A review of habitat use, home range and connectivity for selected New Zealand species

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Summary

Marine protected areas (MPAs) can be effective management tools for the protection of marine biodiversity, and scientific data on movement patterns for target species can enhance aspects of MPA planning and design, particularly size and configuration of MPA networks. Information on species habitat use and home range movement can inform optimal MPA sizes to protect core populations. Connectivity data (which includes the extent and direction of dispersal) can allow the identification of important source populations, and can aid in establishing a comprehensive and representative network of MPAs.

In this report, we reviewed habitat use, home range size, dispersal and connectivity patterns for selected New Zealand marine species. We first investigated commercially and culturally important invertebrates and fish in New Zealand, including the sea urchin (kina), spiny rock lobster, abalone (pāua), blue cod and snapper. We then reviewed information on bladder kelp (*Macrocystis pyrifera*), which acts as a good model for other brown algae that have two life stages (sporophyte and gametophyte) and disperses using kelp rafts. We also highlighted traits for endangered marine mammals (New Zealand sea lion, Hector's and Māui dolphin) that are likely to benefit from MPA protection. Finally, we compared three New Zealand penguin species (little blue, yellow-eyed, and Fiordland crested penguin) to demonstrate that while some similarities may exist for organisms belonging to related species, habitat, home range and connectivity patterns are often species-specific.

We found that ontogenetic shifts in habitat preference for invertebrates and fish were common, highlighting the need to protect habitats used throughout all life stages. For example, juvenile kina and spiny rock lobsters were found to remain more cryptic than adults, and juvenile pāua were found more often in sheltered intertidal cobble environments compared to adults (which preferred exposed subtidal rocky reef). Juvenile snapper were more associated with estuary and seagrass habitats, while adult habitat use included estuaries, rocky reef, soft sediment and offshore environments. Some species required both terrestrial and marine habitats, like the New Zealand sea lion and all three penguin species. These species are exposed to threats both on land and at sea, and therefore protection across both habitats may provide optimal conservation benefits.

Home ranges varied between species. Sedentary kina and pāua had small home ranges and were not recorded to move greater than 5 m and 150 m, respectively. Spiny rock lobster, blue cod and snapper had home ranges on the scale of 5-10s km and generally showed some site fidelity and/or residency, but some individuals (predominately juveniles) underwent longer movements between populations. For the terrestrial and marine species, the area occupied on land was small (colonies contained within 10 km^2, but often much less), but foraging ranges, varying from 10s-1000s of km from the colony, increased home range sizes considerably. Identification and protection of areas where home ranges of different populations may sometimes overlap is important, especially for Hector's dolphins. Hector's dolphins had a small home range (>150 km along coast), and distances between populations were greater than home range sizes, resulting in fragmented populations.

Dispersal by invertebrates and fish occurred either during the larval stage or through migration of individuals. Pelagic larval duration (PLD) varied considerably between species, ranging from a few days (pāua, blue cod), to months (snapper, kina) to years (spiny rock lobster). The dispersal for giant kelp occurred either by zoospores (which dispersed locally; scale of 1-100s m), or by kelp rafts (which dispersed far; scale of 10-1000s km). For marine mammals and penguin species, dispersal was through migration of individuals between groups. Oceanographic models and tag-recapture data revealed dispersal potential of both larvae (for invertebrate species) and individuals (for invertebrate species, mammals and penguins), and these ranged from meters to thousands of kilometres.

Some trends in genetic connectivity emerged, and in general, dispersal data supported genetic patterns. For instance, organisms that were found to disperse far or move long distance between populations had little to no genetic differentiation between populations (blue cod on mainland New Zealand, bladder kelp, New Zealand sea lions). Oceanographic features identified as important for dispersal and movement, including currents, eddies and fronts, resulted in an apparent north-south differentiation for some species (pāua, spiny rock lobster, snapper, Hector's dolphins), and an east-west differentiation for some species on the North Island (spiny rock lobster, pāua, snapper) and the South Island (Hector's dolphins). For organisms that had a short PLD or limited ability of long-distance movement (<1000 km), populations at the Chatham Islands were genetically distinct from the mainland (pāua, blue cod).

