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RESEARCH ARTICLE

Phylogeographic structure and historical demography of tarakihi (*Nemadactylus macropterus*) and king tarakihi (*Nemadactylus* n.sp.) in New Zealand

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ABSTRACT

Tarakihi (*Nemadactylus macropterus*) is a demersal fish that supports valuable commercial, recreational, and customary fisheries in New Zealand. However, little is known about its stock structure. The population genetic structure, genetic diversity, and demographic history of *N. macropterus* were investigated using the hypervariable region one of the mitochondrial control region. 370 samples from 14 locations around New Zealand were collected. While weak genetic breaks were detected between Hawke's Bay and East Northland and between the west and east coasts of South Island, no clear genetic structure was detected for the overall New Zealand area ($\Phi_{ST} = 0.002$, $P = 0.18$), indicative of a panmictic genetic structure. *N. macropterus* display a high level of genetic diversity and appear to have a historically large and stable population with a long evolutionary history. Bayesian skyline analysis indicates that the historic population has gone through two expansions, likely caused by repeated glacial cycles during the second half of the Pleistocene. The addition of 15 king tarakihi samples (*Nemadactylus* n.sp.) collected from the Three Kings Islands showed a clear genetic differentiation between the two morphotypes. These findings can inform the future management of *N. macropterus* and *N.* n.sp. to ensure a sustainable harvest.

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Introduction

Understanding the patterns of connectivity and stock boundaries of a commercial fishery is essential for effective management. Catch levels are usually set for each stock to limit fishing-induced mortality to a sustainable level (Beddington et al. 2007). The success of this regulatory tool depends on the accuracy of a stock assessment model, which in turn requires a clear definition of biological stocks boundaries (Begg et al. 1999; Waples et al.

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2008; Cadrin et al. 2014). A mismatch between the assessment/management area and the size and boundaries of biological stocks can lead to unintentional overfishing and risk collapsing a fishery (Laikre et al. 2005; Reiss et al. 2009; Cadrin 2020). The ability to properly align management areas to natural reproductive units and combine it with knowledge of the degrees of recruitment and genetic diversity is a central goal for ensuring stock resilience and maximising spawning potential. Clearly defining the patterns of genetic diversity among stocks can also prevent the adverse effects of a reduction in population size or disrupting gene flow that may cause stronger genetic drift and the potential to reduce genetic diversity (Hauser et al. 2002; Pinsky and Palumbi 2014). Loss of diversity would make a stock less adaptable (i.e. more vulnerable to environmental changes and disease outbreaks) and potentially expose it to the risk of inbreeding depression (Carvalho and Hauser 1994; Laikre et al. 2005).

While a variety of approaches have been used in an effort to identify stock boundaries, DNA-based approaches have the potential to greatly assist fisheries management (Waples et al. 2008; Ovenden et al. 2015; Papa et al. 2021) by identifying stock structure, estimating degrees of connectivity, and detecting reductions in effective population size (Ovenden et al. 2016). Since mitochondrial DNA (mtDNA) is haploid and usually considered to be maternally inherited, it should have a smaller effective population size compared to nuclear DNA, which is diploid and inherited by both parents. This and the lack of recombination makes it more sensitive to changes in the effective population size and potentially more suited to detect population subdivisions than a nuclear DNA marker (Birky et al. 1989; Harrison 1989; Brown 2008). The non-coding control region is a region of mtDNA that mutates at a relatively fast rate (Lee et al. 1995). It has been shown to be well suited to detect genetic structure in marine fishes (Aboim et al. 2005; Clarke et al. 2015), including in New Zealand species (Smith and Paulin 2003; Lévy-Hartmann et al. 2011; Smith 2012).

Tarakihi (*Nemadactylus macropterus* (Forster 1801)) is a demersal marine fish belonging to the Latridae (Kimura et al. 2018; Ludt et al. 2019; Fricke et al. 2020). The species is widely distributed throughout inshore areas of New Zealand (Figure 1), from the Three Kings Islands in the north to the Snare Islands in the south and the Chatham Islands in the east (Annala 1987; Roberts et al. 2015). It also occurs around the south of Australia and Tasmania (Roberts et al. 2015) where it is commonly known as jackass morwong. It is relatively long-lived (>30 years), has a pelagic larval duration of approximately 10 months, and the potential to disperse over large distances (Annala 1987). The adults are broadcast spawners that form serial spawning aggregations during summer and autumn (Tong and Vooren 1972). *Nemadactylus macropterus* is a valuable fishery species in New Zealand, with annual commercial landings approximating 5000–6000 tonnes for the past 30 years, mainly using bottom trawling (Fisheries New Zealand 2018). While *N. macropterus* are commercially caught in all non-protected Quota Management Areas of New Zealand Exclusive Economic Zone, 80% of the catches occur off the east coast of the North and South Islands (Langley 2018).

A similar but distinct morph of *N. macropterus*, commonly known as 'king tarakihi' (*Nemadactylus* n.sp. *sensu* Roberts et al. (2020), formerly designated as *Nemadactylus rex* (Roberts et al. 2015)), is caught in the northern parts of the *N. macropterus* range in New Zealand and also occurs in Australia (Roberts et al. 2015; Langley 2018). However, due to the difficulty of identification on the field, fishers are not required to

