH891634**	**MH918597**	**MH918628**
***C. virgata* H. Adams & A. Adams, 1853**	**64**	**M.105361**	**McGregors Bay, Whangarei**	**MH891640**	**MH918598**	**MH918629**
***C. virgata* H. Adams & A. Adams, 1853**	**65**	**M.105361**	**McGregors Bay, Whangarei**	**MH891640**	**MH918599**	**MH918630**
***C. virgata* H. Adams & A. Adams, 1853**	**66**	**M.105361**	**McGregors Bay, Whangarei**	**MH891641**	**MG918600**	**MH918631**
***C. virgata* H. Adams & A. Adams, 1853**	**67**	**M.092949**	**Whangaumu Bay, Ngunguru**	**MF161373**	**MH918604**	**MH918635**
***C. virgata* H. Adams & A. Adams, 1853**	**68**	**M.092949**	**Whangaumu Bay, Ngunguru**	**MF161373**	**MH918605**	**MH918636**
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

material examined is at NMNZ (six-digit registration numbers prefixed 'M.').

RESULTS

In total, 126 *CO1* sequences of *C. maculosa* from eight sample localities were added to the dataset reported by Fleming *et al.* (2018) to give a combined dataset of 658 DNA sequences from 30 localities (Table 1). An analysis of the genetic diversity showed there were 47 haplotypes based on 43 segregating sites ($\pi = 0.0057$, SD < 0.001; $h_d = 0.801$, SD = 0.013). Thirty-three haplotypes were private to one locality (Table 1). GenBank accession numbers are: MF161329–MF161369 for haplotypes CM1–CM41 (from Fleming *et al.*, 2018) and MH891644–MH891650 for haplotypes CM42–CM48 (present contribution).

For *C. virgata*, 156 *CO1* sequences from nine new sample sites were added to the dataset of Fleming *et al.* (2018), giving a total of 497 DNA sequences from 22 localities (Table 1). An analysis of that dataset showed there were 41 haplotypes based on 45 segregating sites ($\pi = 0.0073$, SD < 0.001; $h_d = 0.817$, SD = 0.014). Thirty-one haplotypes were private to one locality (Table 1). GenBank accession numbers are: MF161370–MF161390 for haplotypes CV1–CV21 (from Fleming *et al.*, 2018) and MH891624–MH891643 for haplotypes CV22–CV41 (present contribution).

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 consisting of several haplotypes that are one or two mutational steps divergent from a predominant central haplotype (Fig. 1A). Samples from the Chatham Islands form a private sub-group to the 'southern' haplogroup. This sub-group contained one haplotype (CM41; $N = 5$) that is one mutational step from the predominant central haplotype of the 'southern' haplogroup, and a second haplotype (CM42; $N = 1$) two mutational steps divergent (Fig. 1A).

Both haplotypes present in the South Island in *C. virgata* are also present in the North Island. One of these haplotypes (CV1) is represented in the South Island by one sequence from Nelson and in the North Island by one sequence from Hauraki Gulf and many sequences from Wellington (Fig. 2A). The second haplotype (CV4) present in the South Island, represented by 89 of the 90 sequences, also occurs at a high frequency in Hauraki Gulf. Haplotype CV4 forms the centre of a recently expanded ('star-shaped') haplogroup (Fig. 2A)

Table 3. *Cominella maculosa* AMOVA a priori groups and results

		Among groups					Among populations within groups					Within populations				
A priori groups		d.f.	var. comp.	%var.	ϕ_{CT}	*P*-value	d.f.	var. comp.	%var.	ϕ_{SC}	*P*-value	d.f.	var. comp.	%var.	ϕ_{ST}	*P*-value
(Marokopa and Hauraki Gulf to Castle Pt) (New Plymouth, Wellington, South Is and Chatham Is)	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
	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) (New Plymouth, Wellington, South Is except Nelson) (Nelson) (Chatham Is)	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
	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

d.f., degrees of freedom; 'var. comp.', variance components; '%var.', percentage variation; 'hapl. freq.', measured by haplotype frequency; 'gen. diff.', measured by pairwise genetic difference.

Table 4. *Cominella virgata* AMOVA a priori groups and resultsd.f.

		Among groups					Among populations within groups					Within populations				
A priori groups		d.f.	var. comp.	%var.	ϕ_{CT}	*P*-value	d.f.	var. comp.	%var.	ϕ_{SC}	*P*-value	d.f.	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

d.f., degrees of freedom; 'var. comp.', variance components; '%var.', percentage variation; 'hapl. freq.', measured by haplotype frequency; 'gen. diff.', measured by pairwise genetic difference.

that has greater diversity in, and probably originated from, the north-eastern North Island (see below).

Populations of *C. virgata* from the southern North Island form two distinct haplogroups (Fig. 2A), one comprising two private haplotypes (CV2 and CV3), and the other featuring a single haplotype (CV1), represented by many sequences from Wellington and a single sequence from both Hauraki Gulf and Nelson (Fig. 2A).