By contrast, organisms with a long PLD and greater ability to move had genetic homogeneity between the Chatham Islands and mainland (spiny rock lobster, little blue penguin). For the Subantarctic Islands, mainland New Zealand sea lions were well connected, corroborating observations of re-sightings of tagged individuals; however, yellow-eyed penguins, where only one tagged individual has been ever recorded as moving between Subantarctic and mainland populations, were strongly differentiated.

Overall, this report summarizes valuable information for selected New Zealand taxa, and can be used when incorporating species-specific requirements into a plan for a network of MPAs that allows for both protection of species within MPA boundaries and for connectivity among MPAs.

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1. Introduction

1.1. Connectivity in the marine environment

In order to adequately manage and protect marine organisms, an understanding of species connectivity is important. Connectivity encompasses both demographic connectivity and genetic connectivity. Demographic connectivity, as defined by Lowe and Allendorf (2010), is the level at which the dispersal of individuals between populations affects the population growth (i.e. survival rates and birth rates). Demographic connectivity depends on the contribution of net immigration into the total recruitment of a population, and this contribution drives source-sink metapopulation dynamics (Pulliam 1988, Figueira 2009, Lowe and Allendorf 2010). As an example, two populations would be demographically connected if one population had low survival of residents, but received a high level of larvae or immigrants from another population; in this example, the population receiving larvae/immigrants would be the 'sink' and the population supplying larvae/immigrants would be the 'source'. Therefore, high levels of demographic connectivity from source to sink populations can result in a stable network of connected populations, and Marine Protected Area (MPA) planning often involves the identification and protection of habitats supporting source populations (Crowder et a. 2000, Lowe and Allendorf 2010, Yan et al. 2020).

Measuring demographic connectivity is often challenging in the marine realm because many organisms have multiple life stages (i.e., larvae, juvenile, adult), which can range in mobility, behaviour, and survival (Cowen and Sponagule 2009). In addition, many organisms experience ontogenetic shifts in habitat and movement, where habitat preference and distribution can change throughout life stages (e.g., Knip et al. 2011, Compton et al. 2012, Clark and Russ 2012). Methods to measure demographic connectivity include collecting tag-recovery data to determine the proportion of the population that remained resident versus the proportion that dispersed, as well as tracking dispersal using GPS loggers and/or satellite telemetry. Further, oceanographic models are often utilized to trace paths of larval and migrant dispersal.

By contrast, genetic connectivity is the level at which gene flow affects evolutionary processes within populations (Lowe and Allendorf 2010). The genetic makeup of an organism is a product of their DNA, which forms alleles that make up genes. Genetic

connectivity is therefore calculated by comparing allele frequencies across populations (Hedgecock et al. 2007). Similar allele frequencies between populations would indicate high levels of genetic connectivity, whereas different levels of allele frequencies would indicate divergence between populations. Two populations that have identical allele frequencies are said to be 'panmictic', meaning there is no reproductive isolation, mating is random and gene flow between them is high (Lowe and Allendorf 2010). Genetic connectivity occurs along a spectrum, and even seemingly low levels of genetic differentiation are defined as considerable and biologically meaningful (e.g., Knutsen et al. 2010). This is because only a few migrant individuals per generation are required to maintain similar levels of allele frequencies; in fact, it is thought that one migrant per generation is enough to effectively reduce the effects of inbreeding (Mills and Allendorf 1996).

Methods to determine genetic connectivity utilize genetic markers to compare the genetic makeup of different populations, which (in this report) include allozymes, mitochondrial DNA, microsatellites and single nucleotide polymorphisms (SNPs). These (as well as other useful genetic terms for this report) are defined in Appendix 1.