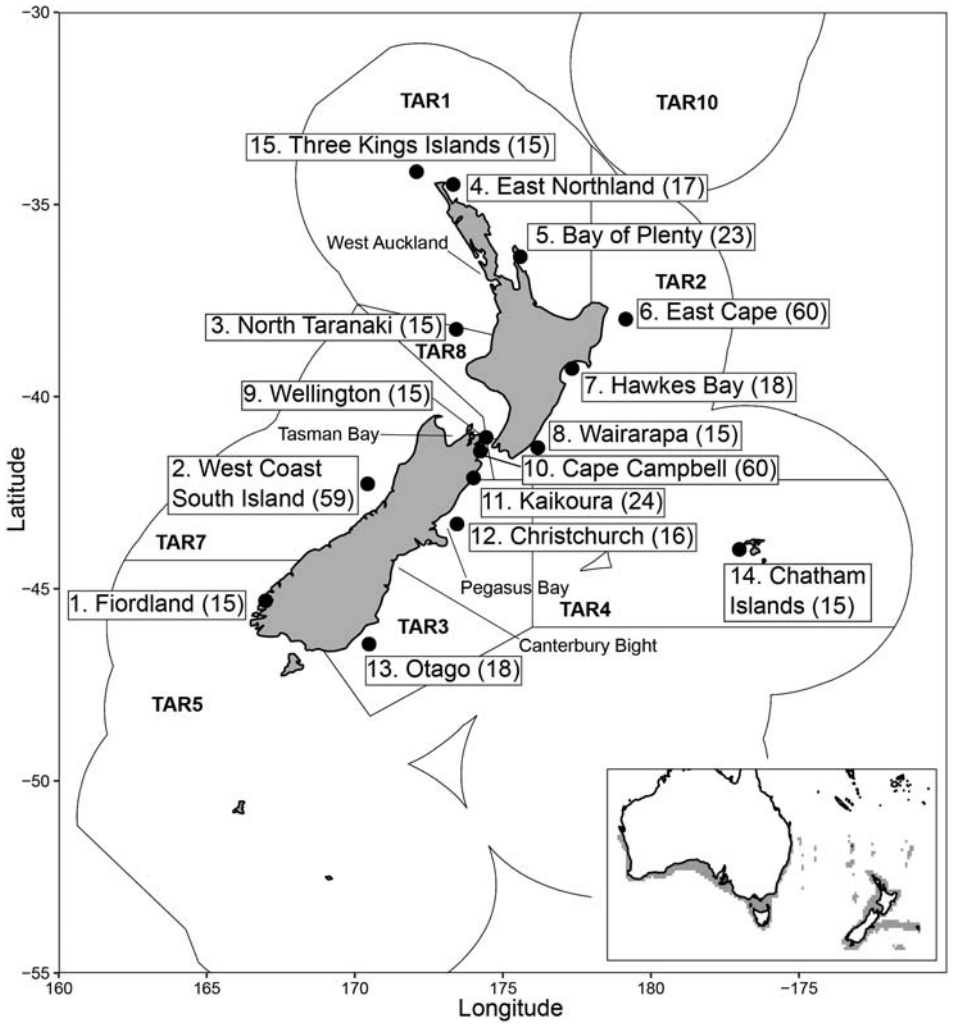

Figure 1. Map of New Zealand showing the 14 sample locations of *Nemadactylus macropterus* and the sample location of *Nemadactylus* n.sp. (Three Kings Islands) in black dots (mean coordinates between start and stop trawls, or approximated to the location midpoint when not provided). Total number of samples collected per location in parentheses. The grey lines correspond to the boundaries of the New Zealand Exclusive Economic Zone (EEZ) and the quota management areas for tarakihi (TAR 1–5, 7–8, 10). Lower right map shows the range of *N. macropterus* in grey area (distribution data from Kaschner et al. (2019)). Plotted with R packages ggplot2 3.3.2 (Wickham 2009), maps 3.3.0 (Becker et al. 2018), and rgdal 1.5.16 (Bivand et al. 2019).

differentiate it from *N. macropterus* when reporting their catches. It is thought to only represent a minor part (20–30 tonnes per annum) of the *N. macropterus* reported catches from the TAR 1 (Figure 1) area (Langley 2018). Previous studies have constantly found a clear genetic differentiation between *N. macropterus* and *N.* n.sp. by using allozymes, random amplified polymorphic DNA, and various mitochondrial DNA markers (Smith et al. 1996; Burridge 1999; Smith et al. 2008). However, *N.* n.sp. have yet to be formally recognised as a species within *Nemadactylus* (Roberts et al. 2020).

Very little is known about the stock structure and connectivity of *N. macropterus* within New Zealand. The North and South Islands are usually considered to be a single population, with the Chatham Islands considered a separate stock due to its geographic isolation and water depth (Morrison et al. 2014; Fisheries New Zealand 2018). Estimates of population connectivity of *N. macropterus* in New Zealand have mainly been derived from catch data provided by fishing vessels and stock assessment surveys (i.e. trends in catch per unit effort indices and age compositions) with a main focus on the east coast area, as well as from a few tagging studies. Relatively recent data analyses showed trends in age and size structure that supported a hypothesis of the Canterbury Bight/Pegasus Bay area on the east of South Island (Figure 1) as the main nursery area for the entire eastern stock, with a northward migration of some of the adult fish along the east coast up to the east Northland area (Langley 2018). Less is known about the connectivity with and within the west coast fishery. Differences in growth rates between east and west Northland may indicate a lack of connectivity between coasts (Langley 2018). However, *N. macropterus* tagged in the Kaikoura area on the east coast of South Island have been recaptured on the west coast of North Island (Hanchet and Field 2001). The number and spatial extent of reproductively distinct groups is a major source of uncertainty in the management of New Zealand *N. macropterus* fisheries (McKenzie et al. 2017).

The only genetic study that has investigated the population structure of *N. macropterus* within New Zealand used the allele frequency of one allozyme from c. 3000 samples collected around the two main islands (Gauldie and Johnston 1980). This study detected some significant population structure based on Z-statistics, with eight geographical stock boundaries proposed between East Northland and East Cape (two), Otago and Solander Islands (two), the lower and the upper parts of the west coast of South Island, the Tasman Bay and Wellington/Cape Campbell, Taranaki and West Auckland, and between West Auckland and the upper west coast of North Island (Figure 1). However, a negative correlation of allele frequency with temperature was also detected, and the geographic variation was no significantly different from the yearly variation observed at one sampling station. The authors could not firmly conclude that the genetic structure observed was due to neutral, adaptive, or temporal genetic variation (see Discussion). Other population genetic studies of *N. macropterus* were based on samples from locations in Australia and included only one location from New Zealand. These studies used enzyme variation (Elliott and Ward 1994), mtDNA restriction fragment length polymorphism (Grewe et al. 1994), and microsatellite DNA markers (Burridge and Smolenski 2003). While none of these detected any significant genetic structure among Australian stocks, the two first studies found a weak but significant genetic disjunction between Australia and New Zealand (Elliott and Ward 1994; Grewe et al. 1994). However, the most recent study did not detect that same genetic separation across the Tasman Sea (Burridge and Smolenski 2003).

In this study, a 500 bp DNA sequence of the hypervariable region 1 (HVR1) in the mitochondrial control region was used to (1) investigate the genetic structure and demographic history of New Zealand *N. macropterus* populations, (2) estimate genetic diversity and historic demography of *N.* n.sp. (king tarakihi), and (3) determine the degree of genetic difference between *N. macropterus* and *N.* n.sp.

Material and methods

Samples and DNA extraction

Samples from 370 adult *N. macropterus* were collected from 14 geographic areas around New Zealand and near the Chatham Islands (Figure 1, Table S1) between October 2017 and April 2018. Samples were purchased from commercial fishing companies (whose associated trawlers in some cases conducted specific tows targeting fish for this study) and Fiordland samples were provided by recreational fishers on charter boats. Three of these areas, known to be important spawning locations (West Coast South Island, Cape Campbell, and East Cape), were sampled during the spawning season (April 2018) to target spawning aggregations. These may be composed of fish from different regions. Additionally, 15 *N.* n.sp. specimens (king tarakihi morphotypes) were collected from the Three Kings Islands by trawling as well. Two sections of muscle tissue were sampled from the tail and stored at −20°C in 99% ethanol. All fish were measured for fork length and weighed. Total genomic DNA was extracted using a Rapid Salt-extraction protocol adapted from Aljanabi and Martinez (1997) and suspended in Tris-EDTA buffer (10 mM Tris-HCl pH 8.0, 1 mM EDTA). Fish were processed for sampling after commercial or recreational harvest, and in any other cases when appropriate, were caught under special permits number 563 and 563–3 from the Ministry of Primary Industries (client number 8730069) and Victoria University of Wellington animal ethics permit number 21765.

PCR amplification and sequencing

A 913 bp portion of the mitochondrial control region, tRNA-Thr, and tRNA-Pro was amplified using polymerase chain reaction in order to target HVR1. The following primers designed for this study were used: L-tRNA-Thr_Tar (5'- GGTCTTGTAAACCG-GATGTCG-3') and H-CCD_Tar (5'-GGGGTCTTTTCTGTTTACGGG-3'). Each PCR (25 µL) included the following: buffer (67 mM Tris-HCl, 16 mM $(NH_4)_2$ SO_4, 0.1% stabiliser), 3 mM $MgCl_2$, 0.6 mg/mL BSA, 0.4 mM dNTPs, 0.4 µM of each primer, 0.05 U/µL Taq polymerase, and 50 ng of template DNA. The following cycles were used for amplification: initial denaturing of 95°C for 2 min, followed by 35 cycles of (1) 1 min at 95°C, (2) 32 s at 64°C, (3) 30 s at 71°C, with a final elongation of 10 min at 71°C. Amplified products were purified by adding 0.5 µL of EXO-SAP-IT and placed in a thermocycler on the following settings: 37°C for 30 min followed by 80 °C for 15 min. Sequencing was carried out by Macrogen Inc. (Seoul, South Korea) using the Sanger method (Sanger et al. 1977). DNA sequences were edited with Geneious Prime 2019.0.4 (http://www.geneious.com) and aligned using the MUSCLE algorithm (Edgar 2004), resulting in clean and aligned sequences of c. 500 bp that cover HVR1.