Comparatively few samples ($N = 5$) were available from Maunganui Bluff (Table 1). Samples of *C. virgata* from Maunganui Bluff and Ahipara form a private haplogroup (Fig. 2A) that comprises a common shared haplotype and another private to Ahipara. Five private haplotypes were present in samples from Paua, in Parengarenga Harbour, forming a private haplogroup (Fig. 2A). The lack of shared haplotypes between many northern populations means that the geographical scale of haplotype transitions cannot be discerned in the region.

With regard to both species, many pairwise genetic differences were statistically significant (Tables S3–S6), probably largely influenced by the presence of many private haplotypes (Table 1; Figs 1A, 2A). Presumably for the same reason, all six AMOVAs proved statistically significant ($P < 0.05$). Given the high number of private alleles, less logical a priori groupings would probably be similarly significant, and as such, the results of the AMOVAs are probably not very informative. 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 dataset of Fleming *et al.* (2018). While most haplogroups are private to a region or have regional affinities, most regions have multiple haplogroups that often do not cluster together (Figs 1A, 2A). Phylogenies recovered the same sub-genus- and species-level clades as Donald *et al.* (2015) (Fig. 3). *Cominella virgata* did not form regionally affiliated clades and the Chatham Islands sequence of *C. maculosa* was sister to South Island sequences, with that from the North Island more distant (Fig. 3).

DISCUSSION

A molecular clock analysis provided by Donald *et al.* (2015: fig. 4) suggested that divergence of *C. virgata* and *C. maculosa* from their sister taxa occurred between 4.8 and 14.9 Mya and 6.2 and 19.1 Mya, respectively, and that their 'northern' and 'southern' clades of *C. virgata* (Donald *et al.*, 2015) diverged sometime in the Pliocene or Pleistocene, between 0.7 and 2.9 Mya. Considering the entire dataset, *C. maculosa* has a less expansive *CO1* haplotype network (Fig. 1A) than *C. virgata* (Fig. 2A), with fewer missing haplotypes, potentially indicating larger population sizes in *C. virgata*. Indeed, *C. virgata* is usually more abundant where the two species co-occur. Unlike *C. virgata*, which was most diverse in northern samples, *C. maculosa* were not sampled from north of Cape Rodney. *Cominella maculosa* and *C. virgata* have broadly similar patterns of phylogeographical structure that are consistent with other species with direct development, but the structure detected differs on a regional scale. Fleming *et al.* (2018) discussed the phylogeographical structure of populations from the Hauraki Gulf to Wellington. Although it is difficult to ascribe causality to observed patterns of genetic structure, regional geography and human movements can potentially explain some of the patterns observed.

Cook Strait geography

During some glacial maxima of the Pleistocene, a land-bridge connecting Whanganui and Golden Bay closed Cook Strait (Fleming, 1979; Proctor & Carter, 1989; Lewis *et al.*, 1994). Between the onset of the Last Glacial Maximum (LGM) roughly 25 kya (Sandiford *et al.*, 2002), and its more gradual end roughly 7 kya (Lambeck *et al.*, 2002), eustatic sea levels dropped to 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 some terrestrial vertebrate taxa across a land-bridge during this period (Worthy & 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).

The shallowest possible connection between the North and South Islands, along Farewell Rise/Egmont Terrace, presently has a maximum depth of between 94 and 100 m (Bowman *et al.*, 1983; Lewis *et al.*, 1994). Admittedly, little is known of the rates of uplift and subsidence on the 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 kya (Proctor & Carter, 1989; Lewis *et al.*, 1994). Such a land-bridge is likely to have comprised mostly low-lying coastal dunes and may have been short lived or ecologically unsuitable for passage of most terrestrial biota (Greaves *et al.*, 2008; O'Neill *et al.*, 2008), such as moa, or rocky-shore species. Several terrestrial species with presumed low dispersal ability show clear evidence of post-Pliocene genetic connectivity between the North and South Islands (O'Neill *et al.*, 2008; Trewick *et al.*, 2011; Trewick & Bland, 2012), although the timing, vectors and scale of the dispersal are unclear.