1.2. Connectivity in the context of NZ MPAs

The establishment of MPAs involves both protecting large (and often remote) areas of the ocean and creating networks of smaller MPAs, each which have their own management implications. Large-scale MPAs (LSMPA, >100,000 km^2; Friedlander et al. 2016) can be advantageous in that large areas can protect species that have large home ranges, enclose the entire extent of dispersal for a particular species, and can encompass climatic transition zones and provide an area where organisms may adapt to or resist change (Edgar et al. 2014, Roberts et al. 2017, White et al. 2017). These areas are often placed in remote areas that experience fewer anthropogenic pressures (Devillers et al. 2015), and can be difficult to manage and enforce (Jones and De Santo 2016). Networks of small MPAs may be more practical for places that experience more anthropogenic influence, and current international agreements for the conservation of nature mandate that nations create networks of well-connected MPAs (Convention on Biological Diversity 2010). Networks of smaller MPAs have the potential to achieve similar conservation benefits as LSMPAs by allowing the protection of well-connected populations across large spatial scales, if well-designed.

To create a representative and biologically viable network of protected areas, the NZ Ministry of Fisheries and Department of Conservation (DOC) have created guidelines for the identification and selection of potential areas for protection, which are divided into three categories (Roberts et al. 2003, MFish and DOC 2008). The first category of guidelines encompasses site identification and protected area design, and suggests the following: (1) to select sites that incorporate a whole habitat and ecosystem; (2) to select a size that is sufficient for population maintenance, where fewer, larger areas are more desirable than numerous smaller areas; (3) to maximise connectivity in order to enhance linkage between individual protected areas within and between biogeographic regions; (4) to represent latitudinal and longitudinal variations (cross-shelf); (5) to consider adjacent land use (including islands) and terrestrial human activity in relation to the sea; and (6) to keep boundaries simple and to keep a low boundary-to-area ratio (i.e., simple shapes, low fragmentation; MFish and DOC 2008). The second and third categories include guidelines for site selection and guidelines for tool selection, respectively (MFish and DOC 2008). Creation of MPAs following these guidelines adheres to objectives and goals for protection that are set in the New Zealand Biodiversity Strategy and its updated Action Plan (see: https://www.doc.govt.nz/ globalassets/documents/conservation/new-zealand-biodiversity-action-plan-2016-2020.pdf).

Determining the 'sufficient size' to allow population protection and maintenance (and to achieve MPA objectives) can be difficult, but scientific data on connectivity of selected species (particularly in relation to habitat use, home range and dispersal) can help inform this. For instance, information on habitat use and home range (i.e., the area that an organism moves for daily activities including feeding, mating, etc.; Powell 2000) can be used to ensure that protection encompasses (at a minimum) the core of a local population.

MPAs that fail to encompass an entire core population may be more susceptible to edge effects (Roberts et al. 2001, Carr et al. 2003). In a study conducted at the Cape Rodney to Okakari Point (CROP) Marine Reserve, Freeman et al. (2009) tagged >5000 spiny rock lobsters occupying three separate reefs within the reserve where one reef was fully protected and the other two had 40% and 9% protection. These authors found that only 1% of individuals from the fully protected reef moved outside

of the reserve; further, the likelihood of migration outside of the marine reserve increased as the proportion of unprotected reef increased. While such spill-over effects may benefit local fisheries in some cases (Goñi et al. 2011), long term loss of individuals to the core population may lead to population collapse (Roberts et al. 2001). For instance, an increased number of male lobsters being fished outside of the reserve boundary at an unsustainable rate could lead to sperm limitation over longer periods of time and have negative impacts on population maintenance. Therefore, understanding movement patterns can allow identification a suitable MPA size, and when such information is not available, cautionary planning may involve protection of larger areas and inclusion of buffer zones, which likely increase the chance of protection of core populations.