Genetic diversity and structure

Summary statistics (number of haplotypes, haplotype diversity, average number of nucleotide differences, nucleotide diversity, and number of segregation sites) were calculated using DnaSP 6.12.03 (Rozas et al. 2017) and Arlequin 3.5.2.2 (Excoffier and Lischer 2010). Molecular and population data was manipulated with R 3.5.0 (R Core Team 2020)

on RStudio (RStudio Team 2020) using packages adegenet 2.1.1 (Jombart 2008) and ape 5.3 (Paradis and Schliep 2018). Rarefaction analysis was performed by random method of haplotype accumulation using spider 1.5.0 (Brown et al. 2012) to estimate how much of the total haplotype diversity was sampled in this study. PopART 1.7 (http://popart.otago.ac.nz/index.shtml) was used to create a Templeton, Crandall and Sing (TCS) network (Clement et al. 2002) of haplotypes to display the number of mutations occurring between individual haplotypes. Population structure was analysed with Arlequin 3.5.2.2 by calculating the pairwise fixation indices (Φ_{ST} and F_{ST}) on the total set of sequences, and analyses of molecular variance (AMOVA) were conducted on clusters of sampling sites to assess the levels of genetic differentiation within populations (Φ_{ST}), among populations within groups (Φ_{SC}) and among groups (Φ_{CT}). Clusters were based on morphotypes and geographic region of samples. Both pairwise Φ_{ST} and AMOVA analyses were run using the distance matrix computed under the T92 + G substitution model with Gamma = 0.65, as estimated with MEGA 7.0.26 (Kumar et al. 2016). The significance of both analyses was assessed with 10,000 permutations, and a false discovery rate correction (Benjamini and Hochberg 1995) was applied to the *p*-values for the pairwise fixation index analysis. The AMOVA was run under several *a priori* groupings for population structure. Structure was further investigated on the presence/absence allele data table of the sequences using a principal component analysis (PCA) with ade4 1.7.15 (Dray and Dufour 2007), and discriminant analyses of principal components (DAPC) with adegenet 2.1.1. The DAPC was conducted both on pre-defined groups based on locality and on groups inferred by K-means cluster identification. Test of isolation by distance was conducted with gdistance 1.3.6 (van Etten 2017) on the matrices of genetic and geographic distances, using a 'least-cost distance' model of geographic dispersal where travel is restricted to the ocean. Specimens' coordinates were obtained by using the mean between start and stop trawl latitudes and longitudes provided by the fishers (or approximated to the location midpoint when not provided), and significance was assessed using a Mantel test with ade4 1.7.15 using 999 replicates. Isolation by distance was also tested using a Mantel test on the F_{ST} and linearised F_{ST} matrices of pairwise genetic distances and using a redundancy analysis as implemented in the R script provided by Meirmans (2015).

Demographic history

Tajima's *D* (Tajima 1989) and Fu's *Fs* (Fu 1997) statistics were calculated using Arlequin 3.5.2.2 to assess sample neutrality with 10,000 simulated samples. A negative value calculated by these statistics can be indicative of past population expansion or purifying selection. Due to the nature of Fu's *Fs* statistic, only *p*-values below 0.02 were considered significant (Fu 1997; Excoffier 2015). The mismatch distribution of pairwise nucleotide differences was calculated using DnaSP 6.12.03 to determine whether the populations have evidence of recent demographic expansion (unimodal pattern) or if the populations are in equilibrium (multimodal pattern). Harpending's raggedness index (Harpending 1994) and the sum of square deviations were estimated in Arlequin 3.5.2.2 to quantify the smoothness of the observed mismatch distribution, with 1000 replicates to test for significant departure from a sudden expanding population model. The demographic parameters τ, θ_0, θ_1, and θ_S were estimated with Arlequin 3.5.2.2. The time since the last

population expansion (t) was estimated under the equation $t = \tau/2u$ (Rogers and Harpending 1992). The parameter u is the mutation rate of the sequence that can be measured as $u = 2\mu k$, where μ is the mutation rate per nucleotide site and k is the number of nucleotides (500 bp). Given the absence of a mutation rate for HVR1 from a closely related species, two nucleotide divergence rates (2μ) of 3.6% (Donaldson and Wilson 1999) and 10% (Bowen et al. 2006) per site per million years were selected. The former has been calibrated in snooks (Carangaria: Centropomidae) and has been commonly used for the control region of fishes with relatively similar size and longevity as *N. macropterus* (Lane et al. 2016; Machado et al. 2020). The latter has been estimated for pygmy angelfishes (Eupercaria: Pomacanthidae) by comparing the rate of divergence of the control region with the relatively well-accepted rate for cytochrome *b* in bony fishes (Bowen et al. 2006). The within-lineage mutation rates were estimated by dividing these divergence rates by two.

Bayesian skyline analysis, as implemented in BEAST2 2.6.2 (Bouckaert et al. 2019), was used to measure population size change through time for *N. macropterus* and *N.* n.sp. A strict molecular clock rate of 1.8×10^{-8} and 5×10^{-8} was applied. For each rate, two independent runs of 10^8 iterations were sampled every 5,000 iterations and then combined after discarding a burn-in of 10% at the start of each run. The HKY + G + I model was selected based on Bayesian information criterion (BIC) from jModelTest 2.1.10 (Darriba et al. 2012). Gamma categories were set to 4, and the following parameters were estimated with the following initial values: Gamma shape = 0.65 [0.6–0.7], proportion of Invariant = 0.67 [0.6–0.8], Kappa = 38 [20–70]. The same clock rates and run protocol were applied to *N.* n.sp. under the HKY model (as determined by BIC from jModelTest 2.1.10). Kappa value was estimated with an initial value of 46.1554. All the other parameters were set to default. Skyline plots of the combined tree files were generated using Tracer v1.7.1 (Rambaut et al. 2018). jModelTest and Bayesian Skyline analyses were run on Rāpoi (Victoria University of Wellington's High-Performance Computer Cluster).

The divergence time between *N. macropterus* and *N.* n.sp. was estimated with the equation: $t = d/2\mu$, where d is the net nucleotide sequence divergence based on nucleotide substitutions between *N. macropterus* and *N.* n.sp. and 2μ is the nucleotide divergence rate reported above. d was calculated with strataG (Archer et al. 2017). In order to compare *N. macropterus* and *N.* n.sp. genetic diversity with other marine fish species, average sequence divergence and haplotype diversity values of the control region were obtained from literature for five other New Zealand fishes, the Atlantic cod (as an example for a species which is expected to have undergone a recent bottleneck, due to the collapse of the Grand Banks cod fishery during the latter half of the twentieth century), and 23 other marine fishes for which these values have been compiled and reported in a former study (von der Heyden et al. 2010).

Results

Genetic diversity and structure

Summary statistics for the 370 *N. macropterus* and 15 *N.* n.sp. sequences are shown in Table 1. *Nemadactylus macropterus* showed very high levels of genetic diversity, with an overall haplotype diversity of 0.999 ranging from 0.99 to 1 across locations. Of the

Table 1. Summary information, estimates of genetic diversity, and neutrality tests for 15 locations.