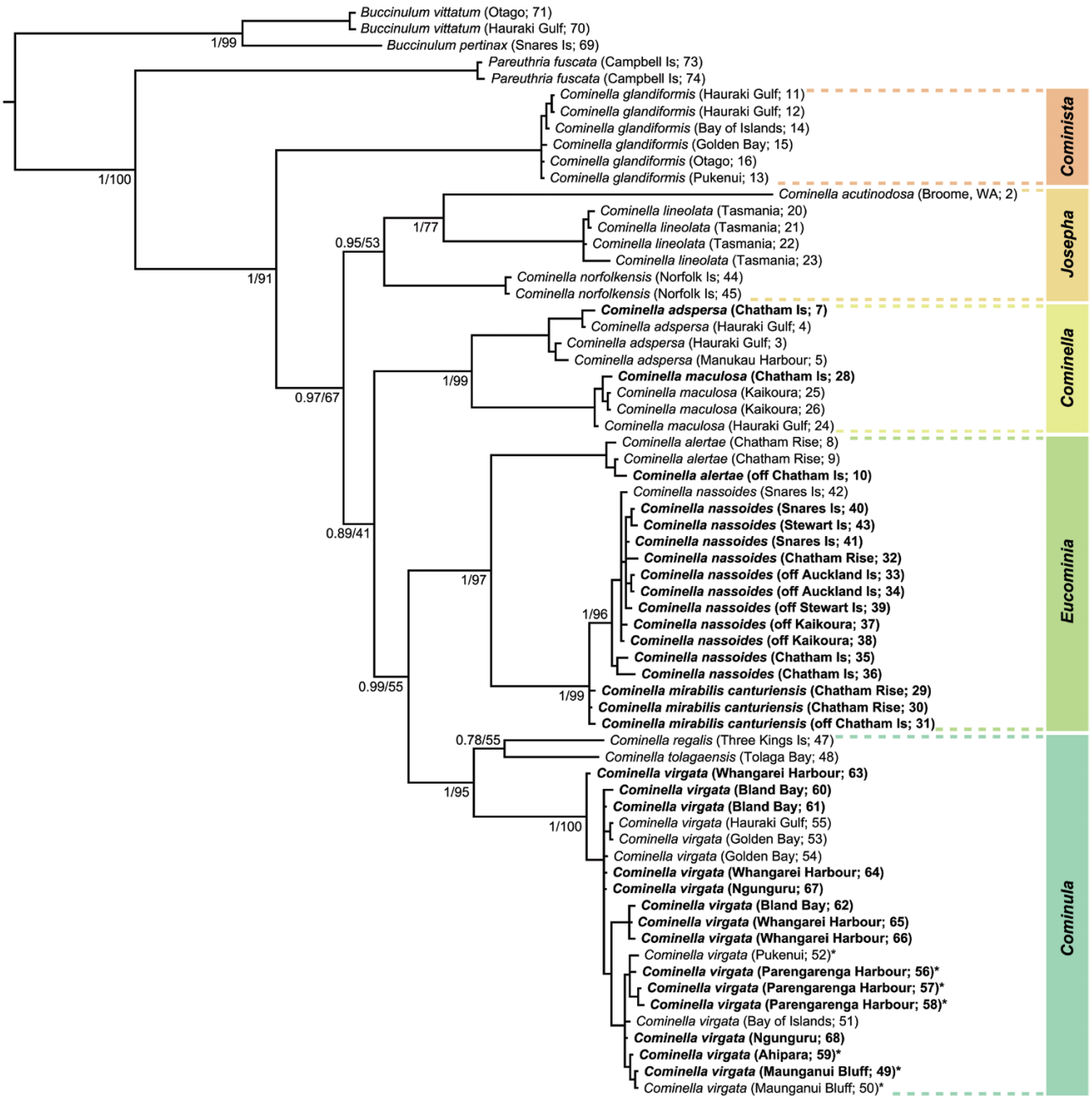

Figure 3. Bayesian phylogenetic tree of concatenated *CO1* (528 bp), 16S (457 bp) and 18S (711 bp) gene sequences from *Cominella* species. Subgenera are indicated by coloured panels. Node labels show Bayesian posterior probabilities (left) and maximum likelihood (ML) consensus bootstrap support percentages (right), the latter from an ML tree with corresponding topologies (Walton 2017). Numbers on sequence labels correspond to those given in Table 2. Bold text indicates samples originating from this study; others originated from Donald *et al.* (2015) that were retrieved from GenBank (Table 2). An asterisk denotes specimens of *C. virgata* of the 'brookesi' shell form.

For most marine species, the emergence of continuous land between the North and South Islands would have severed gene flow between the western and eastern coastlines of central New Zealand. Conversely, for terrestrial or coastal species with little or no long-distance over-water dispersal ability, this closure could have facilitated increased gene flow between the North and South Islands (Fleming, 1979; Liggins *et al.*, 2008; O'Neill *et al.*, 2008; Trewick & Bland, 2012). As direct developers, *C. maculosa* and *C. virgata*

have relatively poor dispersal ability (Fleming *et al.*, 2018; Dohner *et al.*, 2018), although infrequent rafting events could potentially facilitate their natural traversal of Cook Strait in the absence of land-bridges.

Distribution of *Cominella virgata*

The distribution of *C. virgata* comprises two separate 'population centres': one situated in the Cook Strait region and the other in the northern and north-eastern North Island (Fig. 2C). Beu (2012) noted similar distribution patterns for other mollusc taxa, including *Murexul octogonus* (Quoy & Gaimard, 1833) (Marshall & Burch, 2000: fig. 37) and *Roseaplagis rufozona* (A. Adams, 1853) (Marshall, 1998b: fig. 63), 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 cause or causes of these north-eastern/south-western distribution patterns remain to be established. While the ages of the disjunctions are also unclear, most or all are likely to pre-date the LGM as some of these taxa (including *M. octogonus* and *R. rufozona*) have fossil records in the Whanganui coastal section (Fleming, 1953).

