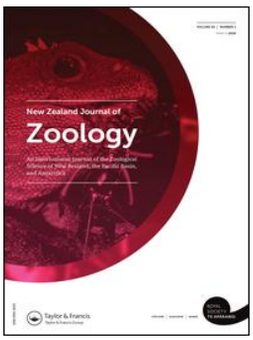

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REVIEW ARTICLE

Genetic stock structure of New Zealand fish and the use of genomics in fisheries management: an overview and outlook

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ABSTRACT

Sustainable management of wild fisheries requires accurate delineation of reproductively isolated stocks to avoid depletion of a commercially and ecologically important resource. However, there is still a lack of reliable information on stock structure for most fishery species in New Zealand. DNA markers can assist in the delineation of stocks, but they also can provide significant insights into other areas related to the genetic diversity and the response to pressures. In this review, we first provide a detailed summary of the population genetic studies of New Zealand fish species, with a particular focus on hoki, orange roughy, snapper, ling, and blue cod. We find that genetic data is uniformly lacking for most species. We then discuss how the global shift from low resolution markers to genomics in fisheries genetics has far reaching consequences for the sustainable management of our aquatic resources, by allowing us to address multiple important pressures that wild fisheries are currently facing, and we introduce some of these briefly. We conclude by emphasising the need for a more systematic and holistic approach for the use of genomics in New Zealand fisheries management, so that the best evidence is available to inform the decisions of policy makers.

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Introduction

The New Zealand Exclusive Economic Zone (EEZ, Figure 1) covers more than 4,000,000 km^2 of ocean and is one of the 10 largest EEZ in the world (Migiro 2018). Wild capture fisheries in the New Zealand EEZ are made up of more than 100 species, and around 600,000 tonnes are harvested annually. In an effort to ensure sustainable utilisation of this resource, spatial, temporal, and size limits are set using a Quota Management System that divides New Zealand waters into Quota Management Areas. Currently, 98 species or groups of species of fishes, invertebrates, and seaweeds are managed as one or more stocks under the Quota Management System (Fisheries New Zealand 2019a). Each stock has an annual Total Allowable Catch, which is supposed to be the upper limit of biomass that can be removed without overfishing the stock. Sustainable catch limits, which Total

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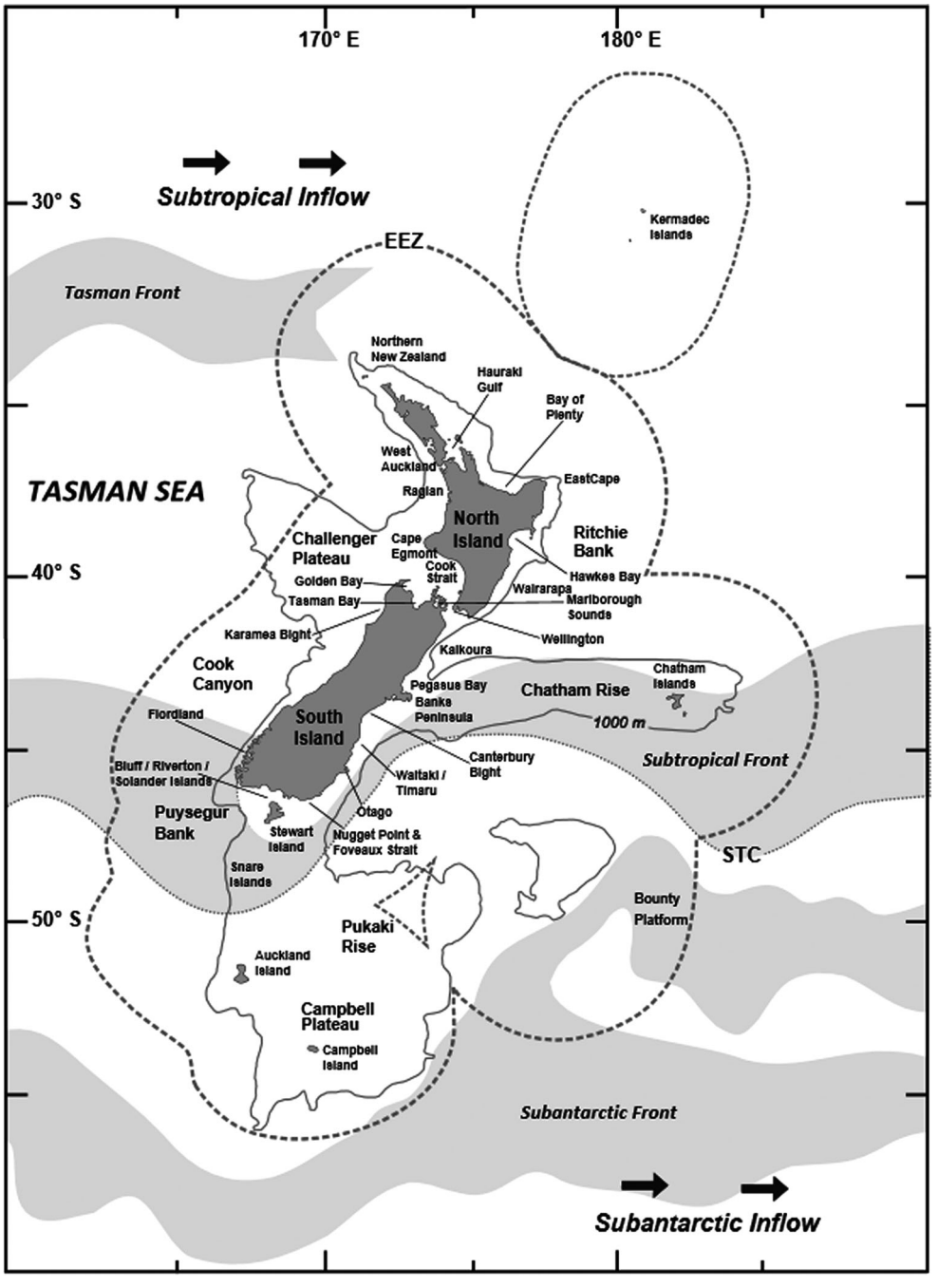

Figure 1. Sampling localities for fish population genetic studies in New Zealand. The dashed line shows the boundary of the New Zealand Exclusive Economic Zone (EEZ), and the continuous line is the 1000 m bathymetric contour, which is the approximate edge of the continental shelf. New Zealand is bathed from the west by water masses of different temperatures: the warm Subtropical Inflow and the cold Subantarctic Inflow. The warm Tasman Front and Subtropical Front are associated with the main flowing surface currents that might influence fish dispersal around New Zealand. The Subtropical Front separates the warmer northern waters from the colder polar water masses of the Subantarctic Inflow at the Subtropical Convergence (STC, dotted line). South of New Zealand and the Campbell Plateau is the deeper Subantarctic Front and associated cold Antarctic Circumpolar Current. (Currents based on a map from the National Institute of Water and Atmospheric Research).

Allowable Catch are based on, are traditionally set using the results of stock assessments when such data are available (Beddington et al. 2007; Gibbs 2008). Properly identifying the boundaries of fisheries stocks is crucial because it is a necessary parameter in any stock assessment model (Begg et al. 1999; Waples et al. 2008; Cadrin et al. 2014a). Moreover, discrepancies between biological populations and management units can result in overexploitation of stocks (Reiss et al. 2009; Benestan 2019) and lack of knowledge of biological spatial structure has already resulted in important fisheries collapses (Cadrin 2020). Overfishing of the infamous Atlantic northern cod in the late 1980s, depletion of small spawning areas of Atlantic herring in the Northwest Atlantic, and overexploitation of crustacean fisheries in the Gulf of Alaska, which all led to dramatic fisheries collapses, have all been attributed, at least partially, to mismatches between the spatial management or assessment units and the actual population structure (Orensanz et al. 1998; Smedbol and Stephenson 2001). In spite of those potential issues, the current lack of knowledge of fisheries biological stock boundaries in New Zealand makes it impossible to know with certainty if they are matched with their assessment and management stock boundaries. Current stock hypotheses that are reported from New Zealand fisheries assessment literature (i.e. Fisheries New Zealand 2018) are either inexistent or are based on various types of observations and scientific data, often sparse, and rarely match the Quota Management Areas (Table S1).

The value of genetics in fisheries stock delineation and fisheries management

Over the last decade there have been increasing efforts to use a holistic approach to delineate fish stocks, by combining the results obtained from multiple methods such as physical tagging, morphometrics, parasites as biological tags, life history data (growth, age composition, reproduction, and distribution), otolith chemistry, and genetics (Abaunza et al. 2008; Espeland et al. 2008; Baldwin et al. 2012; Tanner et al. 2014; Zemeckis et al. 2014; Cadrin et al. 2014b; Izzo et al. 2017; Corrigan et al. 2018). The rationale is that these methods capture evidence from different biological processes which can operate over different temporal and spatial scales. As an example, differences in levels of metal ions and trace elements accumulated in otoliths during time spent at a particular locality can be used to infer residency or migratory events on an ecological time scale (months–a few decades). Otolith microchemistry markers thus provide *direct* measures of what an individual has done and where it has been. In contrast, genetic loci are markers that can be used to estimate levels of connectivity at evolutionary time scales (decades–thousands of years). The latter utilises a sample of characters that remain permanent in individuals and are partially passed down from one generation to the next (Tanner et al. 2016). These markers are *indirect* because they measure the consequences of what other individuals (the ancestors) have done and where they have been. Information from genetic markers is said to provide the most definitive inference of reproductive isolation (Cadrin 2020), although it is important to take into account the intrinsic characteristics of the markers studied, i.e. the mutation rate and the vulnerability to natural selection, in order to interpret results properly.