Map location	Sample location	Code	n	H_n	h	k	π	S	Indels	Tajima's D	Fu's F_S
1	Fiordland	FRDL	15	14	0.99	14.38	0.029	57	1	−0.78	−3.45
2	Spawning West Coast South Island	SPWCSI	59	57	0.999	14.38	0.029	91	4	−0.87	−24.25*
3	North Taranaki	NT	15	15	1	14.63	0.029	55	1	−0.58	−5.51*
4	East Northland	ENLD	17	16	0.993	13.4	0.027	51	0	−0.47	−5.07*
5	Bay of Plenty	BPLE	23	22	0.996	13.15	0.026	63	2	−0.85	−9.64*
6	Spawning East Cape	SPEC	60	58	0.999	14.9	0.03	84	1	−0.60	−24.25*
7	Hawke's Bay	HB	18	17	0.993	11.32	0.023	60	2	−1.45	−6.53*
8	Wairarapa	WAI	15	15	1	10.9	0.022	44	1	−0.82	−6.77*
9	Wellington	WGTN	15	14	0.99	16	0.032	57	1	−0.38	−3.07
10	Spawning Cape Campbell	SPCC	60	58	0.999	13.05	0.026	81	2	−0.87	−24.34*
11	Kaikoura	KAIK	24	23	0.996	10.91	0.022	56	2	−1.01	−12.25*
12	Christchurch	CHCH	16	16	1	12.44	0.025	51	1	−0.81	−7.00*
13	Otago	OTAG	18	18	1	12.06	0.024	57	0	−1.13	−8.99*
14	Chatham Islands	CHAT	15	15	1	15.07	0.03	57	1	−0.61	−5.38*
	All tarakihi locations		370	324	0.999	13.25	0.027	130	8	−0.80	−10.47*
15	King tarakihi	KTAR	15	12	0.971	4.74	0.01	22	1	−1.23	−4.71*

Notes: *Nemadactylus macropterus* sampled from 14 locations with a total of 370 sequences. *Nemadactylus* n.sp. sampled from one location with a total of 15 sequences. Key: sample size (n), number of haplotypes (H_n), haplotype diversity (h), average number of nucleotide differences (k), nucleotide diversity (π), number of segregation sites (S), and number of nucleotide insertions/deletion sites (Indels). (*): indicate statistical significance ($P \leq 0.05$, Tajima's D or 0.02, Fu's F_S).

370 samples, 324 haplotypes in total were detected, of which 290 were unique. This high genetic diversity is also evident in the TCS haplotype network (Figure 2). While *Nemadactylus* n.sp. (red on the TCS network), have multiple nucleotide differences (13) separating them from *N. macropterus*, the number of nucleotide differences among the *N.* n.sp. samples is relatively low (1–2). In contrast, *N. macropterus* display multiple nucleotide differences ranging from 1 to 9 between each haplotype, and an apparent lack of structure in the network.

Pairwise Φ_{ST} conducted between *N. macropterus* and *N.* n.sp. indicated that *N.* n.sp. are significantly different from all *N. macropterus* sampling locations ($\Phi_{ST} > 0.5$, $P < 0.001$) (Table 2). A weak but significant difference between Hawke's Bay (HB) and east Northland (ENLD) ($\Phi_{ST} = 0.099$, $P = 0.007$) was detected after applying a false discovery rate correction to the *p*-values (Table 2). None of the pairwise F_{ST} among *N. macropterus* were significant before false discovery rate correction. AMOVA analysis comparing *N. macropterus* and *N.* n.sp. showed that more than half of the total molecular variance (50.62%) came from between these two groups ($\Phi_{CT} = 0.506$, $P < 0.001$) (Table 3). Overall, there were no significant genetic structure among *N. macropterus* sampling locations ($\Phi_{ST} = 0.002$, $P = 0.175$). AMOVA analyses conducted on *a priori* groupings of only *N. macropterus* always detected low (<0.01) Φ_{CT} values, implying low genetic structure overall. A significant but very low differentiation was detected between the west coast and

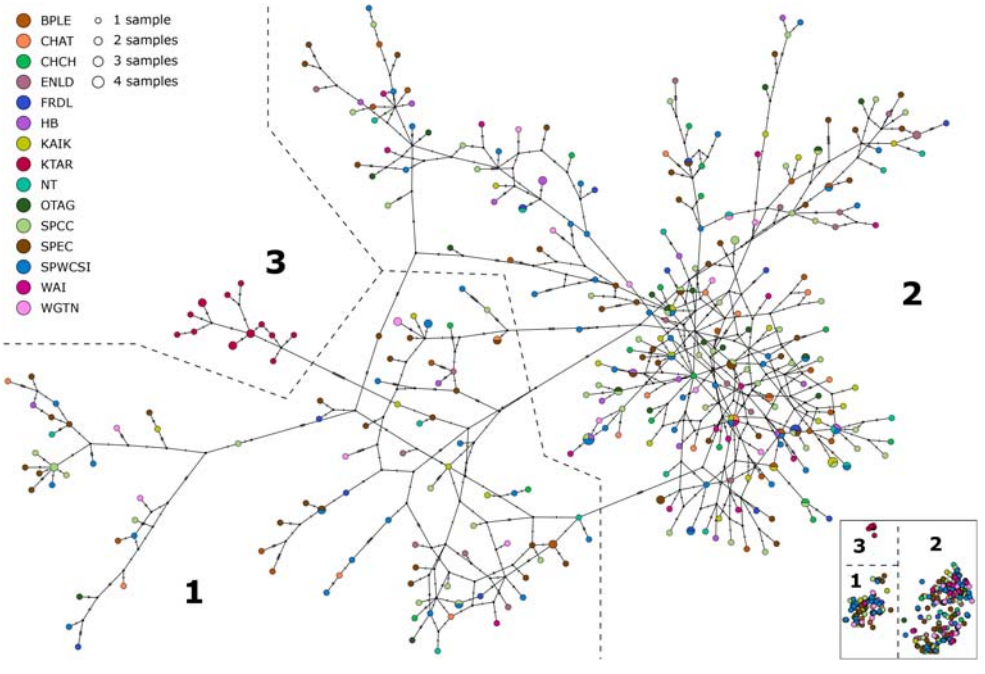

Figure 2. The Templeton, Crandall and Sing network depicts the relationships between 336 haplotypes present in the sample. The circle size is relative to the number of individuals who possess the haplotype, while individual substitutions between two haplotypes are signified as a hatch mark across the connecting line. The smaller black circles represent the node between haplotypes. The three groups separated by the dashed lines correspond to the three clusters identified on the two first axes of the PCA (bottom right and Figure 3). Sampling location codes as referred in Table 1.

Table 2. Pairwise Φ_{ST} values of haplotype diversity between sampling sites.