In *C. virgata*, the present distribution gap on the west coast between the two population centres falls between Maunganui Bluff and Paekākāriki. This region includes seemingly favourable rocky habitats interspersed between large tracts of unfavourable sandy beach habitat. On the east coast, the distribution gap lies 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 with short stretches of unfavourable sandy beach habitat interspersed throughout. Both the eastern and the western distribution gaps seem unlikely to be sampling artefacts. Extensive searches in seemingly suitable habitat yielded no *C. virgata* between Napier and Palliser Bay, or near Hāwera, New Plymouth, Raglan or Port Waikato (all localities where *C. maculosa* occurs). *Cominella virgata* as well as *M. octogonus* and *R. rufozona* were all notably omitted from published records of the west coast fauna of the central North Island (Morley *et al.*, 1997; Hayward *et al.*, 1999, 2002), except for a 'dubious' record of *C. virgata* from off Ngā Motu in New Plymouth (Hayward & Morley, 2002: 3).

Cook Strait populations of *Cominella virgata*

Low *CO1* diversity and a lack of private haplotypes in South Island populations of *C. virgata* suggest recent population size and/or range expansion, probably resulting from translocation events. One of the two haplotypes present (CV1) in the South Island was represented by a single sequence from Nelson (out of 30). Additionally, CV1 was detected at high frequency in Wellington and at low frequency in Hauraki Gulf. Cook Strait does not seem to have presented an impermeable barrier to the natural dispersal of *C. maculosa* (see below), the dispersal potential of which is presumably similar to that of *C. virgata*. However, the absence of CV1 in geographically intermediate Picton samples of *C. virgata* and the high historical and contemporary volume of shipping traffic between Wellington and Nelson make translocation the most likely explanation for the presence of CV1 in Nelson. Not using additional markers to evaluate patterns of phylogeographical structure was a limitation of this study. As such, it was often not possible to confidently determine the effect or presence of translocated lineages.

The highest frequency haplotype in the South Island (CV4), comprising the remaining 89 (of 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 1; Fig. 2A). CV4 forms the centre-point of a recently diversified ('star-shaped') haplogroup featuring several haplotypes that are divergent by one mutational step from CV4. All of the one-step divergent haplotypes are from north-eastern North Island samples, suggesting that this haplogroup has had a longer presence and probable origin in 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 the north-eastern North Island and Wellington, accounting for both haplotypes present.

The timing of the proposed translocation events and the subsequent rate of range expansion in the South Island are unknown. By the mid 1960s, *C. virgata* was well established in the Marlborough Sounds (M.278694), Tasman Bay (M.023105) and Golden Bay (M.278701). The lack of earlier records may be a sampling artefact, but it is impossible to tell this from museum collections. Explanation for the failure of *C. virgata* to spread further south, where there is seemingly suitable habitat on both the western and the eastern coastlines, remains to be established. It may simply be a matter of time.

It is unclear from the presently available data if populations of *C. virgata* in the Wellington region are naturally occurring or if they originated from human-mediated translocations from northern populations. The earliest Wellington records date from 1953 (M.005888), neither supporting nor contradicting either contention (not recorded by Iredale &

Mestayer, 1908). Two of the three haplotypes present in Wellington (CV2, $N = 4$ and CV3, $N = 6$) form a haplogroup private to Wellington (Fig. 2A). The third haplotype (CV1) clusters on its own and occurs at the highest frequency (60 out of 70 sequences from Wellington) of the three (Fig. 2A; Table 1). In addition to samples from Wellington, CV1 is represented by a single sequence from Hauraki Gulf (out of 98 Hauraki Gulf sequences) and another from Nelson (out of 30 Nelson sequences, see above); both of the latter occurrences probably resulted from translocated lineages as all three locations constitute major ports.

Had the Wellington populations originated through translocation events, several haplotypes otherwise undetected by the present sampling must have been translocated. Wellington haplotypes cluster distant from haplogroups containing sequences from the northern population centre (Fig. 2A). The presence of multiple private haplotypes suggests that Wellington populations may be naturally occurring. However, there are few haplotypes divergent by a single mutational step in Wellington samples, which may indicate a recent bottleneck and/or founder effect and divergence from a lineage that is no longer present, or occurring at low frequency elsewhere.

Cook Strait populations of *Cominella maculosa*

In the Cook Strait region, *C. maculosa* and *C. virgata* have very different patterns of genetic structure. *Cominella maculosa* has nine haplotypes private to the South Island and shares a high-frequency haplotype (CM1) with populations from the southern North Island (Fig. 1A), indicating a natural occurrence on either side of Cook Strait. A second haplotype (CM6) is shared between the North and South Islands. CM6 was detected only from Nelson in the South Island but occurs at high frequency in the north-eastern North Island and forms the centre of a primarily 'northern' haplogroup. It is unclear if the presence of CM6 in Nelson is natural or the result of translocations as in *C. virgata* (see above). Nelson samples of *C. maculosa* were considerably more diverse ($h_d = 0.61$) than any other sampled South Island locality (Table 1). Four haplotypes were unique to Nelson in our sampling, two of which are divergent by two mutational steps from any other sampled haplotype and one of these (CM32, $N = 3$) clustered roughly with the primarily 'northern' haplogroup (Fig. 1A).