Using genetic markers either as a standalone method or as part of an integrative approach has led to numerous advances towards establishing the levels of connectivity and structure of fisheries stocks. Recent examples include the discovery of four

reproductively isolated stocks of beaked redfish in the North Atlantic (Cadrin et al. 2010), three stocks of Atlantic cod that reproduce at different times of year on the East Coast of North America (Kovach et al. 2010), five global populations of silky sharks based on mitochondrial DNA control region sequences (Clarke et al. 2015), significant genetic population structure among Greenland lumpfish (Garcia-Mayoral et al. 2016) and Greenland halibut (Westgaard et al. 2017), two mitochondrial lineages of night sharks in the West Atlantic (Domingues et al. 2019), and two genetic stocks of Australasian snapper along the east coast of Australia (Morgan et al. 2019). See also reviews by Cadrin et al. (2014b) and Cuéllar-Pinzón et al. (2016) for more examples. Some of these studies have provided information to fisheries management which could then be used to respond accordingly with practical measures. Examples of these practical applications in North Atlantic fisheries are reviewed in Kerr et al. (2017): they include the setting of temporal and spatial closures of Atlantic cod in North America and the alteration of management stock boundaries of redfish. Detection of morphologically similar mixed stocks through population genetics has also been shown to successfully assist in the management of fragile Atlantic cod populations in Norway. Since allele frequencies of the gene *Pan*I can be reliably used to differentiate between the declining Norwegian coastal cod and the stable Northeast Atlantic cod populations (Sarvas and Fevolden 2005), 'real-time' genotype monitoring of landings could then be routinely undertaken in order to close some fisheries areas when the proportion of Norwegian coastal cods in catches was considered too high (Dahle et al. 2018).

Additionally to stock delineation, genetic tools have other numerous applications for fisheries-related studies and questions. Traditionally, long-term patterns and evolutionary processes are investigated with genetic data to explore population structure, levels of gene flow and connectivity, adaptive differentiation, levels of gene diversity, effective population size (N_e), and inter-species phylogenetic relationships. In the context of fisheries management, the useful applications can extend to age estimation, ecosystem monitoring, and biosecurity, among others. All these well-established and new potential applications for genetics have already been thoroughly reviewed by Ovenden et al. (2015). Now that the levels of resolution have significantly improved with the use of genome-wide DNA sequencing (Bernatchez et al. 2017), that is referred here as 'genomics', the power of these methods has substantially increased. Among all those applications, maintaining levels of genetic diversity in a stock is often an important goal of fisheries management that cannot be addressed without non-genetic methods (Hoarau et al. 2005; Pinsky and Palumbi 2014; Domingues et al. 2018). However, it is not often monitored and testing for a decline would require long-term sampling that is very rarely undertaken. Despite the importance of both levels of genetic variation and structure, it has been difficult to include them into fisheries management and planning in New Zealand and globally because there has been limited interest or appropriate support for long-term comprehensive studies (Waples et al. 2008; Bernatchez et al. 2017). Yet, even newer issues related to the genetic integrity of fisheries have started emerging in the scientific literature. As examples, the response of fisheries to new selective pressures due to our current way of size-selective fishing (which might cause a 'fishing-induced evolution') or to the current wave of global warming is still uncertain. Those issues are thus expected to become important topics in the field of fisheries genomics (Bernatchez et al. 2017; Benestan 2019).

The first part of this review aims at providing an overview of the current state of knowledge on genetics in New Zealand wild fisheries, with a detailed review of the population genetic studies that have been reported for New Zealand fisheries species. The second part is a more general overview of how the field of fisheries genetics is currently evolving towards new methods and tools and how they will be beneficial to New Zealand (and global) fisheries management to address the question of stock structure and some other issues related to genetics.

The current state of New Zealand fisheries genetics

In 2019, 68 fishes were managed under the Quota Management System with a total allowable commercial catch limit. Several of the fish quotas consist of taxonomic units which do not require separate catch reports, usually because it is difficult to distinguish among the grouped species (however, most of them are still assessed separately whenever it is possible). These 68 fishes thus consist of 86 recognised species *sensu stricto* (Table 1). To date, only 23 out of the 86 species have been studied for genetic population structure (Figure 2, Table 2. See Table S1 for a more detailed report of all genetic studies that include New Zealand EEZ fishes). Only 11 of them have been studied using microsatellites and/or DNA sequencing (as opposed to allozymes and fragment length polymorphism) and none with genome-wide DNA sequencing methods.

Here we focus on commercially important marine finfish and cartilaginous fish species, for which population genetic data are available. Whenever possible, species were classified into one or more of five categories of population genetic structure: (I) panmixia: no genetic differentiation detected within the population; (II) isolation by distance (IBD): a semi-continuous population where gene flow between two locations decreases as a function of distance (Wright 1943); (III) spatially distinct populations: two or more areas were shown to have significant genetic differences; (IV) temporal variation: significant genetic differences were detected between samples collected in same localities at different times; (V) sympatric: two or more genetic lineages were detected in the population, without evidence of link with spatial or temporal variation.

*Hoki or blue grenadier (*Macruronus novaezelandiae*, Merlucciidae)*

Hoki is a schooling bentho-pelagic fish distributed throughout the southwest Pacific, most abundant between depths of 200–800 m. This is New Zealand's largest and most valuable fishery with a reported commercial catch of more than 122,000 tonnes in 2019, i.e. almost a third of the total commercial catches for the same year (Fisheries New Zealand 2019b). They are mainly targeted in spawning aggregations during the winter in the Hokitika Canyon on the West Coast of the South Island and in Cook Strait on the East Coast of the South Island. The lifespan of the species is around 25 years, with a long pelagic larval and juvenile phase (4–7 years). Although it only comprises one Quota Management Area around North and South Island, Hoki are effectively managed as separate western and eastern sub-stocks. These were defined based on differences in growth and maturation rates, as well as morphometric characters, between west and east coast stocks (Horn and Sullivan 1996; Livingston and Schofield 1996). There is some evidence of spawning stock fidelity for those sub-stocks on the east coast (Cook Strait) and the west coast (off South

Table 1. List of 68 fishes corresponding to 86 taxonomic units that are managed under the New Zealand quota management system and for which total allowable commercial catch limits are set.

Common name(s)	Scientific name(s)	Taxonomic units	Reported commercial catch in 2019 (kg)
Hoki	*Macruronus novaezelandiae*[†]	1	122,404,872
Jack mackerel	*Trachurus declivis*[†], *T. murphyi*[‡], *T. novaezelandiae*	3	40,734,597
Southern blue whiting	*Micromesistius australis*[‡]	1	31,887,837
Barracouta	*Thyrsites atun*[†]	1	18,415,124
Ling	*Genypterus blacodes*[†]	1	16,740,636
Blue mackerel	*Scomber australasicus*[†]	1	10,299,535
Oreo	*Pseudocyttus maculatus*[†], *Allocyttus niger*[†], *Neocyttus rhomboidalis*, *A. verrucosus*	4	8,949,515
Silver warehou	*Seriolella punctata*	1	8,607,869
Orange roughy	*Hoplostethus atlanticus*[†]	1	8,018,783
Snapper	*Chrysophrys auratus* [†]	1	6,349,644
Tarakihi	*Nemadactylus macropterus*[†], *Nemadactylus* sp.[§] (King Tarakihi)	2	5,149,627
Spiny dogfish	*Squalus acanthias*[‡]	1	5,053,718
Gurnard	*Chelidonichthys kumu*[†]	1	4,028,509
Trevally	*Pseudocaranx dentex*[†]	1	3,089,874
Common warehou	*Seriolella brama*	1	2,928,547
Red cod	*Pseudophycis bachus*[†]	1	2,904,727
Frostfish	*Lepidopus caudatus*[§]	1	2,869,061
Giant stargazer	*Kathetostoma giganteum*[§]	1	2,839,591
School shark	*Galeorhinus galeus*[†]	1	2,733,332
Redbait	*Emmelichthys nitidus*	1	2,673,588
Hake	*Merluccius australis*[†]	1	2,641,532
Alfonsino & Long-finned beryx	*Beryx splendens*[†], *B. decadactylus*	2	2,342,198
Gemfish	*Rexea solandri*[†]	1	2,194,494
Kahawai	*Arripis trutta*, *Arripis xylabion*	2	2,042,298
Flatfish	*Colistium nudipinnis*, *Peltorhamphus novaezelandiae*, *C. guntheri*, *Rhombosolea retiaria*, *R. plebeian*, *R. leporine*, *R. tapirine*[‡], *Pelotretis flavilatus*	8	1,939,211
Blue cod	*Parapercis colias*[†]	1	1,843,655
Rough skate	*Zearaja nasuta*	1	1,431,725
Ghost shark	*Hydrolagus novaezealandiae*	1	1,402,288
Rig	*Mustelus lenticulatus*[†]	1	1,364,148
Elephant fish	*Callorhinchus milii*	1	1,353,839
Hāpuku & Bass (Gropers)	*Polyprion oxygeneios*[†], *Polyprion americanus*[‡]	2	1,259,378
Sea perch	*Helicolenus percoides*[§]	1	1,160,885
White warehou	*Seriolella caerulea*	1	1,027,749
Ribaldo	*Mora moro*	1	1,020,763
Southern bluefin tuna	*Thunnus maccoyii*	1	956,979
Grey mullet	*Mugil cephalus*	1	851,969
Pale ghost shark	*Hydrolagus bemisi*	1	840,215
Smooth skate	*Dipturus innominata*	1	701,929
Cardinal fish	*Epigonus telescopus*	1	696,222
Bluenose	*Hyperoglyphe antarctica*[‡]	1	671,119
John dory	*Zeus faber*[§]	1	611,135
Blue moki	*Latridopsis ciliaris*[§]	1	543,325
Lookdown dory	*Cyttus traversi*	1	420,470
Short-finned freshwater eel	*Anguilla australis*[†], *A. reinhardtii*	2	346,798
Pilchard	*Sardinops sagax*	1	343,381
Leatherjacket	*Meuschenia scaber*	1	320,447
Kingfish	*Seriola lalandi*[‡]	1	316,421
Swordfish	*Swordfish*[‡]	1	262,437
Rubyfish	*Plagiogeneion rubiginosum*	1	225,005
Ray's bream	*Brama brama*	1	140,150