	BPLE	CHAT	CHCH	ENLD	FRDL	HB	KAIK	NT	OTAG	SPCC	SPEC	SPWCSI	WAI	WGTN	KTAR
BPLE		0.978	0.764	0.392	0.942	0.598	0.911	0.911	0.764	0.911	0.859	0.911	0.889	0.883	0.000*
CHAT	0		0.911	0.488	0.978	0.513	0.911	0.911	0.825	0.978	0.92	0.996	0.634	0.942	0.000*
CHCH	0	0		0.244	0.911	0.652	0.911	0.911	0.598	0.764	0.254	0.7	0.883	0.652	0.000*
ENLD	0.026	0.019	0.048		0.46	0.007*	0.108	0.722	0.21	0.108	0.598	0.296	0.108	0.598	0.000*
FRDL	0	0	0	0.022		0.392	0.883	0.942	0.78	0.911	0.767	0.942	0.911	0.911	0.000*
HB	0.011	0.016	0.008	0.099	0.024		0.742	0.709	0.883	0.634	0.09	0.465	0.942	0.244	0.000*
KAIK	0	0	0	0.059	0	0.001		0.911	0.764	0.911	0.21	0.742	0.93	0.563	0.000*
NT	0	0	0	0.004	0	0.006	0		0.911	0.93	0.722	0.911	0.911	0.742	0.000*
OTAG	0	0	0.011	0.044	0	0	0.001	0		0.889	0.598	0.767	0.911	0.742	0.000*
SPCC	0	0	0.001	0.035	0	0.005	0	0	0		0.392	0.911	0.911	0.598	0.000*
SPEC	0	0	0.025	0.007	0	0.043	0.023	0.003	0.007	0.007		0.911	0.21	0.911	0.000*
SPWCSI	0	0	0.003	0.022	0	0.014	0	0	0	0	0		0.716	0.911	0.000*
WAI	0	0.009	0	0.067	0	0	0	0	0	0	0.031	0.001		0.455	0.000*
WGTN	0	0	0.009	0.015	0	0.038	0.015	0.001	0.004	0.008	0	0	0.028		0.000*
KTAR	0.589	0.581	0.63	0.608	0.608	0.651	0.624	0.596	0.632	0.549	0.517	0.515	0.662	0.577	

Notes: Φ_{ST} values are below the diagonal while the *p*-value associated with each comparison is above the diagonal. (*): indicate statistical significance ($P \leq 0.05$) after false discovery rate correction. Sampling location codes are listed in Table 1.

Table 3. Results from locus-by-locus Analysis of Molecular Variance of *Nemadactylus macropterus* (and *Nemadactylus* n.sp.) hypervariable region 1 (HVR1) sequences with seven *a priori* groupings.

		Among groups			Among populations within groups			Within populations		
A priori grouping	*n* groups	%Var	Φ_{CT}	*P*	%Var	Φ_{SC}	*P*	%Var	Φ_{ST}	*P*
King TAR vs. TAR	2	50.62	0.506	<0.001*	0.16	0.003	0.171	49.23	0.508	<0.001*
TAR (all locations)	1				0.21			99.79	0.002	0.175
North and South Island vs. Chatham Islands	2	0	−0.017	1	0.36	0.004	0.055	100	−0.013	0.165
Spawning locations: SPWCSI vs. SPEC vs. SPCC	1				−0.03			100.03	<0.001	0.538
West vs. East	2	−0.31	−0.003	0.948	0.53	0.005	0.017*	99.78	0.002	0.049*
North Island: West vs. East	2	−2.09	−0.021	0.996	2.1	0.021	<0.001*	99.99	<0.001	<0.001*
South Island: West vs. East	2	0.59	0.006	0.023*	−0.8	−0.008	0.97	100.21	−0.002	0.925
North Island vs. South Island	2	−0.12	−0.001	0.761	0.46	0.005	0.041*	99.66	0.003	0.045*

Notes: %Var = variance component in percentage of the total variation. *Nemadactylus* n.sp. were only included in the first grouping. Both 'West vs. East' groupings did not include the Wellington and Chatham Islands locations. (*): indicate statistical significance ($P \leq 0.05$). Sampling location codes as referred in Table 1.

the east coast of the South Island ($\Phi_{CT} = 0.006$, $P = 0.023$). The significant but low differentiation between Hawke's Bay and East Northland may be responsible for the significant differentiation observed among some populations within groups (Φ_{SC}) that include the North Island (West vs. East, North Island West vs. East, and North Island vs. South Island). PCA conducted on all *Nemadactylus* samples showed that *N.* n.sp. form a distinct cluster separate from *N. macropterus* (Figure 3, Figure S1). Although *N. macropterus* individuals form one large cluster with two possible subgroups (that are corroborated by the haplotype network, Figure 2), sampling locations appear to be randomly distributed throughout the *N. macropterus* cluster, indicating a lack of genetic structuring. The PCA conducted on the *N. macropterus* dataset only did not detect any structure related to location, size, or weight of fish (Figures S2–S7). DAPC conducted on *a priori* groupings based on locality (Figures S8 andS9) and K-means clustering (Figures S10 and S11) both failed to infer any *a posteriori* groups related to geographic locations. There was no isolation by distance detected (Figure 4) when using a matrix of least-coast distance restricted to ocean travel on the 370 *N. macropterus* ($R = 0.029$, $P = 0.105$). Tests of isolation by distance using different models (great-circle distance, Figure S12), data (by not including the Chatham Islands, Figure S13), and genetic transformation (F_{ST} and linearised F_{ST}) led to similar results ($R < 0.03$, $P > 0.1$), and no spatial variable could be forward-selected in order to perform a redundancy analysis (Supporting information: R scripts).

Demographic history

Tajima's *D* and Fu's *Fs* were all negative for both *N. macropterus* and *N.* n.sp. (Table 1). While none of Tajima's *D* values were significant, almost all Fu's *Fs* were, with the exception

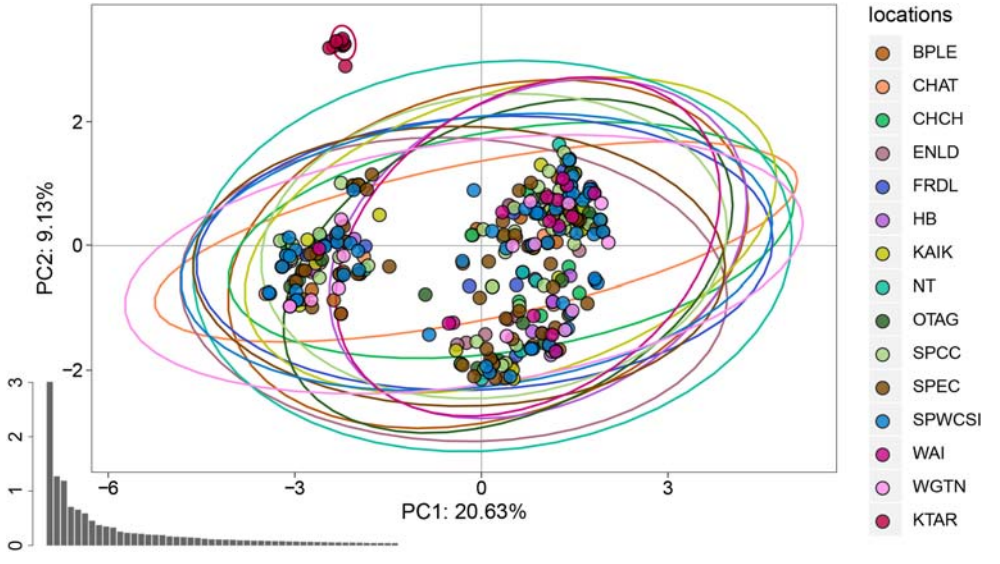

Figure 3. Principal Component Analysis of presence/absence alleles in hypervariable region 1 (HVR1) for all *Nemadactylus macropterus* ($n = 370$) and *Nemadactylus* n.sp. (KTAR) samples ($n = 10$). Ellipses represent the 95% confidence intervals. Bottom left: Eigenvalues. Sampling location codes as referred in Table 1.