An MPA within a network should be able to sustain itself through local population growth, or through immigration from other populations (i.e., from sources; Roberts et al. 2003). Estimates of dispersal and/or population connectivity allow for an understanding of how widely individuals may be dispersing, and allow the identification of key source populations. For example, Yan et al. (2020) examined the genetic diversity and genetic structure of squat lobster populations across deep sea habitats of the southwest Pacific Ocean and found high levels of larval connectivity between sites. These authors further identified important squat lobster source populations (populations from the Tasmanian slope) and the direction of gene flow to sink populations (populations from the Kermadec Ridge), providing important considerations for the management of vulnerable marine ecosystems that cross international boundaries. While this was found for squat lobster, for other species this was not the case, such as sponges and coral (Zeng et al. 2017, 2019). High levels of connectivity can therefore be important in supporting adjacent fisheries, and/or ensuring individual marine reserves or MPAs within a network are linked, but levels of connectivity can be highly species-specific.

Important considerations should be made for different taxa in MPA design. For instance, for invertebrates, which often produce larvae that disperse into the water column, the identification of larval sources and sinks is important to understand how populations are connected (Shanks et al. 2003). For mobile species, like fish, spacing between MPAs where distance between MPAs is less than the home range of the

organism may allow high degrees of population mixing and reduce the risk of population fragmentation (Mann et al. 2016). By contrast, for organisms that cannot actively move, like seaweeds, it is important to understand habitat requirements and dispersal in order to identify hotspots where these organisms will settle and grow. Marine mammals and birds have both land and sea requirements that need to be considered, and large migrations between populations may require the protection of 'corridor' areas in addition to the population's home range (Pompa et al. 2011). Furthermore, MPA design should consider species interactions, such as predator-prey relationships (Pilyugin et al. 2016). For instance, protection of only one species that relies on another species with a different home range size may lead to inadequate achievement of protection objectives. Thus, the design of an MPA may have different considerations depending on certain life-history traits of the desired organism of protection and depending on species interactions.

In 2016, the Government consulted on reform of New Zealand's marine protection legislation (Ministry for the Environment 2016), and is currently working to progress this initiative. This provides an opportunity to develop scientific guidance on MPA design and implementation that is directly applicable to the New Zealand context. Additionally, countries are being called to define global post-2020 conservation strategies based on sound scientific approaches (e.g., Visconti et al. 2019). Information on ecological processes like dispersal and connectivity of New Zealand marine organisms will therefore be important to inform future systematic conservation planning of New Zealand's MPA network (Geange et al. 2017).

1.3. Factors that influence connectivity

There are many factors that often dictate the level and direction of demographic and genetic connectivity, including dispersal of individuals, life-history traits (i.e., reproductive method, body size, age or life stage, life span, survival, home range), hydrodynamic forces (i.e., currents, mixing layers, fronts), and habitat features (Cowen et al. 2007, Pineda et al. 2007, Cowen and Sponaugle 2009, Lowe and Allendorf 2010, Yan 2020).

Dispersal can be by larvae (from broadcast spawners) or occur after an organism has settled (migration). Pelagic larval duration (PLD), defined as the time spent in the water

column during development as the planktonic larval stage, is said to play an important role in the extent of dispersal for an organism (Pineda et al. 2007, Cowen and Sponaugle 2008). For example, PLDs are often positively correlated to gene flow, whereby the longer a larva can travel in the water, the greater chance for populations to be connected (e.g., Ross et al. 2009). This is not always the case, and oceanographic features also strongly influence dispersal of larvae (Pineda et al. 2007, Cowen and Sponaugle 2008). For instance, hydrodynamic features (like currents, eddies, and fronts) as well as geographic features (like trenches and shelves) can either promote or act as barriers in the transportation of larvae between populations. Environmental factors can also influence larvae distribution; for instance, El Niño-Southern Oscillation (ENSO) may result in changes to currents, upwelling and/or surface mixing, which consequently may change the paths for larval dispersal (e.g., Bailey and Picquelle 2002, Hsiung et al. 2018). Therefore, the sinks for larvae are largely a product of the PLD and of oceanographic features, and can vary temporally due to environmental conditions. Movement or migration of adults are similarly affected by similar oceanographic and environmental parameters, as well as by life-history traits and physiological capability of a particular species. For instance, organisms that swim and are mobile can travel further than sedentary or sessile ones.