(*Continued*)

Table 1. Continued.

Common name(s)	Scientific name(s)	Taxonomic units	Reported commercial catch in 2019 (kg)
Butterfish	*Odax pullus*	1	110,807
Blue shark	*Prionace glauca*	1	100,183
Parore	*Girella tricuspidata*	1	81,364
Long-finned freshwater eel	*Anguilla dieffenbachii*†	1	65,971
Trumpeter	*Latris lineata*‡	1	62,499
Porae	*Nemadactylus douglasii*	1	54,594
Bigeye tuna	*Thunnus obesus*	1	54,417
Moonfish	*Lampris guttatus*‡	1	45,367
Red snapper	*Centroberyx affinis*	1	37,739
Porbeagle shark	*Lamna nasus*	1	36,222
Yellow-eyed mullet	*Aldrichetta forsteri*	1	33,175
Mako shark	*Isurus oxyrinchus*	1	26,180
Pacific bluefin tuna	*Thunnus orientalis*†	1	21,629
Garfish	*Hyporhamphus ihi*	1	16,418
Yellowfin tuna	*Thunnus albacares*	1	4919
Anchovy	*Engraulis australis*	1	3628
Patagonian toothfish	*Dissostichus eleginoides*	1	20
Sprats	*Sprattus antipodum, S. muelleri*	2	3

(†): Fishes for which genetic population structure hypotheses have already been tested among New Zealand locations. (‡): Fishes that have only been part of a broader population genetic study with one or few sampled locations in New Zealand. (§): Fishes that have only been part of studies at an inter-specific scale with one or few sample locations or specimens in New Zealand.

Island), but no characteristics (otolith rings, mean number of gill rakers or otolith microchemistry) appear to be reliable predictors of spawning ground origin (Hicks et al. 2003; Francis et al. 2011).

No evidence in support of genetic differentiation of *M. novaezelandiae* stocks in New Zealand has been found to date. Allozyme studies of nine locations (Smith et al. 1981), cytochrome *b* direct sequencing on the west coast, Cook Strait, and Chatham Rise (Baker et al. 1995) and mitochondrial DNA restriction fragment length polymorphism (RFLP) on the west coast and Cook Strait (Smith et al. 1996) were unable to detect any significant genetic structure. Microsatellites have only been used on two east coast locations as part of a broader geographical study, again showing no substructure between locations (Takeshima et al. 2011). This means that the hypothesis of two main hoki stocks with spawning ground fidelity has not been confirmed by genetic studies to date. This apparent lack of genetic structure could be explained by a level of migration that is high enough to homogenise sub-populations at neutral sites or that the markers used to date (allozymes, cytochrome *b*) were of too low-resolution for a species with such large population size and thus lacked discriminatory power. On a broader geographical scale, comparing New Zealand and Tasmanian populations led to contrasting results. While Baker et al. (1995) detected significant differences in haplotype frequencies between these populations using cytochrome *b* sequences, Smith et al. (1996) found no structure using RFLP.

*Orange roughy (***Hoplostethus atlanticus***, Trachichthyidae)*

A large deep-sea fish that is widely distributed in the South Pacific, Indian, south-east, and north-east Atlantic oceans. It mostly occurs along continental slopes, ocean ridges, and

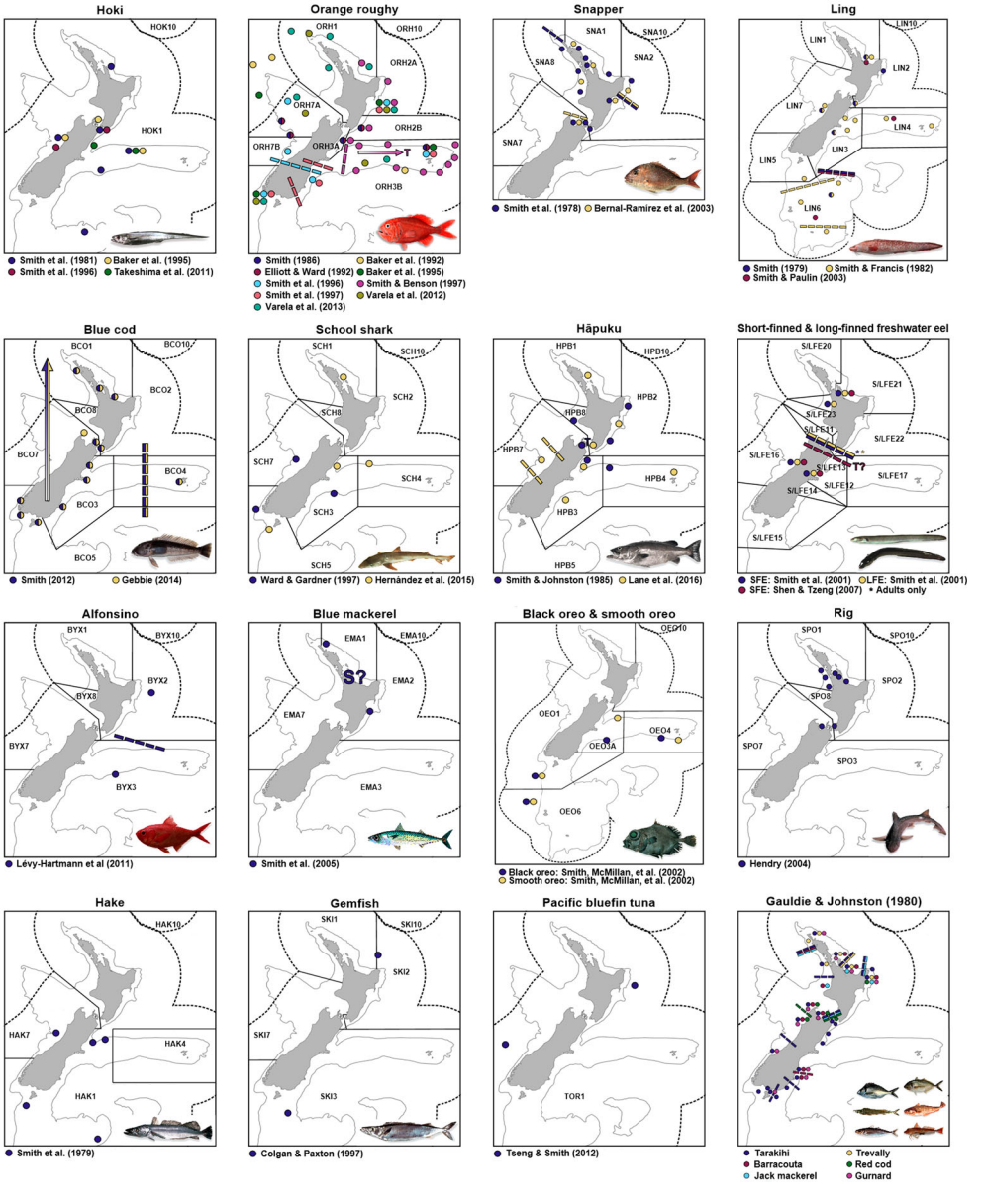

Figure 2. Maps of fish population genetic studies in New Zealand. Dots represent sample points. Dashed lines are spatial genetic breaks that have been reported as significant by their respective studies. Gradient arrows represent isolation by distance. T: temporal variation. S: sympatric lineages. Colours correspond to the respective reported study, except in the last map were they represent the respective species from the multi-species allozyme study of Gauldie and Johnston (1980). Half-dots are samples that have been re-used across studies. Solid black lines represent Quota Management Area boundaries, with names in black capital letters (not represented in the last map for visibility). The black dashed line shows the boundary of the New Zealand Exclusive Economic Zone (EEZ) and the continuous line is the 1000 m bathymetric contour. Sample points particularly close spatially were merged for visibility. When studies only reported broad sampling areas, points were placed arbitrarily in the centre of the reported area. Maps are scaled to cover their relevant areas. Only studies that have tested genetic population structure hypotheses among at least two New Zealand locations are reported here. Images of fish were used with permission from Seafood New Zealand (https://www.seafood.co.nz/) or are in the public domain.