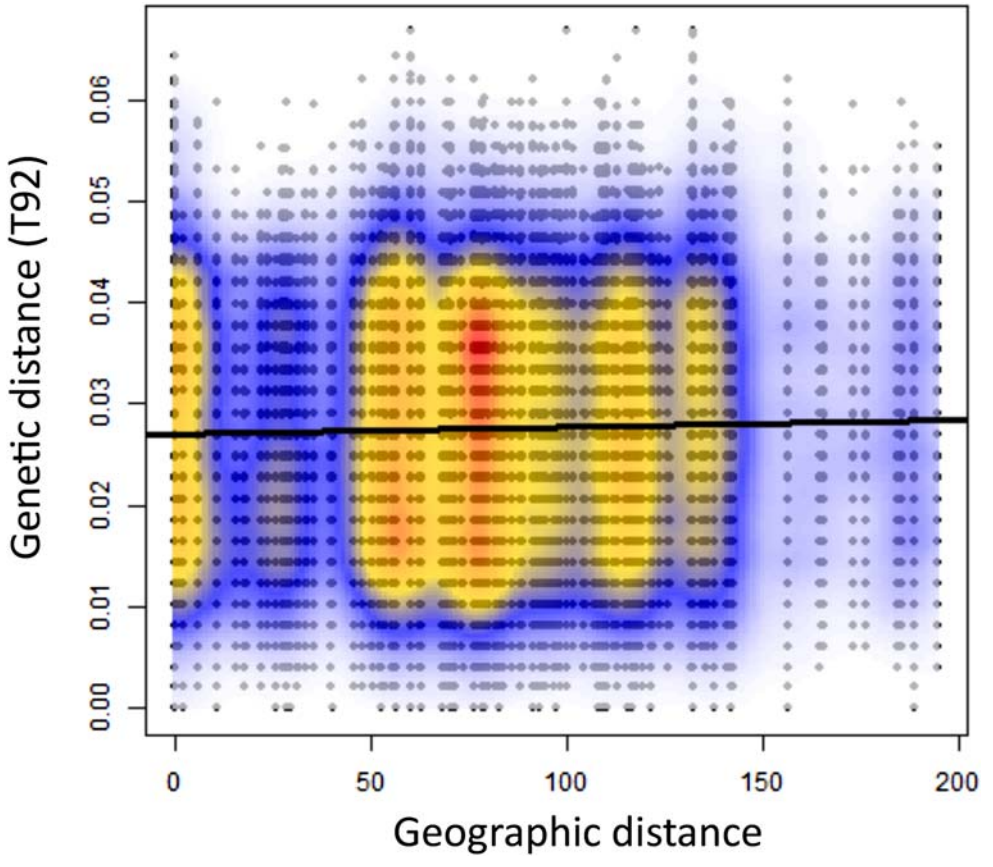

Figure 4. Isolation By Distance plot for all *Nemadactylus macropterus* sampling locations. A least-cost distance model restricting travel to the ocean was used to compute the geographical distance matrix.

of Fiordland and Wellington. However, *p*-values for these two locations were still low (P = 0.051 and 0.070 respectively). A negative Fu's *Fs* statistics implies recent or current population expansion. The mismatch distribution graph for *N. macropterus* showed a unimodal distribution (Figure S14) and Harpending's raggedness index and sum of square distributions values were low and not statistically significant ($Hr = 0.001$, $P = 0.94$ and $SSD = 0.003$, $P = 0.39$). These results are all indicative of a past or current population expansion. The mismatch distribution graph for *N.* n.sp. showed a twin-peaked distribution that could be interpreted as bimodal, thus indicating a more stable population (Figure S14). Indeed, the goodness of fit of Harpending's raggedness and the sum of squared deviation statistics significantly departed from an expanding population model ($Hr = 0.077$, $P = 0.05$ and $SSD = 0.021$, $P = 0.03$). Estimates of time since last population expansion based on demographic parameters (Table S2) varied from c. 240,000 to c. 86,000 years before present (BP) for *N. macropterus* and from c. 110,000 to c. 40,000 yr BP for *N.* n.sp., depending on the mutation rate. Bayesian skyline plots were generated to investigate historic changes to the female effective population size (Figure 5). *Nemadactylus macropterus* historic effective population (N_{ef}) has undergone two possible expansion periods over the last 800,000 yr. N_{ef} has increased from c. 1×10^6–2×10^6 to c. 1×10^8–2×10^8 individuals

over this period, with a first burst c. 200,000–800,000 yr BP and a second one c. 60,000–300,000 yr BP. *Nemadactylus* n.sp. historic effective population appears to have been rather stable for the last 60,000–180,000 years with the N_{ef} staying between 300,000 and 1,000,000 individuals depending on the mutation rate. Based on these results, *N. macropterus* effective population size is at least 100 times larger than that of *N.* n.sp.

Divergence time

Only one fixed substitution was found between *N. macropterus* and *N.* n.sp., which corresponded to a net nucleotide sequence divergence of 2.88%. Based on this result, the

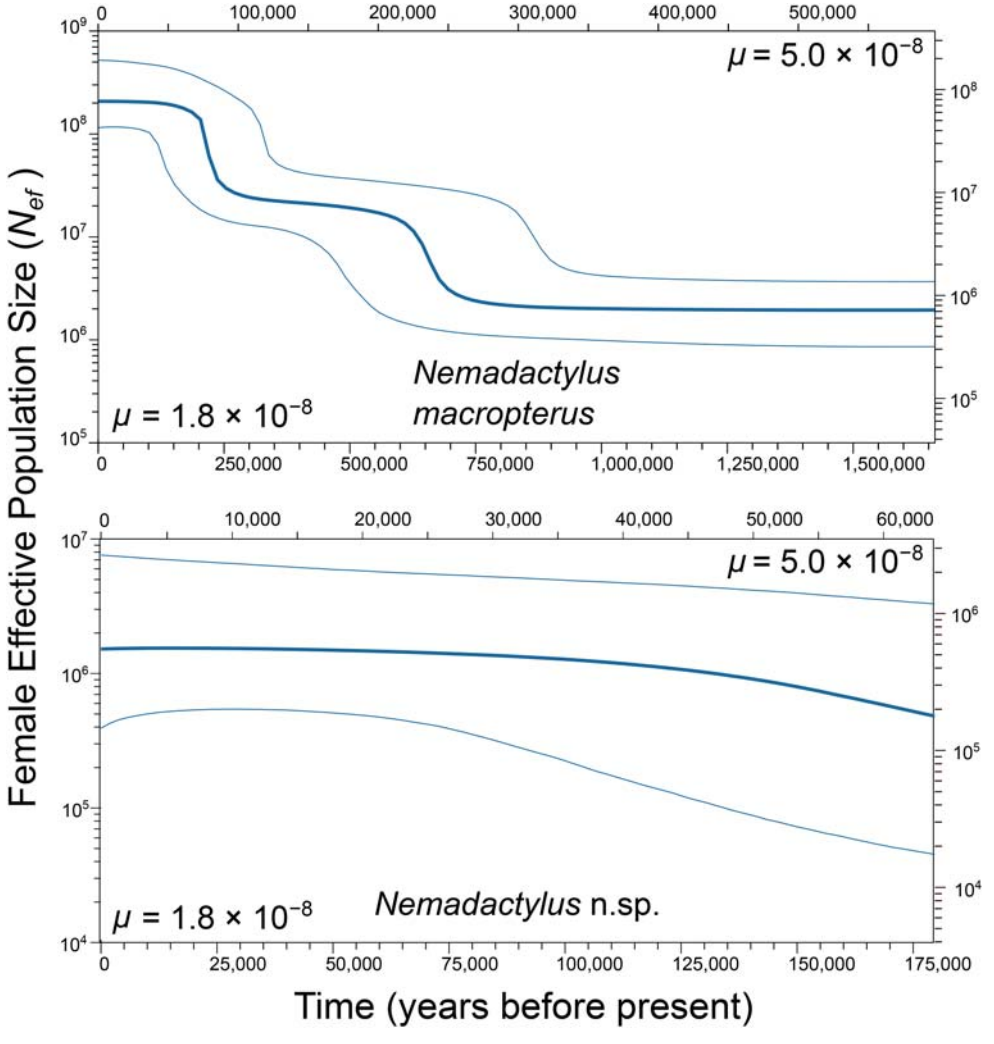

Figure 5. Bayesian Skyline Plot illustrating estimated female effective population size through time (years before present) for *Nemadactylus macropterus* and *Nemadactylus* n.sp. The darker middle line is the mean female effective population size through time and the light blue lines are the 95% confidence intervals. The bottom and left axes are the values for a mutation rate of 1.8×10^{-8}. The top and right axes are the values for a mutation rate of 5×10^{-8}.

time since divergence between the two 'species' was estimated to be at least 0.3–0.8 million yr BP, depending on the divergence rate.