Excluding Nelson (see above), all haplotypes sampled 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 (Fig. 1A). These 'southern' populations have far less diversity than populations from further north (Fig. 1A), potentially resulting from smaller historical population sizes and/or shorter regional occupancy times. Low genetic diversity in southern regions may reflect southward range expansion by isotherm tracking following the LGM (Fraser *et al.*, 2012a), which would be characterized by both population size expansion and founder events (Fraser *et al.*, 2012a; Waters *et al.*, 2013), leading to low diversity. Isotherm tracking has been reported for several New Zealand molluscs, including the congener *C.* (*Eucominia*) *nassoides* (Reeve, 1846) (K.W. & B.A.M., unpubl. data), the scallop *Zygochlamys delicatula* (Hutton, 1873) (Beu, 1969, 1999; Beu & Maxwell, 1990; Dijkstra & Marshall, 2008) and the trochoid gastropod *Maurea blacki* (Powell, 1950) (Marshall, 1995). 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 relatively poor dispersal ability of *C. maculosa*, blocking effects could maintain low levels of genetic diversity in southern populations (Fleming *et al.*, 2018).

As with *C. maculosa* and *C. virgata*, amphipod species of the genus *Paracorophium* Stebbing, 1899 (Stevens & 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 markedly different patterns of genetic structure. Phylogeographical breaks have been identified in the Cook Strait region for a range of taxa, although break locations are poorly constrained and vary considerably from species to species (Ross *et al.*, 2009; Gardner *et al.*, 2010). Very few marine taxa have a North Island/South Island break as in *C. virgata*, but, as discussed above, this example probably results from human-mediated translocation events. Where a north/south genetic split is identified (as per: Apte & Gardner, 2002; Apte *et al.*, 2003; Star *et al.*, 2003; Waters & Roy, 2004; Ayers & Waters, 2005; Goldstien *et al.*, 2006; Veale & Lavery, 2011; Ross *et al.* 2012; Wei *et al.*, 2013a, b), the so-called 'northern group' usually includes populations from the northern South Island.

Phylogeographical breaks have been recorded or implied for several taxa near or to the south of Te Hapu in the north-western South Island (Apte & Gardner, 2002; Waters & Roy, 2004; Ayers & Waters, 2005; Ross *et al.* 2012; Wei *et al.*, 2013a, b). Te Hapu is the southernmost west-coast site sampled for *C. maculosa* (Table 1) and not far north of the southernmost recorded west-coast locality, Cape Foulwind (Fig. 1C). There are no obvious geographical or hydrological features immediately to the south of Te Hapu that appear likely to cause phylogeographical disjunction in *C. maculosa*.

Refugia during glacial maxima may have been located to the north of Wellington if sea temperatures in the Cook Strait region were too low for *C. maculosa* or *C. virgata*, at least on open coasts rather than in harbours. Different refugial populations could have founded the various mitochondrial DNA (mtDNA) lineages of *C. virgata* in Wellington. In *C. maculosa*, the phylogeographical break between Marokopa and New Plymouth (Fleming *et al.*, 2018; Fig. 1A) and relative homogeneity of populations to the south suggest a possible refugium near New Plymouth. The cause(s) of a phylogeographical break in *C. maculosa* between Castle Point and Cape Palliser (Dohner *et al.*, 2018; Fleming *et al.*, 2018; Fig. 1A) are unclear but it seems unlikely that they reflect prevailing conditions in Cook Strait or along the Wairarapa Coast. This presumably relictual break may result from the confluence of two lineages spreading southwards along the western and eastern coastlines during the period of warming following the LGM. The patterns of a phylogenetic break that can be detected using mtDNA markers may take considerable time to disestablish through admixture due to high-density blocking effects (Waters, 2011; Waters *et al.*, 2013), so the historical causes of a break might not reflect contemporary geography or ocean conditions. The Cook Strait region occupies almost the central third of mainland New Zealand, extending far to the west of 'the Narrows', which are often incorrectly treated as directly synonymous with Cook Strait (Lewis *et al.*, 1994). To refer to a 'Cook Strait phylogeographical break' without qualification is to some degree misleading (Goldstien *et al.*, 2006; Ross *et al.*, 2009; Walton, 2017). Without considering evidence from multiple taxa and a wide range of markers, deducing historical drivers of patterns in genetic structure remains conjecture at best.