Table 2. 23 fish species for which genetic population structure hypotheses have already been tested among New Zealand locations.

Species	Current stocks hypothesis (Fisheries New Zealand 2018)	New Zealand Genetic structure	Trans-Tasman differentiation	Markers (no. loci)	Sample distribution (no. sites)	References
Hoki (*Macruronus novaezelandiae)*	2 stocks: west coast and east coast	(I) panmictic[1,2,3,4]	yes[2]/no[3]	[1] allozymes (15), [2] mt seq (cyt *b*), [3] mt RFLP (6), [4] mt seq (cyt *b* + CR), msat (4)	[1] CR (2), WCSI (2), CS (2), PR(2), BP, [2] WCSI, CS, CR, Tas, [3] WCSI, CS, Tas, [4] CR (2), Chile (3)	[1] Smith et al. (1981), [2] Baker et al. (1995), [3] Smith et al. (1996), [4] Takeshima et al. (2011)
Orange roughy (*Hoplostethus atlanticus)*	>8 stocks	(I) panmictic[1,2,4,8,9], (II) IBD[6], (III) distinct populations[5,6,7], (IV) temporal variation[6]	no[3,4,5,8,9]	[1] allozymes (22), [2] VNTR (3), [3] allozymes (11). [4] mt seq (cyt *b*), [5] mt RFLP (6), [6] allozymes (11), [7] allozymes (11), RAPD (29), mt CAPS (3), [8] mt seq (COI + cyt *b*), [9] msat (9)	[1] ChP (2), Kai, Wai, CR, Atl (2), [2] CR, LHR (2), [3] [1], Aus (6), Tas (5), [4] PB, CR, ChP, RB, LHR, Tas, SA, [5] PB, Wait / WCSI, ChP, RB, CR, Tas, [6] BP, EC, RB, Wai, Kai / CR (10), [7] PB / Wait / CR, RB, [8] LHR, NNZ, ChP, PB, CR, RB, LR, Aus (2), Chile, Atl (3), [9] ChP, PB, CR, RB, BP (4), NNZ (8), Aus (2), Chile, Atl (3)	[1] Smith (1986), [2] Baker et al. (1992), [3] Elliott and Ward (1992), [4] Baker et al. (1995), [5] Smith et al. (1996), [6] Smith and Benson (1997), [7] Smith et al. (1997), [8] Varela et al. (2012), [9] Varela et al. (2013)
Snapper (*Chrysophrys auratus)*	possibly 7 stocks	(III) distinct populations[1,2]	yes[†]	[1] allozymes (23), [2] mt seq (CR), msat (7)	[1] CE, West NNZ (2) / East NNZ (2), HG, BP, EC / HB, MS, TB, Wel, [2] East NNZ, HG, EC / TB / Raglan, HB	[1] Smith et al. (1978), [2] Bernal-Ramírez et al. (2003)
Ling (*Genypterus blacodes)*	5 stocks	(III) distinct populations[1,2,3]	yes[3]	[1] allozymes (2), [2] allozymes (1), [3] mt seq (cyt *b* + CR)	[1] EC + BP, CS, CB, WCSI / PR, [2] [1], Kai, WCSI, BP, SI, CR (10) / PR (3), AI (2) / CI (2), [3] BP, CR / CP / Tas (2)	[1] Smith (1979), [2] Smith and Francis (1982), [3] Smith and Paulin (2003)
	>8 stocks		–			

(*Continued*)

Table 2. Continued.

Species	Current stocks hypothesis (Fisheries New Zealand 2018)	New Zealand Genetic structure	Trans-Tasman differentiation	Markers (no. loci)	Sample distribution (no. sites)	References
Blue cod (*Parapercis colias*)		(II) IBD[1,2], (III) distinct populations[1,2]		[1] mt seq (CR), [2] mt seq (CR), msat (7)	[1] NNZ, BP, MS (3), Wel, Kai, Banks, Ota, Stl, Fio (2) / Chl, [2] [1], GB	[1] Smith (2012), [2] Gebbie (2014)
School shark (*Galeorhinus galeus*)	1 stock	(I) panmictic[1,2]	no[1,2,†]	[1] allozymes (29), mt RFLP (10), [2] mt seq (CR), msat (8)	[1] WCSI (2), ECSI, Atl, Arg, SA, Aus (2), Tas (3), [2] East NNZ, Kai, CR, BRSI, Aus (4), Tas (2), Chile (1)	[1] Ward and Gardner (1997), [2] Hernández et al. (2015)
Hāpuku (*Polyprion oxygeneios*)	Unknown, probably 1 stock	(IV) temporal variation[1], (III) distinct populations[2]	–	[1] allozymes (2), [2] mt seq (CR), msat (9)	[1] CS (18), Kai, EC, CR, Wai (2), CE (2), [2] NNZ, HB,CS (2), Kai, Ota, CI / WCSI	[1] Smith and Johnston (1985), [2] Lane et al. (2016)
Short-finned freshwater eel (*Anguilla australis*)	1 stock	(III) distinct populations[2] (adults only)[1]	yes[2]	[1] allozymes (10), [2] msat (7)	[1] Rivers: WCSI (2), ECSI (2) / BP, Raglan (2), [2] Rivers: WCSI, Banks, BP	[1] Smith et al. (2001), [2] Shen and Tzeng (2007)
Long-finned freshwater eel (*Anguilla dieffenbachia*)	1 stock	(III) distinct populations (adults only)	–	allozymes (9)	Rivers: WCSI (3), ECSI / BP, Raglan	Smith et al. (2001)
Alfonsino (*Beryx splendens*)	unknown	(III) distinct populations	yes (ECNI)	mt seq (cyt *b*)	NC (7), Japan, ECNI / CR, Aus (2), West Indian Ocean, / Atl	Lévy-Hartmann et al. (2011)
Blue mackerel (*Scomber australasicus*)	At least 3 stocks	(V) sympatric?	no[†]	mt seq (CR)	NNZ, HB, Aus	Smith et al. (2005)
Black oreo (*Allocyttus niger*)	4 stocks	(I) panmictic	yes[†]	mt CAPS (10), nuc CAPS (11)	ECSI (2), CR (2), PSM (6)	Smith, McMillan, et al. (2002)
Smooth oreo (*Pseudocyttus maculatus*)	4 stocks	(I) panmictic	no[†]	mt CAPS (10), nuc CAPS (11)	ECSI (1), CR (2), PSM (6)	Smith, McMillan, et al. (2002)
Rig (*Mustelus lenticulatus*)	5 stocks	(I) panmictic	–	allozymes (17), mt RFLP (12)	TB, CS, Raglan, West NNZ (2), BP, HG (2)	Hendry (2004)
Hake (*Merluccius australis*)	3 stocks	(I) panmictic	–	allozymes (2)	WCSI, Banks, CR, SI, CP	Smith et al. (1979)
Gemfish (*Rexea solandri*)	2 stocks	(I) panmictic	no	allozymes (17), mt RFLP (11)	NNZ, WCSI, Aus (8)	Colgan and Paxton (1997)

Pacific bluefin tuna (*Thunnus orientalis)*	1 Pacific stock	(I) panmictic	–	msat (7), mt seq (CR + cyt *b*)	NNZ, WCSI, Taiwan	Tseng and Smith (2012)
Tarakihi (*Nemadactylus macropterus)*	1 stock	(III) distinct populations or adaptive cline	yes† / no†	allozymes (2)	NNZ, HG / BP / EC (2), CS (2), Kai (2), Wait, Ota / NPFS (2) / BRSI (3), WCSI / KB, GB, TB / WA	Gauldie and Johnston (1980)
Trevally (*Pseudocaranx dentex)*	c. 3 stocks, may be more	(III) distinct populations or adaptive cline	–	allozymes (2)	NNZ (2), HG / BP, EC, CE, WA	Gauldie and Johnston (1980)
Barracouta (*Thyrsites atun)*	At least 4 stocks	(III) distinct populations or adaptive cline	–	allozymes (2)	WA / HG, BP, EC, Wait / Ota, KB, GB, TB	Gauldie and Johnston (1980)
Red cod (*Pseudophycis bachus)*	unknown	(III) distinct populations or adaptive cline	–	allozymes (2)	KB / GB, TB / CS, EC	Gauldie and Johnston (1980)
Jack mackerel (*Trachurus declivis)*	unknown	(III) distinct populations or adaptive cline	–	allozymes (2)	CE / BP / EC /	Gauldie and Johnston (1980)
Gurnard (*Chelidonichthys kumu)*	unknown	(I) panmictic?	–	allozymes (2)	EC, WA, NNZ (2), HG, BP, EC, Wait, Ota, BRSI, WCSI, KB, GB, TB	Gauldie and Johnston (1980)