Discussion

Nemadactylus macropterus

Genetic structure

The mtDNA data analysis conducted in this study indicates that *N. macropterus* have a panmictic population structure throughout its distribution around mainland New Zealand and the Chatham Islands. Although the haplotype network and the PCA hint at the possibility of two genetic groups in New Zealand, these are not congruent with any geographical sub-grouping (including the spawning locations and the remote Chatham Islands) or measured morphological variables. If there are two (partially) reproductively isolated populations in New Zealand, extensive spatial intermixing of individuals in sampled schools have obscured this in the present dataset. Overall this is not congruent with the study from Gauldie and Johnston (1980) who detected several genetic breaks around New Zealand. It is possible that their study was more powerful given the larger sample size (c 3000 individuals), although it is important to note that these findings were based on allozymes for which selective neutrality was uncertain (as opposed to the non-coding control region), and no correction for multiple statistical tests was applied. The authors were cautious about drawing any conclusions because they found a correlation between genetic variation and temperature and could therefore not rule out the possibility of a selective cline instead of geographically isolated fish stocks.

Even if there was no overall genetic structuring of the population, we found a significant genetic break between Hawke's Bay and East Northland. It has been reported that juvenile *N. macropterus* disperse from nursery grounds in Canterbury Bight/Pegasus Bay area and travel north along the east coast of New Zealand passing through the Hawke's Bay region, eventually making their way to east Northland and settling as adults (Langley 2018). The genetic break might be indicative of a boundary at the northern extent of the eastern stock, where a portion of northward migrating individuals settle, and the remainder skips the Bay of Plenty area and continue north to eventually settle in east Northland. Gauldie and Johnston (1980) also detected two successive genetic breaks for *N. macropterus* samples between East Cape (directly North of Hawke's Bay) and East Northland. However, a recent stock assessment of the eastern *N. macropterus* stock (TAR 1, TAR 2 and TAR 3) estimated that the spawning biomass in these areas has been depleted below the fisheries management soft limit of 20%, and was already close to this soft limit in the 1970s (Langley 2018). The migrating fish transit through these quota fishing areas, in which the majority of the commercial catches are landed (Hanchet and Field 2001). The genetic boundary that we found could have been established after the development of a long-term pattern of skipping Bay of Plenty during the northward migration. However, the reduction of population size due to high levels of fishing and ocean warming could in the near future disrupt this natural process of genetic structuring.

A very small genetic break was also detected using the AMOVA of West Coast (Fiordland and West Coast South Island) vs. East Coast (Kaikoura, Christchurch, and Otago) locations of the South Island only, although the same pattern was not detected by pairwise

Φ_{ST} of those same locations. This could be explained by a mostly northward migration of adults (as is known to occur on the East Coast), which would lead to mixing of adult populations around the North Island, with a homing behaviour of reproductive stocks to their respective spawning grounds on the west and the east of the South Island.

The remote Chatham Islands sample location is not genetically divergent from mainland locations. The maximum depth that *N. macropterus* is known to occur is 250 m (Annala 1987). However, the shallowest parts on the Chatham rise seabed between the Chatham Islands and the mainland is 500 m (Chiswell et al. 2015), which means regular demersal movement by adults between the two areas is, while not impossible, unlikely. Hydrographic models of the region estimate that it would take 30–50 days for larvae to cover this 850 km stretch of water (Chiswell 2009). *Nemadactylus macropterus* have a pelagic larval duration of approximately 10 months (Annala 1987) making it possible to cover this distance, especially with the dominant easterly currents over the Chatham Rise (Ross et al. 2009). Larvae from mainland coastal locations could be transported to the Chatham Islands via the East Cape, Wairarapa, Southland, Westland and D'Urville currents to the Chatham Islands.

Demographic history and genetic diversity

Patterns of genetic variation can provide insight into the demographic history of a species. *Nemadactylus macropterus* display a high level of nucleotide ($\pi = 2.7\%$) and haplotype ($h = 0.999$) diversity within HVR1. In this study, 324 haplotypes were discovered from 370 *N. macropterus* samples. This is a much greater degree of variation than many other New Zealand marine species when comparing homologous control region fragments from similar sample sizes and life histories (Figure 6, Table S3). High amounts of nucleotide and haplotype diversity are suggested to be characteristic of a large stable population with a long evolutionary history, or secondary contact between previously isolated lineages (Grant and Bowen 1998). The numerous past glacial cycles of the Pleistocene are often cited as being responsible for changes in demographic history observed in modern fauna (Hewitt 2000; 2004), including marine species (Hickey et al. 2009). The last glacial maximum was approximately 20,000 yr BP in New Zealand (Alloway et al. 2007). It occurred during the last glaciation period, Otira, which lasted from c. 75,000 to c. 14,500 yr BP (McSaveney 2007; Shulmeister et al. 2019). During this period, sea levels

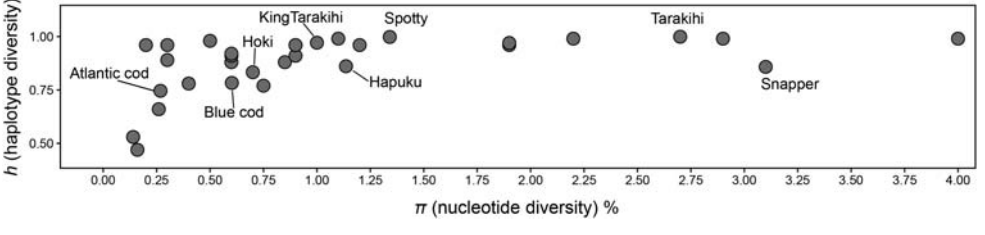

Figure 6. Haplotype (*h*) and nucleotide (π) diversity values of the mtDNA control region in a range of marine fish populations (adapted from Grant and Waples (2000)). Values from the New Zealand species and the Atlantic cod are labelled: Atlantic cod (*Gadus morhua*), blue cod (*Parapercis colias*), hāpuku (*Polyprion oxygeneios*), hoki (*Macruronus novaezelandiae*), snapper (*Chrysophrys auratus*), spotty (*Notolabrus celidotus*). See Table S3 for names and genetic diversity values of all plotted species.

around New Zealand had dropped to a point at which land bridges connected the North, South and Stewart Island (Wallis and Trewick 2009). These drops might have exposed most of the continental shelf, leaving a reduced and more fragmented area of available habitat to coastal species. Some fish species in New Zealand have probably undergone their most recent expansion after the last glacial maximum when ocean levels rose again and marine populations could expand and connect (e.g. hāpuku (Lane et al. 2016), blue cod (Smith 2012)). However, *N. macropterus* population size does not show an increase after the end of the last glaciation period. The species might have been unaffected by the last glaciation due to its life history and habitat preference (i.e. relatively deep species and high potential for dispersal). The last population expansion detected by demographic parameters happened earlier than the last maximum glaciation (c. 240,000–86,000 yr BP) and these values are concordant with the second expansion detected by the Bayesian skyline plot (c. 300,000–60,000 yr BP). The two expansions probably happened during some older interglacial periods. For example, if the mutation rate of 5×10^{-8} is assumed to be most appropriate, *N. macropterus* populations could have been expanding during the Karoro interglacial period. They reached their first maximum capacity during the Waimea glacial period, which started c. 180,000 yr BP (Suggate 1990; McSaveney 2007). The second expansion could have started during the Kaihinu interglacial period (125,000–75,000 yr BP) with their final maximum carrying capacities reached during the Ōtira glaciation (75,000–14,500 yr BP). This maximum carrying capacity might not have been affected by the end of the last glacial maximum and the current interglacial period. Population expansions estimated at similar time scales have been reported for yellow croaker based on the same genetic marker (50,000–197,000 yr BP (Xiao et al. 2009)). However, the time scale and absolute number in term of individuals (N_{ef}) of these two expansions should be interpreted with caution. These values are highly dependent on the molecular clock rate. Moreover, since connectivity with Australia is presumably high, it is possible that these signatures of large expanding populations are not reflective of the local New Zealand situation.