Habitat and home range also play an important role in connectivity. Habitat requirements of an organism determine where it can successfully live, ultimately driving its distribution. Marine organisms are often associated with specific habitat types, including substrates, algal cover, depths, exposure, proximity to land, etc. Reliance on specific types of habitats can limit population movements and ultimately species distributions. Home range size of a population also influences the level of connectivity to other populations. Organisms that show high site fidelity with small home ranges have less of a chance of interacting with other populations, especially those populations that are further away than their home range size (Kramer and Chapman 1999). Lack of overlap between home ranges of different populations can result in population fragmentation.

2. Objective of this report

The objective of this report was to review habitat use, home range and connectivity patterns for selected marine species in New Zealand, with an emphasis on:

1. commercially and culturally important invertebrate and fish species including sea urchins (kina), spiny rock lobster, abalone (pāua), blue cod, and snapper.

2. bladder kelp (*Macrocystis*), which provides and supports a highly productive and diverse ecosystem, and is a good model for other brown algae that have two life stages (sporophyte and gametophyte) and use kelp rafts for dispersal.

3. threatened marine mammals that may benefit from MPA protection, including New Zealand sea lions and Hector's and Māui dolphins. New Zealand sea lions and Hector's dolphins are both classified as 'endangered' by the International Union for Conservation of Nature (IUCN) and 'nationally vulnerable' by the New Zealand Threat Classification System (NZTCS), and Maui dolphins are classified as 'critically endangered' by the IUCN and 'nationally critical' by the NZTCS (Baker et al. 2019).

4. penguin species that may benefit from MPA protection, including three species that are experiencing varying levels of threats: little blue penguin (IUCN = least concern, NZTCS = at risk – declining), yellow-eyed penguin (IUCN = endangered, NZTCS = nationally endangered), and Fiordland crested penguin (IUCN = vulnerable, NZTCS = nationally vulnerable). Comparing these three species demonstrates that habitat requirements, home range sizes and movement patterns can vary significantly even among organisms belonging to the same taxonomic group.

3. Methods

For each species, we searched for literature on Elsevier's Scopus (www.scopus.com) and Google Scholar with keywords: species name + 'habitat', 'home range', 'movement', 'connectivity', or 'population structure'. We then consulted the reference lists of these papers to identify any missing literature. Our review includes relevant information compiled from published scientific papers, reports, and grey literature. For

a list of references in relation to their study location and information extracted, see Appendix 2.

In order to gain a broad understanding of population structure for each species, we plotted general genetic differentiation for each species based on the latest study (or studies) containing genetic information for population structure (Fig. 1-5). For these figures, we indicated the sample locations and coloured the populations based on genetic differentiation, which was achieved by adapting figures from respective papers, or when figures were absent, comparing measurements of genetic differentiation reported in the papers (F_{ST} or divergence values, see Appendix 1 for definitions). For instances when no to little genetic differentiation, colours for the populations were the same (and indicate genetic similarity). For instances of low to moderate genetic differentiation colours for populations were different shades of the same colour. For populations that had high genetic differentiation, colours for populations were different colours. Note, these figures are meant as a qualitative summary of genetic differentiation, and original studies should be consulted for greater detail.

4. Summary of findings: patterns in New Zealand

In examining the habitat, home range size and connectivity patterns of selected marine species in New Zealand (see Table 2 for summary), patterns and key findings emerged.

4.1. Habitat use

Habitat preferences for the invertebrates and fish investigated here often changed with life stage (larvae, juvenile, adult). For instance, pāua juveniles tended to occupy different habitats to that of adults (calm, intertidal, barren versus exposed, subtidal, reef; respectively; Aguirre and McNaught 2013, Laferriere 2016). An ontogenetic shift in habitat was also observed for snapper, where juveniles tended to occur more in seagrass and estuarine habitats compared to adults in reef and offshore habitats (Crossland 1981, Compton et al. 2012, Parsons et al. 2014a). Similarly, blue cod juveniles were generally found shallower and in cobbled habitats, whereas adults occurred more on reef fringes and deeper (Carbines 2004). Spiny rock lobster and kina both remained more cryptic until later life stages (Edmunds 1995, Cole and

Keuskamp 1998, Booth and Ayer 2005). Such shifts in habitat dependency highlight the importance of incorporating the protection of the entire range of habitats used by all life-history stages in MPA design.