Notes: Only population genetic studies which have sampled more than one area in New Zealand are reported here. Studies with genetic data from only one area (†) are reported in Table S1. mt: mitochondrial DNA; nuc: nuclear DNA; seq: direct sequencing; cyt *b* = cytochrome *b*; CR = control region; COI = cytochrome *c* oxidase subunit I; RFLP: restriction fragment length polymorphism; VNTR: variable number tandem repeat; RAPD: random amplified polymorphic DNA; CAPS: cleaved amplified polymorphic sequence; msat: microsatellites. '/' indicates a significant genetic differentiation. New Zealand locations: CR = Chatham Rise, WCSI = West Coast of South Island; CS = Cook Strait, PR = Pukaki Rise, B*P* = Bay of Plenty, Ch*P* = Challenger Plateau, Kai = Kaikoura/Pegasus Bay, Wai = Wairarapa, PB = Puysegur Bank, RB = Ritchie Bank, Wait = Waitaki/Timaru, EC = East Cape, NNZ = Northern NZ, CB = Canterbury Bight, SI = Snare Islands, AI = Auckland Island, CI = Campbell Island, *CP* = Campbell Plateau, MS = Marlborough Sounds, Wel = Wellington, Banks = Banks Peninsula, Chl = Chatham Islands, Fio = Fiordland, Ota = Otago, Stl = Stewart Island, GB = Golden Bay, ECSI = East Coast South Island, CE = Cape Egmont, HB = Hawkes Bay, PSM = Puysegur-Snares-Macquarie Ridge, TB = Tasman Bay, HG = Hauraki Gulf, NPFS = Nugget Point/Foveaux Strait, BRSI = Bluff/Riverton/Solander Islands, KB = Karamea Bight, WA = West Auckland, ECNI = East Coast North Island; other locations: LHR = Lord Howe Rise, LR = Louisville Ridge, Tas = Tasmania, Aus = Australia, SA = South Africa, Atl = Atlantic Ocean, Arg = Argentina, NC = New Caledonia. Current stocks hypotheses are reported from New Zealand fisheries assessment literature and are based on various types of observations and scientific data that sometimes include genetics.

seamounts at depths between 700 and 1500 m and is targeted by trawling. In spite of their extensive distribution, the adults do not appear to be highly migratory. The movement data inferred from seasonal catches only show migration of a few hundred kilometres (Francis and Clark 1998). Absolute and relative fecundity is low. They are also slow-growing, reaching maturity at 20–30 years of age and evidence from otoliths suggest they can live for more than 100 years (Fenton et al. 1991; Branch 2001). The low productivity of orange roughy makes it particularly vulnerable to overfishing. Indeed, stocks have rapidly declined globally: orange roughy fisheries have collapsed in several countries, resulting in closures. While New Zealand hosts the last large-scale commercial fishery in the world (>8000 tonnes reported commercial catches in 2018), several stocks are depleted (Dunn and Forman 2011). In the New Zealand EEZ, the Quota Management System divides orange roughy fisheries into eight areas, each one probably containing several discrete stocks (Fisheries New Zealand 2018), with the main fisheries being off the southeast of the North Island and the northern South Island, and on the Chatham Rise. There have been numerous attempts to determine the stock structure of New Zealand orange roughy by using several methods, such as genetics, morphometrics, parasite analysis, life history parameters, size structure and timing of spawning. While most of these studies were able to find some differences between areas, it is difficult to infer persistent patterns of geographic variation inside the EEZ based on these, as reviewed in Branch (2001) and Clark et al. (2016). Evidences of an isolated stock on Challenger Plateau based on parasite analysis were corroborated by an age and length at maturity study, but not by further studies using the same method or genetics. The Challenger Plateau area (ORH7A) is however still managed as a single separate stock, based on evidence (genetics, size structure, time of spawning, fishery distribution …) of differentiation with nearby fishing areas outside the EEZ (Clark et al. 2016). At least two main stocks are recognised in ORH 3B (Chatham Rise and Puysegur), based on genetic evidence (but see below). Biological stock structure is considered uncertain or unknown across other New Zealand management areas and the separation of stocks for assessment purposes is mainly putative and based on sparse evidence like spawning grounds location, inference of migration and catch-per-unit effort trends (Fisheries New Zealand 2018).

The findings reported for population genetic studies of *H. atlanticus* in New Zealand waters have been inconsistent. The first studies used samples from several locations and found no genetic differentiation between western and eastern fishing grounds using 22 allozyme loci (Smith 1986), variable number tandem repeat 'fingerprinting' (Baker et al. 1992), and cytochrome *b* sequences (Baker et al. 1995). However, subsequent analyses of mitochondrial DNA RFLP, allozymes, and random amplified polymorphic DNA (RAPD) have detected genetic heterogeneity among populations from the Challenger Plateau, West Coast South Island, Chatham Rise, east coast of North Island, and off the southern coasts of Puysegur and Waitaki (South Island). The detection of genetic differences appears to depend on the type of marker used (Smith et al. 1996; Smith et al. 1997; Smith and Benson 1997). Among studies a significant level of genetic differentiation between southern stocks (Puysegur and Waitaki) and all other stocks was reported. This could be due to the fact that these southern stocks lie within the convergence between sub-Antarctic and subtropical water (Figure 1), a barrier that appears to be associated with a major faunal disjunction for many fishes (Paul 1986). Multiple sampling along the Chatham Rise also showed spatial and temporal heterogeneity at two allozyme loci,

genetic divergence with the North and South Island coasts and evidence for IBD (Smith and Benson 1997). In contrast, more recent analyses using cytochrome *c* oxidase subunit I (COI) and cytochrome *b* sequences as well as microsatellites on samples collected from all around New Zealand did not detect any genetic structure (Varela et al. 2012; Varela et al. 2013). Likewise, some genetic structure has been detected among Australian localities and between Australia and New Zealand (Ovenden et al. 1989; Smolenski et al. 1993) although further studies did not corroborate those findings (Elliott and Ward 1992; Baker et al. 1995; Varela et al. 2012; Varela et al. 2013). As a result, patterns of population differentiation in orange roughy have been deemed inconsistent (Ward and Elliott 2001). Allozymes and RFLP, coupled with non-genetic methods were able to validate the independent stock status of three fishing grounds in New Zealand EEZ and international waters: south-west Challenger Plateau, north-west Challenger Plateau, and Lord Howe Rise (Smith, Robertson, et al. 2002). On a more global scale, there was a small but significant level of genetic differentiation between north Atlantic and southern hemisphere populations (Smith 1986; Elliott et al. 1994; Varela et al. 2012; Varela et al. 2013). In the Southern Hemisphere, no significant differentiation has been detected among populations from South Africa, Australia, and New Zealand (Smolenski et al. 1993; Baker et al. 1995), while the multi-continental study using DNA microsatellites by Varela et al. (2013) revealed a pattern of IBD at the global scale as well as significant genetic differentiation between stocks sampled from Chile, Namibia, and Australia / New Zealand that was undetectable using mitochondrial DNA sequence data (Varela et al. 2012).

*Australasian snapper (*Chrysophrys auratus*, Sparidae)*

A coastal species commonly referred to as 'snapper' that inhabits the rocky reef ecosystems around Australia and New Zealand. While recognised as a single species, snapper between New Zealand and Australia are genetically distinct (Tabata and Taniguchi 2000). Snapper can be found at depths down to 200 m but most commonly occur between 10 and 50 m. Juvenile snapper require sheltered estuaries for development. This species reaches sexual maturity at 3–4 years of age. Areas around North Island such as Parengarenga, Rangaunu, Mahurangi, Whangapoua, Whangarei, Whangape, Kaipara, and Huruhi harbours have been identified as the key locations for snapper recruitment (Parsons et al. 2014). Snapper is one of New Zealand's most important inshore fisheries with c. 6400 tonnes of total allowable commercial catch and an additional recreational allowance of c. 3700 tonnes per year (Fisheries New Zealand 2019b). There are thought to be seven or eight distinct stocks of snapper, which are being managed over four areas around the North Island (three stocks off the North Coast (SNA1), two off the East Coast (SNA2, one of which may be associated with the North Coast), and one off the West Coast (SNA8)) and northern parts of the South Island (SNA7, two stocks). North Coast (Northland, Hauraki Gulf, and Bay of Plenty) and West Coast comprise the majority of the fisheries with 4500 and 1300 tonnes of total allowable commercial catch respectively. Snapper stocks have been heavily fished over the last 100 years. Although the North Coast is thought to have been reduced to less than 20% of its original biomass, current estimates show signs of recovery. The West Coast stock is considered to be depleted below the soft limit of 20%. South Island stocks (Tasman Bay and Marlborough Sounds) were severely depleted (<10% original biomass) but now show a trend of increasing size. Statistical

projections estimate that the South Island stocks will be above its soft limit by 2022 and under current conditions could return to 40% of its original biomass (Fisheries New Zealand 2018). The severe population size bottleneck in the South Island stocks is supported by the observed loss of genetic variation (Hauser et al. 2002), likely caused by increased genetic drift following exploitation. Population trends for the East Coast stocks are less clear. Although there is evidence, based on catch at age sampling, for two separate sub-stocks with the boundary at the southern tip of Mahia Peninsula (Walsh et al. 2012), the East Coast is still managed as a single administrative area. Both sub-stocks showed fluctuating trends over the last two decades (Fisheries New Zealand 2018).