As eustatic sea levels rose following the LGM, the New Zealand coastline advanced many tens of kilometres inland to its present location. This introgression would have been most pronounced along the western North Island where the continental shelf extends far out to sea. The rate of sea-level rise during this period remains unclear. Without continuous suitable habitat during this transition, and on a relatively fine geographical scale, many populations of obligate rocky-shore species with poor dispersal ability, such as *C. maculosa* and *C. virgata*, may have become isolated or extirpated.

The Chatham Islands

Situated roughly 700 km east of the New Zealand mainland, the Chatham Islands straddle the Subtropical Convergence, along which relatively warm temperate water and cool subantarctic water flow eastwards along the Chatham Rise (Chiswell, 1994; Marshall & Walton, 2015). This confluence results in a productive local marine fauna (Bradford, 1983) comprising species with affinities to the northern North Island and others with affinities to the southern South Island (Finlay, 1928; Dell, 1960; Craw, 1988, 1989; Marshall & Walton, 2015). Despite the Chatham Islands having been isolated from the mainland for at least tens of millions of years (Campbell *et al.*, 1993; Emberson, 1995; Trewick, 2000) and by several hundred kilometres of ocean deeper than 200 m, the region has remarkably 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 & Walton, 2015; K.W. & B.A.M., unpubl. data) has suggested that no more than ten named marine mollusc species or subspecies are truly unique to the Chatham Islands. The Chatham Islands are considered to have become fully emergent in about the middle Pliocene following a period of submergence (Campbell *et al.*, 1993; Campbell, 1998; Stevens & Hogg, 2004), so the terrestrial and coastal marine faunas comprise relatively recent arrivals dispersed from the mainland (Trewick, 2000).

In *C. maculosa*, two haplotypes (CM41, $N = 5$ and CM42, $N = 1$), a divergent from one another by a single mutational step, were detected in the few ($N = 6$) Chatham Islands samples available (Table 1), and both are detected only at the Chatham Islands. The higher frequency Chatham Islands haplotype was divergent by a single mutational step from the high-frequency haplotype forming the centre of the 'southern' haplogroup, which was detected through the southern North Island and northern South Island (Fig. 1A; Table 1), suggesting a relatively recent but natural divergence of Chatham Islands populations from 'southern' populations.

Northern populations of *Cominella virgata*

Northland populations of *C. virgata* had particularly high genetic and morphological diversity and fine-scale regional structure (Figs 2A, 4). Throughout its distribution, the shell of *C. virgata* has a sculpture of commarginal axial costae, strongest at the edge of the subsutural concavity, becoming evanescent near the abapical third of the base and often obsolete on later teleoconch whorls. Although normally restricted to hard substrate environments, *C. virgata* inhabits mudflats in Parengarenga and Houhora Harbours. Specimens from these localities have larger and more persistent axial costae and a broader shoulder (Fig. 4D) than specimens from adjacent open coasts and the rest of New Zealand, perhaps local adaptations to reduce