Further evidence of a past population expansion is provided with the mismatch distribution supported by non-significant sum of squared deviation and Harpending's raggedness index values. The mismatch distribution is unimodal, indicating a population expansion, and over time would have been shifting to the right of the graph due to the high nucleotide diversity shown as pairwise difference. This indicates that the population has undergone a rapid population expansion in the past but has since become a large stable population that has accumulated a high level of nucleotide diversity. Fu's F_s, which is more sensitive to demographic expansions on neutral markers than Tajima's D (Fu 1997; Excoffier 2015), also indicated a past population expansion for the whole of New Zealand, and for every locality except Wellington and Fiordland. The TCS haplotype network also supports this finding by showing multiple nucleotide segregations between haplotypes instead of only a few. This is characteristic of a recently expanding population.

Nemadactylus n.sp.

Genetic variation and demographic history

Nemadactylus n.sp. display a high degree of haplotype diversity ($h = 0.971$) within HVR1, which might be indicative of a large or expanding population. These values are similar to

N. macropterus, although the lower nucleotide diversity ($\pi = 1.0\%$, $k = 4.74$) could indicate that the population size is smaller and/or it has had less time to accumulate mutations during expansion after a past bottleneck (Grant and Bowen 1998). Significant Fu's F_s support the conclusion of population expansion, but the N_{ef} of *N.* n.sp. shows a less than twofold increase in the Bayesian skyline plots for at least the last 60,000 years (albeit with a very wide 95% confidence interval). The hypothesis of expansion was not supported by the sum of squared deviation and the Harpending's raggedness index. These results should be taken with caution because of the unique sampled location and the small sample size. The rarefaction curve for our sample size did not asymptote (Figure S14), indicating that further sampling is required to better capture the extent of genetic diversity of the *N.* n.sp. population.

Evidence for separate species

None of the haplotypes sampled in this study were shared between *N. macropterus* and *N.* n.sp, which is evidence of long-term reproductive isolation of these sympatrically distributed fish. *Nemadactylus* n.sp. formed a separate cluster from *N. macropterus* in the PCA and TCS haplotype network and were separated from the closest *N. macropterus* haplotype by 14 nucleotide substitutions. Pairwise Φ_{ST} analysis provided further strong evidence of a substantial genetic divergence between both species ($\Phi_{ST} = 0.515–0.662$, $P < 0.001$ between all sampling locations). AMOVA between *N.* n.sp. and *N. macropterus* also provided additional supporting evidence, as the majority of the genetic variation (66.315%, $P < 0.001$) could be contributed to the difference between *N.* n.sp. and *N. macropterus*. The estimated minimum time since divergence between *N. macropterus* and *N.* n.sp., 0.3–0.8 million yr BP, is concordant with the radiation time estimated from molecular clock calibrations for the most closely related species of *Nemadactylus* and *Acantholatris* (Burridge 1999), which was reported to be possibly during the last 0.6 million years and at least within the last 2.6 million years.

Comparison of genetic diversity in marine fishes

The patterns observed in Figure 6 are concordant with the results reported in Grant and Waples (2000), who plotted the nucleotide diversity against the haplotype diversity of coding regions of several marine species. The authors argued that species could be assigned to historical demography categories depending on their position in the graph.

Species plotted on the lower left of the graph are characterised by having shallow mtDNA divergence. It has been suggested that species that fall into this category have typically undergone a recent bottleneck or are a founding/recolonising population (Grant and Bowen 1998; Grant and Waples 2000). As haplotype diversity increases through time, so does nucleotide diversity. Species displaying a higher haplotype diversity, but low nucleotide diversity (e.g. king tarakihi, spotty) represent populations that could have undergone rapid expansion but have not had the time for nucleotide diversity to increase. As haplotype diversity reaches a plateau, nucleotide diversity only increases in large stable populations (e.g. tarakihi), which would be projected on the upper right of the graph. No species are projected in the lower right of the graph, a category that could be indicative of contacts between small formerly isolated populations. However, this is

unlikely to be the case in coastal and ocean organisms for which the potential for gene flow is typically high (Grant and Waples 2000).

Conclusions and prospects

This is the first study to utilise DNA sequencing to investigate genetic diversity, structure, and demographic history of *N. macropterus* from sample sites around New Zealand. The analysis of *N. macropterus* genetic structure supports the conclusion of a panmictic population. This genetic pattern is probably maintained by their longevity, high migration/dispersal potential, and long pelagic larval dispersal. Our finding is concordant with the results of panmixia for the Australian populations (Elliott and Ward 1994; Grewe et al. 1994; Burridge and Smolenski 2003). An analysis of demographic history classified *N. macropterus* as having a long-term large and stable population that contains a high degree of genetic variation. Moreover, rarefaction analysis and expansive PCA indicate that a larger sample that we were able to obtain is required to fully capture the genetic diversity of the New Zealand population (Figure S14). Although our results suggest that gene flow might be high between management areas at an evolutionary scale, this is not a guarantee of rapid recovery of regional stocks that could be overexploited (Waples 1998; Burridge and Smolenski 2003). Moreover, genetic panmixia can result from very infrequent movement, even when there is a demographic structure. Higher-resolution markers will be required to gain a more definitive understanding of the stock status and connectivity of *N. macropterus* in New Zealand. Genome-wide markers can be used to detect shallow genetic structure in marine species with large populations, which are typically highly mobile (Allendorf et al. 2010; Bernatchez et al. 2017; Benestan 2019; Papa et al. 2021). Focusing genetic sampling on larvae or early-settlement individuals could help in countering the confounding effect of adults being highly mobile, although *N. macropterus* larvae are also subject to long-distance dispersal due to oceanic currents (Annala 1987) and juvenile *N. macropterus* are highly elusive (M. Morrison, personal observation). Nevertheless, a high certainty in the conclusions about *N. macropterus* stock structure is crucial, given the concerns about the current state of the tarakihi fisheries on the New Zealand east coast (Langley 2018). A genetic comparison of *N. macropterus* and *N.* n.sp. provided further evidence in support for their status as separate species under the *Nemadactylus* genus. The taxonomic status of *N.* n.sp. should be formally investigated, which will likely assist the conservation management of king tarakihi.

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Disclosure statement

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Data availability statement

DNA sequences have been submitted to GenBank under accession numbers MW147766 – MW148150. DNA sequence alignments are available on Figshare (DOI: 10.6084/m9.figshare.13317128 and 10.6084/m9.figshare.13317131). All R scripts used in the analyses are openly available on GitHub at https://github.com/yvanpapa/tarakihi_NZ_population_genetics.

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