Genetic analyses support in part stock structure models used for fisheries management. Early work using allozymes identified a North and a West coast population along the North Island (Smith et al. 1978). Using mitochondrial and microsatellite DNA data, Bernal-Ramírez et al. (2003) found a genetic pattern consistent with population differentiation. Sampling sites along the North Coast of the North Island did not show any significant divergence. The population in Tasman Bay (South Island) was identified as an isolated population, and the Hawkes Bay (East Coast North Island) population was genetically more similar to the West Coast North Island. This led the authors to hypothesise that gene flow was promoted via the D'Urville and Wairarapa coast current. This finding also supports the two recognised sub-stocks along the North Island East Coast, with a gene flow barrier around the Mahia Peninsula. Recent genomic work on snapper involved genome assembly, quantitative trait loci (QTL)-mapping and creation of a 95% optically mapped linkage map (Ashton, Ritchie, et al. 2019; Ashton, Hilario, et al. 2019).

*Ling or pink cusk-eel (*Genypterus blacodes*, Ophidiidae)*

An eel-like bottom dwelling fish distributed throughout the southern hemisphere, including off the coasts of New Zealand, southern Australia, and Patagonia at depths from 200 to 800 m. They have constantly been in the list of the top five most heavily fished species in New Zealand for the past few years (more than 18,500 tonnes in 2018) and are mainly caught by bottom trawling on the Southern Plateau and the Chatham Rise, although they are also targeted by long line along West Coast South Island and across the North Island coast south of East Cape. Spawning grounds are relatively well documented and distinct but the patterns of larval transport are unknown (Morrison et al. 2014). An integrative review of ling population stock structure around New Zealand concluded that they comprised at least five distinct stocks: Campbell Plateau, Bounty Plateau, Chatham Rise, West Coast South Island, and Cook Strait (Horn 2005). Those conclusions were mainly based on differences in life history traits like growth rates, length and age at maturity, and timing of spawning.

Only three genetic studies have been conducted on ling from New Zealand (Smith 1979; Smith and Francis 1982; Smith and Paulin 2003) and all of them have detected some level of stock structure. Smith (1979) used data from the polymorphic enzyme glucose phosphate isomerase, collected from sampling of a few New Zealand locations, to suggest a differentiation between stocks from Pukaki Rise (southern continental shelf) and from mainland (i.e. North and South Island). The subtropical convergence zone (Figure 1) was suspected to be acting as a geographical barrier to gene flow and mixing of stocks

could potentially occur to the north in the Canterbury Bight. This dataset was expanded with the same allozyme and more samples by Smith and Francis (1982). They also did not detect any heterogeneity among mainland locations but found differentiation, based on allele frequencies, between Campbell Island and Pukaki Rise / Auckland Islands samples ($P < 0.10$), as well as some heterogeneity among Chatham Rise samples. These results were interpreted as further evidence for a mainland stock that extends as far south as the Snares, a second stock on the northern Campbell Plateau (Pukaki Rise / Auckland Islands), and a possible third one around Campbell Island, with mixing of stocks along the Chatham Rise. It is important to note that none of the population boundaries suggested in both these studies had strong statistical support. As a result, evidence for population structure from these studies has been considered weak (Daley et al. 2000; Horn 2005). The third study by Smith and Paulin (2003) primarily aimed at re-assessing the taxonomic status of some *Genypterus* species in New Zealand and Australia, but these data from the mitochondrial DNA control region were also able to show a significant genetic differentiation between pink ling populations from the Campbell Plateau and the two northern locations investigated (Bay of Plenty and Chatham Rise), as well as between populations from New Zealand and from Tasmania. Although the results reported in the two first studies lacked strong statistical support and the existence of genetic stock structure has been questioned due to its high mixing potential (Horn 2005), all genetic studies conducted so far indicate the presence of a barrier to gene flow between ling stocks from the mainland and the southern plateau. This separation is most likely due to the subtropical front acting as a barrier to migration. A more extensive genetic sample of ling fishing grounds and high-resolution genetic markers would be helpful to resolve this uncertainty.

*Blue cod (*Parapercis colias*, Pinguipedidae)*

A bottom dwelling, territorial reef fish endemic to New Zealand. It is widely distributed in coastal waters that have a rocky substrate and found throughout the country at depths down to 150 m. It is most abundant south of Cook Strait and around the Chatham Islands. The major commercial fisheries are off Southland (lower South Island) and the Chatham Islands, with catches also happening regularly off the east coast of the South Island (Otago, Canterbury) and Cook Strait (Marlborough Sounds and Wanganui). More than 1800 tonnes of blue cod were commercially caught in 2019, and the recreational fishery is also quite significant with more than 500 tonnes of allowed catch (Fisheries New Zealand 2019b). Blue cod seem to have a relatively low capacity for dispersal compared with other similar fisheries species. Eggs and larvae have a pelagic phase of only 10 days before settling (Henderson 2009). Males are territorial and tagging studies have shown that most adults do not travel distances of more than 1 km (Gebbie 2014). Blue cod are managed in eight Quota Management Areas based on their distribution and abundance. Studies of stock structure are sparse. The findings of tag-recapture studies suggested low dispersal of adults (Carbines and McKenzie 2004) and spatially structured populations with limited mixing within relatively small areas, which was a finding also supported by evidence from otolith microchemistry in Fiordland and Banks Peninsula (Beer and Carbines 2012).

Two unpublished studies have investigated blue cod population genetic structure using an extensive New Zealand-wide sampling. Using the mitochondrial control region, Smith (2012) found significant genetic differentiation between samples from the Chatham Islands and mainland New Zealand. However, no clear population boundaries were detected among regions from both the North and South Islands, although sampling consisted of catches as far apart as Puysegur Point and Northland. However, pairwise F_{ST} results from mainland samples were positively correlated to geographic distance, albeit very weakly ($R^2 = 0.26572$, $P = 0.08$) which could be a pattern of IBD across the North and South Islands. Identical results were found by Gebbie (2014) when expanding the sampling by one more site and using the same genetic marker. However, investigating microsatellite DNA polymorphisms in samples from a sub-set of those locations did not detect any structured genetic pattern around mainland New Zealand, be it IBD or population boundaries. Blue cod is a good example of a species for which genetic structure should be expected given its low capacity for dispersal (i.e. short egg/larval stage and sedentary adult life). Since there only needs to be a small number of effective migrants exchanged each generation to homogenise genetic variation even which such low levels or movement, genetic differentiation might not be detected using those markers. Although blue cod from the Chatham Islands clearly consist of a separate stock, it is possible that a single nucleotide polymorphism (SNP)-level analysis on a similar sampling scale will provide the needed resolution to detect stronger patterns of neutral and/or adaptive heterogeneity among mainland populations.

Other fishery species

Few other New Zealand EEZ fishes have population genetic information available, with New Zealand-wide studies being very sparse and often restricted to a few locations encompassing only a small portion of their range.

An early study by Gauldie and Johnston (1980) used two allozymes to conduct a New Zealand-wide study on six fish species (tarakihi, trevally, barracouta, red cod, jack mackerel and gurnard), with a sampling of thousands of individuals that was impressive in quantity and in spatial distribution. This study was able to detect significant population structure based on Z-statistics in all of the species examined, except for the red gurnard. Some of the geographic stock boundaries were shared by some of the species. However, the year-to-year levels of genetic variation in one location for tarakihi and trevally (the two species with temporal samples available) was not significantly different from spatial levels of genetic variation. Moreover, correlations between allele frequencies and water temperature were detected. As a result, the authors strongly suspected that these genetically distinct groups were due to selective clines and not genetic isolation.

School shark (*Galeorhinus galeus)* is a species which occurs in coastal waters of the Pacific, Antarctic, and Indian oceans and is listed as *vulnerable* due to global overexploitation. Two global genetic studies suggest that school shark populations are isolated at the continental level. The first used mitochondrial control region sequences to detect (at least partially) isolated populations from North America, South America, Europe, South Africa, and Australia (Chabot and Allen 2009), while the second detected three clades (South America, South Africa and Australasia) with microsatellites and nuclear sequencing data (Bester-van der Merwe et al. 2017). New Zealand and Australian school sharks,

however, seem to consist of one genetically homogenous group (Ward and Gardner 1997; Hernández et al. 2015; Bester-van der Merwe et al. 2017; Devloo-Delva et al. 2019), a hypothesis that is supported by evidence of recurring trans-Tasman migration.