The identification and protection of source populations is also important in MPA planning, and oceanographic models have allowed the identification of potential sources and/or habitats conducive for source populations for invertebrates (i.e., kina in Wing 2011; spiny rock lobster in Chiswell and Booth 2008; pāua in Stephens et al. 2006). Wing et al. (2003), Wing (2009) and Wing (2011) highlighted that potential source populations of kina in Fiordland were not in current Fiordland marine reserves. For fish, otolith microchemistry was another important tool in identifying discrete populations of blue cod (Beer et al. 2011, Beer 2014), and genetic analyses of parents versus offspring also allowed the extent and direction of larval dispersal to be characterized for snapper (Le Port et al. 2017).

Furthermore, it was apparent that organisms that depend on both terrestrial and marine environments (i.e., sea lion, penguins) were vulnerable to threats both above and below sea. As an example, terrestrial habitat loss due to deforestation and farming as well as reduced prey availability due to competition with fisheries both have been reported as being factors in the decline of the yellow-eyed penguins. Therefore, protection may focus on terrestrial and/or marine requirements of these organisms.

4.2. Home range

Home range varied from small (10s m) to large (1000s km) across all species investigated here. Sedentary invertebrates (pāua, kina) stayed within a small area (distance moved <150 m), and movement was linked to food availability (Dix 1970a, Poore 1972a). For instance, pāua and kina were found to remain more sedentary in the presence of large amount of drift algae, while greater movements were observed in the absence of algae due to the need to move to actively search for food (Andrew and Stocker 1986, Poore 1972b). More mobile species (spiny rock lobster, blue cod, snapper) tended to be associated to a certain area (within ~5 km from the shore or >5 km between tag-recapture locations), but a portion of the population underwent long distance migrations (10s-100s km), potentially promoting population mixing (Booth 1997, Kelly and MacDiarmid 2003). Bladder kelp also had two modes of dispersal:

zoospores which stayed more local, and kelp rafts that allowed dispersal over 1000s of km (Macaya 2010). MPAs that are spaced apart in a way that home ranges overlap may be more effective in mitigating exchange of organisms between population and preventing population fragmentation.

Organisms that had terrestrial and marine requirements often occupied a small area on land (<10 km^2), but foraged far out from land at sea (100s km from shore). New Zealand sea lions showed regional variability where Subantarctic populations foraged farther and deeper than the mainland population (Auge et al. 2011a). A concern particularly for the Hector's and Māui dolphins was that home ranges were smaller than distances between populations (Pichler 2001, 2002, Slooten et al. 2010, Rayment et al. 2010, McKenzie and Clement 2016), meaning a lower chance of breeding between populations and consequently a higher chance of more fragmented populations. This situation leaves the population at a particular risk because of their already low numbers and low genetic diversity. MPAs may benefit these organisms directly if placed in an area that is important for breeding or for particular life stages, and indirectly by benefiting prey species.

4.3. Dispersal and connectivity

Connectivity occurred over multiple scales and was highly variable across taxa. PLD (applicable for organisms that are broadcast spawners with pelagic larvae, such as many invertebrate and fish species) has been shown to play an important role in connectivity. It has been that found for many New Zealand marine species, PLD is positively correlated with gene flow; that is, populations are more likely to be connected if their larvae are in the water column for longer (Ross et al. 2009, Gardner et al. 2010). The spiny rock lobster produces larvae that remain in the water column 1-2 years and as a result, populations were generally well-mixed (though low to moderate genetic differentiation was also reported; Thomas and Bell 2013, Ilyushkina 2018); with larvae being able to disperse from Australia to New Zealand (Chiswell et al. 2003, Thomas and Bell 2012). However, the relationship between PLD and high levels of connectivity is not always the rule, and many other factors also influence connectivity. For instance, pāua were found to have a short PLD (~72 hr) and a small home range (Poore 1972a, Tong et al. 1992); however, populations were relatively well-mixed, possibly owning to the large population size of pāua (Will et al. 2011, Will

et al. 2015). Furthermore, because only a few migrant individuals are required to maintain levels of gene flow (Mills and Allendorf 1996), even for well genetically connected populations this could be the result of only a few immigrants.