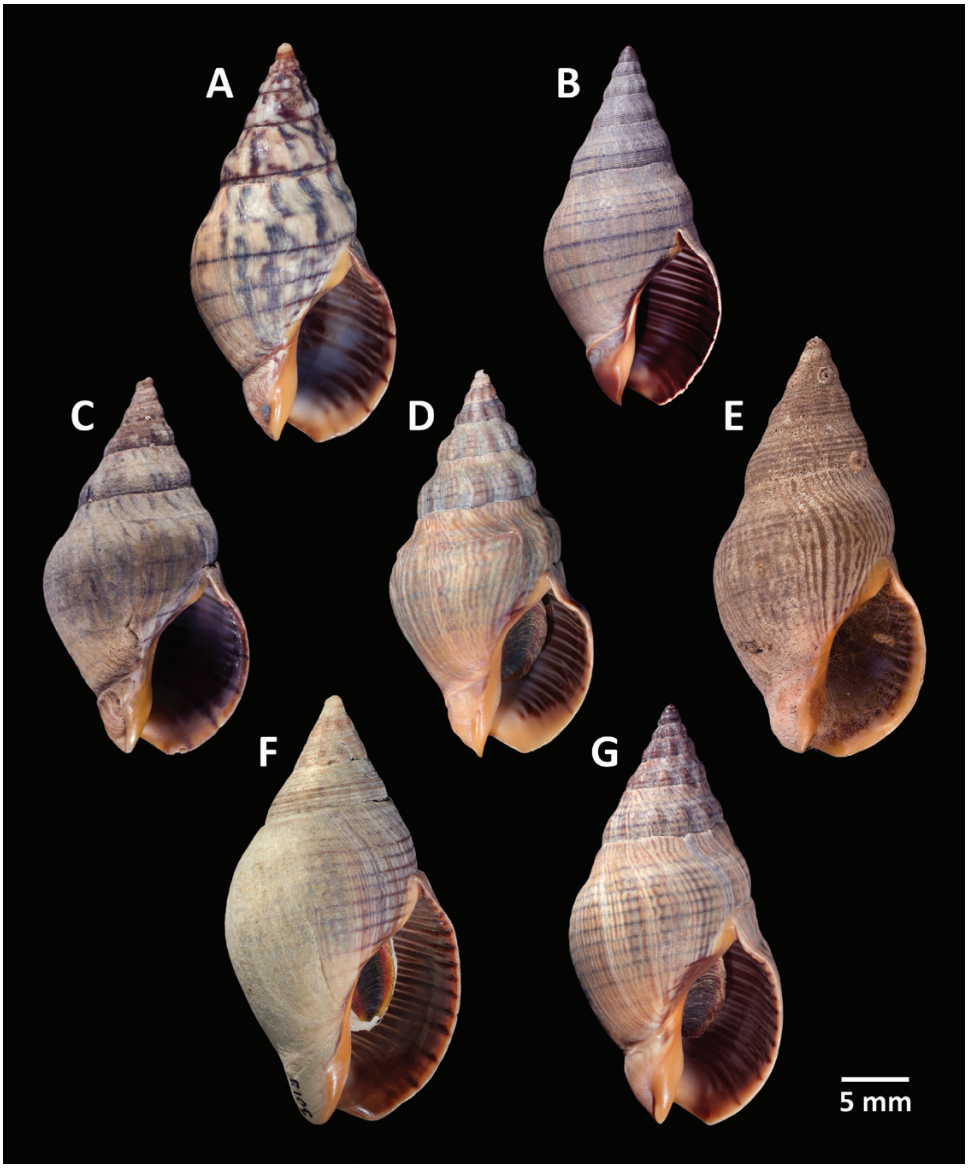

Figure 4. Type specimens and morphological variations of *Cominella virgata* to scale. A, Pink Beach, Leigh, M.090919. B, Waihau Bay, Raukumara Peninsula, M.321237. C, Bay of Islands, lectotype (here designated) of both *Buccinum lineolatum* Quoy & Gaimard, 1833 and *C. virgata* H. Adams & A. Adams, 1853, MNHN-IM-2000-6968. D, Te Hapua, Parengarenga Harbour, M.278721. E, Whatuwhiwhi, Karikari Peninsula, holotype of *C. virgata brookesi* Powell, 1952, AM MA.71191. F, The Bluff, Ninety Mile Beach, M.278743. G) Reef Point, Ahipara, M.278752.

sinking in mud (Thayer, 1975). Five private haplotypes were detected in Parengarenga Harbour samples, forming a private haplogroup, itself forming part of an even larger haplogroup that includes all samples from the west coast of Northland, some samples from the east coast of Northland and, more distantly related, several samples from Wellington (Fig. 2A).

Specimens from and north of Maunganui Bluff on the west coast and north of the Bay of Islands on the east coast (Fig. 4D–G) generally have more numerous (eight or more) and crowded spiral chords, as well as a colour pattern of crowded, narrow, flexuous, axial flammules (Powell, 1952), rather than the broad and highly irregular lines or blotches characteristic of southern populations (Fig. 4A–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 along the west coast of Northland

(Fig. 4F, G). Apart from the presence of narrow axial colour bands, the holotype of *C. v. brookesi* (Fig. 4E) is indistinguishable from *C. v. virgata* (type locality: 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 unambiguously of the nominal form.

The phylogenies reported by Donald *et al.* (2015) recovered two clades within *C. virgata*. Donald *et al.* (2015) interpreted the 'northern' clade, comprising specimens from Pukenui (*c.* 25 km from Whatuwhiwhi), Maunganui Bluff, Bay of Islands and Taupiri Bay, as conforming to the subspecies *C. v. brookesi*. The 'southern' clade, comprising specimens from Waitemata Harbour and Golden Bay, was treated as *C. v. 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 of the nominal form. That from the Bay of Islands could be argued to be a topotype, although 'Bay of Islands' is a broad locality descriptor.

The expanded phylogeny (Fig. 3) did recover the two clades within *C. virgata* reported by Donald *et al.* (2015), but which were obscured by numerous additional clades. None appears to warrant any formal taxonomic distinction. Neither the Northland forms nor typical *C. virgata* formed monophyletic clades (Figs 2A, 3).

Considering only the *CO1* data (Fig. 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 haplotypes from other regions. In addition, the various shell forms of *C. virgata* from throughout its distribution, including the holotype of *C. v. brookesi* and the type series of *C. v. virgata* (see below), intergrade fluidly, and therefore continued recognition of separate subspecies is unjustified. The name '*brookesi*' is here interpreted as a form of *C. virgata* rather than a subspecies, describing specimens with more than eight dark spiral threads as well as relatively narrow and crowded axial flammules. It is known only from north of the Bay of Islands, but the nominal shell forms and intermediate forms 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. 4A–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. **Syn. nov**.

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 MA.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. 4C) 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, Walton, 2017).

H. Adams and A. Adams (1853–1854) 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 that of Quoy and Gaimard (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).