Both hāpuku (*Polyprion oxygeneios*) and bass (*P. americanus*) are managed in New Zealand as a single fishery under the name 'groper', despite being recognised as different biological species with different distributions. Both species lack reliable information about their stock structure in New Zealand. An early study on hāpuku detected temporal variation of allozyme frequencies in the Cook Strait area (Smith and Johnston 1985), while microsatellite DNA analysis showed that individuals sampled from West Coast South Island (Hokitika) were genetically distinct from individuals sampled at all other New Zealand sites (Lane et al. 2016). Bass have been investigated with genetic markers in two global studies using only one New Zealand location. Both studies did not detect any significant lack of gene flow between New Zealand and Australia (Sedberry et al. 1996; Ball et al. 2000).

Short-finned (*Anguilla australis*) and long-finned (*A. dieffenbachia*) freshwater eels show allozyme genetic differentiation between North Island and South Island adults, but no heterogeneity was detected among glass eels (i.e. juveniles). Although treated separately, those results were identical for both species. It was concluded that both species consisted each of a single panmictic population with adults subjected to selection or a 'sweepstake' type reproduction event (Smith et al. 2001). A significant level of genetic differentiation was found between North and South Island short-finned eels using microsatellite DNA, although the authors were unsure if this was due to geographic or temporal variation (Shen and Tzeng 2007).

Mitochondrial DNA control region haplotype frequencies of Alfonsino (*Beryx splendens*) showed that the Chatham Rise and East Coast North Island populations were significantly different (Lévy-Hartmann et al. 2011). Moreover, hierarchical analysis of molecular variance and neighbour-joining tree analysis of the data showed that Chatham Rise alfonsinos were genetically more similar to the ones from Australia and the Indian Ocean, while another cluster consisted of fish sampled from East Coast North Island, New Caledonia, and Japan.

Mitochondrial control region sequences of the blue mackerel (*Scomber australasicus)* were used to build a neighbour-joining tree which showed strong support (bootstrap > 90%) for the presence of two phylogroups in the dataset. However, there was no geographical structure because specimens from all of the sampled areas (North Cape and Hawke's Bay (New Zealand) and South Australia) were found in both phylogroups and there was no detectable differentiation among populations (Smith et al. 2005).

Complete genetic homogeneity was observed for the pacific bluefin tuna (*Thunnus orientalis)* between New Zealand East Coast North Island, West Coast South Island, and Taiwan based on several genetic markers using a neighbour-joining tree reconstruction (Tseng and Smith 2012).

Other fishes for which the hypothesis of panmixia has not been rejected by genetic analyses of New Zealand-wide sampling include black oreo and smooth oreo (Smith, McMillan, et al. 2002), rig (Hendry 2004), hake (Smith et al. 1979), and gemfish (Colgan and Paxton 1997). None of them have yet been investigated using microsatellite DNA, Sanger direct sequencing, or genome-wide sequencing. Some other species have been investigated as part of broader studies with only one location (or none) in New Zealand and are reported in Table S1. Some highly migratory fishes with a wide distribution have shown

patterns of structure at the inter-oceanic scale only, thus genetic heterogeneity within New Zealand or Australasia can be considered unlikely (e.g. swordfish (Chow and Takeyama 2000), spiny dogfish (Veríssimo et al. 2010)). A similar Australasian-wide finding of genetic homogeneity could reasonably be expected from other fish with high dispersal capacity and broad distribution like blue shark, moonfish or most tunas. Conversely, some species with only one New Zealand location sampled have shown evidence of trans-Tasman differentiation (e.g. tarakihi (Elliott and Ward 1994; Grewe et al. 1994) and trumpeter (Tracey et al. 2007)), which suggests that within-New Zealand EEZ structure might be found. It is also interesting to note that evidence of trans-Tasman connectivity in a species does not necessarily mean that there is a panmictic 'Australasian' stock. Several studies have reported a genetic distinction between west and east Australia but not between east Australia and New Zealand. This is the case for kingfish (Nugroho et al. 2001; Miller et al. 2011), gemfish (Colgan and Paxton 1997) and mako shark (Corrigan et al. 2018).

Overall, very few New Zealand fisheries species have good population genetic data which has been used to define their stock boundaries. Snapper is the only species showing a population genetic structure that has been deemed consistent across studies and that is also partially supported with other methods of stock identification (Bernal-Ramírez et al. 2003; Parsons et al. 2014). Findings based on genetic data from other species have either been inconsistent (orange roughy), lacked in statistical support (ling), failed to reject selective neutrality (Gauldie and Johnston 1980) or did not detect any genetic structure. This lack of genetic heterogeneity found in most fishes could be because: (1) their stocks are genetically panmictic, but because this is typically the null hypothesis it is not easily tested (especially with non-genomic studies); (2) the genetic markers used up until this point in time lacked the resolution required to detect genetic differentiation; (3) there has been insufficient spatial sampling to properly test for genetic structuring.

Moving forward: use of genome-wide sequencing techniques

Genetic differentiation can be undetectable using traditional genetic approaches, such as microsatellite DNA or short stretch DNA sequencing, because these only sample a small portion of the genome. Signals of population genetic difference can be difficult to detect in some cases, because isolation may have only recently been established, low levels of persistent gene flow are homogenising most loci, or a large N_e makes genetic drift a weak force (Palsbøll et al. 2007; Attard et al. 2018). A lack of strong levels of population genetic structure is a common finding for studies of marine organisms. This is particularly pronounced in the many marine species with large populations and hence high levels of genetic diversity, and is further compounded in the many species with a high dispersal power (Sandoval-Castillo et al. 2018). Until recently, genetic markers had to be chosen carefully to give an accurate estimate of the amount and distribution of variation, to properly address the question asked, and be suitable for the practical limitations of data collection (Anne 2006). These constraints also make the comparison of results from different markers difficult (Portnoy and Heist 2012).

The development of genome-wide DNA sequencing technology, often referred to as 'Next Generation Sequencing', has fundamentally changed the type of population genetic data sets now available. These 'high-throughput' methods allow whole genome

sequencing data to be collected, and for species with large genomes, reduced-representation methods like restriction site associated DNA markers (RAD-Seq and ddRAD), and genotyping-by-sequencing (GBS), continue to make genome-wide population studies affordable. As DNA sequencing costs continue to decrease and research laboratories switch to these methods, genome-wide DNA sequencing data for fisheries species are slowly becoming more common, as is already the case in farm-based primary production sectors (Kumar and Kocour 2017; Li and Wang 2017). The large genome-wide amounts of SNPs obtained from these methods should provide higher levels of resolution to estimate more accurately F_{ST} and N_em than the small number of loci microsatellites could sample (Benestan 2019). Direct comparison of RAD sequencing and microsatellites on great scallop (Vendrami et al. 2017) showed that the genome-wide method could resolve population structure that was undetectable using typical suit of microsatellite loci. Genome-wide sequencing techniques can also provide more accurate estimates of relatedness (Thrasher et al. 2018) and genetic variation at the individual level (Lemopoulos et al. 2019) and are also better at detecting evidence of introgression (Bradbury et al. 2015). In some cases genetic structure can be detected by only sampling a few individuals per population (c. 8–10) as long as the genome-wide SNP density is high (Jeffries et al. 2016; Nazareno et al. 2017). Moreover, genome-wide SNP datasets can detect genomic regions under selection, while there is growing incentive for adaptive diversity to be relevant to fisheries management (Funk et al. 2012; Valenzuela-Quiñonez 2016). Before genomics made it possible to detect outlier loci, separating neutral from adaptive variation was either impossible (allozymes) or sometimes based on wrong assumptions (e.g. microsatellites (Cadrin 2020)). Genome-wide SNP data is becoming the preferred approach for addressing important fishery management issues (Allendorf et al. 2010; Portnoy and Heist 2012; Andrews et al. 2016). Although studies using genome-wide SNP data to resolve population structure of marine species have been growing in numbers in the last few years (e.g. European lobster (Jenkins et al. 2019), yellowfin tuna (Pecoraro et al. 2018), sea cucumber (Xuereb et al. 2018), and more …) none have been reported for New Zealand fish stocks.

Other issues in fisheries management that will benefit from a more systematic use of genetics and genomics

As we showed above, although the use of genomics will improve the resolution and confidence in testing genetic structure hypotheses, the advantages of that type of data are not limited to this specific question. The development of genome-wide markers has become an important tool for understanding some of the emerging issues in fisheries (Valenzuela-Quiñonez 2016; Bernatchez et al. 2017; Benestan 2019). For example, reliable estimation of stock size and resilience to environmental stressors are critical measures for sustainable fisheries management. In this section, four critical fisheries issues are briefly introduced and discussed, namely (1) the loss of diversity, (2) fishing-induced evolution, (3) the influence of climate change on stock sizes and range, and (4) the measurement of absolute abundance. These issues are only a few examples among the numerous applications of genetics in fisheries as thoroughly reviewed in Ovenden et al. (2015), but we focussed on what we think might be the main point of interests that could have been overlooked by fisheries managers in New Zealand.