Hydrodynamic features also greatly influenced the dispersal of larvae, spores, juveniles and adults. The movement of larvae and spores is often dictated by local currents, eddies and fronts, and oceanographic models have predicted how hydrodynamic features shape the paths of dispersal for invertebrates, fish and algae investigated here. Along New Zealand's west coast, a north-south phylogenetic break occurs in the Cook Strait region for many marine taxa, where South Island populations are genetically different to North Island populations (i.e., for some amphipods, brittlestars, limpets, green mussels, seagrasses; see Ross et al. 2009 and Gardner et al. 2010 for a review of connectivity among New Zealand species). This break was reported for pāua (low to moderate differentiation; Will et al. 2011, Will et al. 2015), snapper (low to moderate differentiation; Bernal Ramirez 2003), Hector's and Māui dolphins (strong differentiation; Hamner et al. 2012), and rock lobster (low to moderate differentiation; Thomas and Bell 2012, Ilyushkina 2018). There is also a recognized east-west phylogenetic break that occurs for many species in New Zealand (i.e., for some amphipods, seagrass; Ross et al. 2009, Gardner et al. 2010), and east-west differentiation was reported for snapper (North island, low to moderate differentiation; Bernal Ramirez 2003), and Hector's dolphins (South Island, strong differentiation; Hamner et al. 2012).

4.4. Species-specific traits

While there are some patterns among marine organisms with similar life-history traits existing in comparable environments that may be applicable to the wider taxon, it is important to consider that there are often high levels of species-specificity. This is exemplified in examining habitat requirements, home range and connectivity patterns in penguin species. For instance, the little blue penguins were more variable in their habitat use and foraging ranges (Braidwood et al. 2011, Poupart et al. 2017), while yellow-eyed penguins appeared to be less flexible in terms of habitat requirements (likely contributing to their decline and current 'endangered' status; Ellenberg and Mattern 2012). At sea, yellow-eyed penguins employed benthic diving strategies, while the little blue and Fiordland crested penguins foraged pelagically (Mattern and

Ellenberg 2018). Furthermore, Fiordland crested penguins had a large home range that encompassed 1000s of km, as they foraged in the Subantarctic and Subtropical Fronts (Mattern et al. 2018); whereas the little blue penguin and yellow-eyed penguin remained ~100 km from shore on the continental shelves to forage (i.e., Chilvers et al. 2014, Chilvers 2019, Ellenberg and Mattern 2012). Genetic and tagging data revealed that little blue penguins were well mixed throughout mainland New Zealand (both North and South Islands) and with the farther away Chatham Islands, due to movement of penguins between colonies (Grosser et al. 2015). Instead, yellow-eyed penguins had a well-mixed population on mainland New Zealand (only distributed on the South Island, southeast coast), but were more genetically distinct with further Subantarctic populations, owing to perhaps a higher site fidelity but also largely a product of the distance between colonies (Boessenkool et al. 2009). Therefore, while some species may share life-history traits and provide baseline information for a broader taxonomic group, designing an effective MPA to protect a certain organism will require knowledge of specific traits of the species of interest.

4.5. Conclusion

Understanding connectivity of marine populations is important for designing effective networks of MPAs. Information on habitat use and home range size can inform MPA size (as well as sizes of specific key habitats within the MPA) to protect core populations in MPA design. Habitat use and home range of organisms also influence connectivity patterns, where habitat requirements dictate the distribution of an organism and home range size either promotes or limits mixing between populations. Information on dispersal and connectivity can inform to what extent populations interact and can inform spacing for MPAs within a network design. Connectivity is affected by factors including mobility of organism, pelagic larval duration, and hydrodynamic features. While this report summarizes and identifies some key commonalities in habitat, home range and movement patterns of selected New Zealand species, it also emphasizes that there are also often species-specific differences. Overall, the information reviewed in this report provides useful data that can be referred to when integrating connectivity of a particular species into MPA planning and design.