ACKNOWLEDGEMENTS

We are grateful to the many people who contributed towards the manuscript, notably: Jean-Claude Stahl (NMNZ) for imaging of specimens; Bruce Hayward (Geomarine Sciences) for comments on Auckland Isthmus geography; Wilma Blom and Severine Hannam (AM) for images of the holotype of *Cominella virgata brookesi*; Virginie Héros (MNHN), Emmanuel Tardy (MHNG) and Andreia Salvador (NHMUK) for comments on, and assistance locating, type material; Cécile Massiot (GNS Science) for translation of French texts, Melanie Dohner and Angela Fleming (VUW) for assistance with lab techniques and making available their data, and Sebastian Logan (VUW) for sequences of *C. adspersa* and *C. glandiformis*; and Meredith Buchholz (Dunedin), Kevin Burch (Whangarei), Kathy Carson (Christchurch), Pete Cresswell (Motueka),

Derrick Crosby (Whakatane), Kevin and Yvonne Mead (Nelson), Jason Plaisted (Wellington), Marc Sykes (Wellington) and Mike Young (Motueka) for assistance with sample collection. The image of the lectotype of *Buccinum lineolatum* Quoy & Gaimard, 1833 was taken by M. Cabeller (MNHN) as part of project E-RECOLNAT (ANR-11-INBS-0004). We greatly appreciated feedback from three anonymous reviewers and the editor which improved the manuscript.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Table S1. *Cominella maculosa* additional statistics and neutrality tests.
Table S2. *Cominella virgata* additional statistics and neutrality tests.
Table S3. *Cominella maculosa* sample site pairwise differences calculated using genetic distance (below) and associated *P*-values (above). BBO = Bowentown; WCP = Cape Palliser; CHM = Purau, Christchurch; CIO = Owenga, Chatham Islands; CIW = Waitangi, Chatham Islands; KKM = Kaikoura; KTM = Kaiteriteri; MBM = Marfells Beach; PBM = Picton Beach; PRM = Patons Rock; WCM = Te Hapu; WPH = Point Howard; WMA = Makara; AAB = Army Bay; ARB = Red Beach; ASB = Snells Beach; TNP = New Plymouth; TMA = Marokopa; BMM = Mount Mounganui; BMA = Maketu; BOM = Omaio; GTA = Te Araroa; GTT = Tatapouri; WCS = Castle Point; NEL = Nelson; WMP = Moa Point; AMB = Mathesons Bay; GMA = Mahia Peninsula; GPA = Napier; GPB = Purere Beach; GWB = Whangaehu Beach.
Table S4. *Cominella maculosa* sample site pairwise differences calculated using haplotype frequencies (below) and associated *P*-values (above). BBO = Bowentown; WCP = Cape Palliser; CHM = Purau, Christchurch; CIO = Owenga, Chatham Islands; CIW = Waitangi, Chatham Islands; KKM = Kaikoura; KTM = Kaiteriteri; MBM = Marfells Beach; PBM = Picton Beach; PRM = Patons Rock; WCM = Te Hapu; WPH = Point Howard; WMA = Makara; AAB = Army Bay; ARB = Red Beach; ASB = Snells Beach; TNP = New Plymouth; TMA = Marokopa; BMM = Mount Mounganui; BMA = Maketu; BOM = Omaio; GTA = Te Araroa; GTT = Tatapouri; WCS = Castle Point; NEL = Nelson; WMP = Moa Point; AMB = Mathesons Bay; GMA = Mahia Peninsula; GPA = Napier; GPB = Purere Beach; GWB = Whangaehu Beach.
Table S5. *Cominella virgata* sample site pairwise differences calculated using genetic distance (below) and associated *P*-values (above). AHV = Ahipara; BBV = Bland Bay; KTV = Kaiteriteri; MAV = Maunganui Bluff; MGV = McGregors Bay; NGV = Ngunguru; PAV = Paua, Parengarenga Harbour; PBV = Picton Beach; PRV = Patons Rock; WPB = Pukerua Bay; WPH = Point Howard; WMP = Moa Point; AMB = Mathesons Bay; AAB = Army Bay; ARB = Red Beach; ASB = Snells Beach; BMM = Mount Mounganui; BMA = Maketu; BOM = Omaio; GTA = Te Araroa; NEL = Nelson; GMA = Mahia Peninsula.
Table S6. *Cominella virgata* sample site pairwise differences calculated using haplotype frequencies (below) and associated *P*-values (above). AHV = Ahipara; BBV = Bland Bay; KTV = Kaiteriteri; MAV = Maunganui Bluff; MGV = McGregors Bay; NGV = Ngunguru; PAV = Paua, Parengarenga Harbour; PBV = Picton Beach; PRV = Patons Rock; WPB = Pukerua Bay; WPH = Point Howard; WMP = Moa Point; AMB = Mathesons Bay; AAB = Army Bay; ARB = Red Beach; ASB = Snells Beach; BMM = Mount Mounganui; BMA = Maketu; BOM = Omaio; GTA = Te Araroa; NEL = Nelson; GMA = Mahia Peninsula.