Loss of genetic diversity and adaptive potential

Genetic diversity is the evolutionary potential of a population (Spielman et al. 2004; Sgrò et al. 2011). Higher levels of genetic diversity increase the likelihood that there will be advantageous variants in a population when a new environmental challenge arises. When population size is reduced the force of genetic drift increases, which eliminates alleles from the population. The consequence of lower diversity is reduced adaptive potential. In highly fecund species like most marine fish, N_e may be much smaller than the census population (N_c) due to a bias in reproductive success, large variation in year class strength, and size-dependant fecundity (Waples 2002). Indeed, harvesting often targets specific sexes or age classes which reduces the N_e:N_c ratio, thereby increasing the rate of loss of heterozygosity without having any detectable effect on population size. Marine finfish species generally display very large population sizes and are consequently assumed to maintain high levels of genetic diversity. It is therefore reasonable to assume that many fisheries species were originally characterised by a high adaptive potential, making them more resilient (Spielman et al. 2004; Sgrò et al. 2011). However, loss of genetic diversity can be significant in just a few generations in small effective populations where genetic drift is strong. Work by Hauser et al. (2002) demonstrated a dramatic loss of genetic diversity in Australasian snapper *Chrysophrys auratus* in New Zealand, despite an estimated minimum N_c size of more than 3,000,000 fish. A meta-analysis using 140 species and more than 10,000 loci showed that allelic richness and heterozygosity are significantly lower in overharvested fish populations (Pinsky and Palumbi 2014). Moreover, size-selective fishing has been experimentally shown to significantly reduce genetic diversity over very few generations (Therkildsen et al. 2019).

Over the last century, populations have been heavily exploited and most population sizes have drastically decreased. As a result, a loss of genetic diversity can be expected due to increased genetic drift. In contrast, it can take many generations for genetic variation to return in a population through random mutation, and immigration levels from other populations may not always be high enough for gene flow to supplement the lost genetic variation in a short time scale (Pinsky and Palumbi 2014). This implies that exploited populations will experience lower genetic diversity for hundreds or thousands of years into the future, and a reduced evolutionary potential compared to their 'baseline' level (i.e. before industrial fishing). This could result in more frequent occurrences of inbreeding depression. In spite of the risks associated with genetic erosion, the target levels of genetic diversity to maintain in a population are difficult to quantify because any advantageous alleles only become relevant when presented with a challenging environment. To understand this better, the extent to which genetic variation is lost in exploited populations could be assessed using temporal sampling, i.e. historic (<100 year old) and ancient (>100 year old) DNA when available (Oosting et al. 2019). By reconstructing the genetic variation present in past populations, it could be possible to assess how much genetic variation has been lost and use this information to set diversity baselines for fisheries management. Maintaining genetic diversity should be of concern to fisheries managers because the future of fisheries species will be one with lower adaptive potential, making them more vulnerable to environmental challenges than they have ever been in their recent evolutionary history.

Fishing-induced evolution

The practice of size-selective fishing has been observed to affect the evolution of key life-history traits, such as maturation age and growth rate. In short, intense fishing pressure has favoured the reproductive success of individuals with 'fast life-history traits. Shifts in life-history traits have been observed in a large number of exploited fish species (Heino et al. 2015). A key question is whether these changes in life-history traits have been facilitated through phenotypic plasticity (e.g. density-dependant) processes or directional selective pressure on genetic loci. The distinction between these two processes is crucial because shifts in allele frequencies could theoretically lead to the loss or fixation of alleles that would otherwise be beneficial or detrimental to the population in an 'unfished' state.

Experimental studies provide strong evidence for the causal link between changes in life-history traits caused by size-selective fishing and directional selection on genetic loci (Conover and Munch 2002; van Wijk et al. 2013; Marques et al. 2018; Therkildsen et al. 2019). Strong support for this causal link in wild populations is currently lacking because the genetic data from a pre-exploited population are difficult to obtain. Notably, Therkildsen et al. (2013) reported changes in allele frequencies in loci which correlate with temporal changes in probabilistic maturation reaction norm (an approach commonly used to assess changes in maturation). These changes were observed through temporal sampling of wild Atlantic cod (*Gadus morhua*) using historic samples. With recent advances in genome-wide sequencing and improved extraction protocols for ancient DNA, this question can now be more easily addressed. SNP datasets generated from ancient DNA samples can be compared to fish in contemporary stocks to test whether loci associated with maturation and growth traits have been experiencing selection (Oosting et al. 2019). Overall, the increasing evidence of the effects of size-selection on fishery stocks indicates that it may be time to re-think the way fish catches are regulated in New Zealand (and elsewhere), e.g. by shifting to a balanced harvesting model (Garcia et al. 2012; Zhou et al. 2019). Such a model change could be particularly effective on the small-scale fisheries which represent more than half of the global catch for human consumption (Plank et al. 2017).

Climate change

Global warming is shifting the geographic distribution of many marine species. Modelling has shown that changes in distribution predominate towards the poles and/or to lower depths (Morley et al. 2018; Stanley et al. 2018; Brooks 2019). Management approaches need to account for this, but surprisingly only few empirical studies have been conducted on the genetic changes in fish populations associated with climate change (Muñoz et al. 2015; Munday et al. 2017; Munday et al. 2019). We expect that there will be both short- and long-term changes to levels of genetic diversity, disruptions to population structure, and adaptive responses to this type of environmental shift (Potts et al. 2014; Ramos et al. 2018; Stanley et al. 2018). Monitoring and studying the genetic diversity in a fishery that is associated with adaptation to warmer waters (as well as related impacts like acidification and decreases in oxygen levels) and genetic founder events as populations expand into new areas will be necessary to avoid overfishing of stocks building at new locations and depletion of those in decline elsewhere.

Measuring abundance and connectivity

Other than stock structure and the resilience capacities of harvested stocks, fisheries managers are mostly concerned with estimating absolute abundance and inter-stock movement. Abundance is traditionally investigated through measures of catch per unit effort, which is only an indicator of change in relative abundance, or through age- and length-composition data, which rely on a lot of assumptions (Maunder and Piner 2015). Stock connectivity and movements are usually investigated with tagging via mark-recapture. However, this method requires fish be brought to the surface, potentially causing barotrauma and high levels of mortality. Tagging is considered impossible on deep-water species, causing large information gaps for species such as orange roughy and hoki. Classical genetic tagging (e.g. Miller et al. (2015)) faces the same issues. Genetic tagging by using biopsy hooks to sample individuals *in situ* (Mace et al. 2020) is a relatively new method that would allow to bypass those constraints, and could simultaneously allow for the estimation of absolute abundance when combined with methodologies like close-kin mark-recapture (Bravington, Skaug, et al. 2016). Using this method, absolute abundance and demographic parameters could even be estimated without the need to resample the same individual (as long as juveniles can also be sampled in the case of close-kin mark-recapture). Genetic tagging coupled with close-kin mark-recapture has already been used to infer the absolute population size of southern bluefin tuna on a large spatial and temporal scale (Bravington, Grewe, et al. 2016) and subsequently the estimation of N_e (Waples et al. 2018), as well as the absolute abundance of white sharks in eastern Australia and New Zealand (Hillary et al. 2018).

A genetic-based tagging programme would open up a range of new possibilities for stock assessment (Mace et al. 2020). If genetic data from enough specimens is collected, this could allow for a more reliable estimation of N_e, an important metric that has suffered from sub-optimal sample size so far (Marandel et al. 2019). Genetic tags are permanent, and the offspring of previously tagged individuals will be detectable for several generations. Depending of the life expectancy of the species, genetic tagging data can remain relevant for many decades, or even for a century or more for long-lived species like orange roughy.

Conclusion

Our review showed that the genetic population structure of fisheries species in New Zealand has been largely under-studied. Prior to the advent of genomics, population genetic markers often lacked the level of resolution needed to study marine species that typically have large populations and are highly mobile. New genome-wide sequencing approaches offer the opportunity to more comprehensively resolve a range of previously intractable stock structure issues. Following are several recommendations for promoting a genomics-enabled approach to New Zealand fisheries management.

1. Long-term sampling and data handling strategy: Develop a plan for regular spatial and temporal sample collection for each fishery and in a way that can be easily integrated into a tagging programme. Tissues will need to be preserved in a way that enables genomic sequencing. Overall, the genetic data collection (including meta-data) should be

standardised as much as possible at a national scale to insure its efficient usability for current and future studies. This requires good coordination among collectors, fisheries data management, and laboratory capabilities. A centralised genomic data storage facility is needed for a range of strategic interests beyond fisheries and is a common need across New Zealand's primary industries and conservation groups. A well-maintained national archive would secure the long-term value of genomics.

2. Prioritise species: A limit on the resources available to support genomic research means priority should be given to the most valuable fisheries that are experiencing the greatest management concerns. For example, deep-water species such as hoki and orange roughy lack good stock assessment information. Genomic markers could be used to enable an in situ deep-water tagging programme to be developed for the first time. Genomic tools could be developed for species (e.g. snapper, trevally, hapuku) that are also good candidates for aquaculture. The dual support of fisheries and aquaculture interests would require a more joined up seafood genomics approach among government, industry and researchers.

The strong pressures that wild fishes are currently facing both nationally and globally require more detailed understanding about the current status of stocks and what changes are occurring, or are likely to occur. Genomics tools fit into the management toolbox as part of a holistic integrative approach to a fishery. There is little doubt that genomics will be a vital component of the response to the challenges fisheries management will face this century.

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