Table 1. Summary information for each species, including distribution, habitat requirements (for different life stages), home range sizes, connectivity and movement patterns and method used to calculate connectivity patterns.

Taxa	Distribution	Habitat	Home range	Connectivity patterns	← Method used
Invertebrates					
Kina	· North and South Islands · Stewart Island · Snares Island · Chatham Islands · Three Kings Island	Rocky reef, shell or coarse substrate · **Larvae** – settle on coralline algae · **Juveniles** – cryptic, in crevices or under rocks · **Adults** – exposed (little algae, no predators) or cryptic (high algae, predators)	**Scale of m** <5 m (Dix 1970a, Andrew & Stocker 1986, Andrew & MacDiarmid 1991, Lamare & Mladenov 2000)	North and South Island genetically the same, except for Fiordland (Mladenov et al. 1997) Genetic differentiation between North Island (+Marlborough Sounds) and South Island (Nagel et al. 2015); and between inner and outer fiords in Fiordland (Perrin et al. 2003) Fiordland inner and outer fiords different demographic variability, where outer = more stable, potential larval source and inner = more variable, potential larval sink (Lamare 1998, Wing et al. 2003, Wing 2009,2011)	Allozymes Microsatellites Oceanographic models, larval tows and collectors, recruitment indices (based on size) over time
Spiny rock lobster	· North and South Islands · Stewart Island · Subantarctic Islands · (but not Campbell Island) · Chatham Islands · Three Kings Island	Rocky reef; sand, horse mussel beds and low lying reef important during inshore-offshore movements · **Larvae** – settle in small holes, crevices; rarely on complex seaweeds / bryozoans · **Juveniles** – occupy small holes same size as body · **Adults** – Holes, crevices, gaps – shelters on rock reef; exposed but in aggregates in sand	**Scale of km** <5 km Inshore-offshore movements associated with foraging, mating and moulting (MacDiarmid 1991, Booth 1997, Kelly 1999, Kelly et al. 1999, Kelly 2001, Kelly & MacDiarmid 2003, Freeman et al. 2009)	Juveniles move between populations (~100 km, largest observed 460 km) (Street 1971, McKoy 1983, Booth 1997) 4 larval sources and sinks (far north, east coast of North Island, Chatham Islands, southern New Zealand); direction of flow south to north (Chiswell & Booth 1999,2008) No genetic differentiation between any populations (Smith et al. 1980, Booth et al. 1990, Ovenden et al. 1992) Low to moderate levels of genetic differentiation between northeast North Island, northwest North Island, and South Island (Thomas & Bell 2013, Ilyushkina 2018)	Tag-recapture Oceanographic models Allozymes Microsatellites, SNPs

Pāua	· North and South Islands · Stewart Island · Snares Island · Chatham Islands	Intertidal and subtidal rocky reef, also barren cobble or boulder fields · **Larvae** – settle on coralline algae · **Juveniles** – higher densities in shallow (<5 m) intertidal; in sheltered barren fields (but growth and survival greater in algal habitats at depth) · **Adults** – subtidal (>5 m) rocky reef; exposed, high energy environments	**Scale of m** <150 m (Poore 1972a)	Larval dispersal 200 m – 4 km in calm conditions, but 50-80 km in high energy conditions with prolonged winds (Stephens et al. 2006) No genetic differentiation between any populations (Dollimore 1977, Frusin 1982) Genetic differentiation between Chatham Islands, Stewart Island, Great Barrier Island, South Taranaki (Smith & McVeagh 2006) Genetic differentiation between populations, identifying 4 phylogenetic breaks = (1) Chatham Islands break, (2) break in Cook Strait, (3) East Cape break, (4) break in southeast coast of South Island (Will 2009, Will et al. 2011,2015)	Oceanographic models Allozymes Mitochondrial DNA Mitochondrial DNA, microsatellites
Fish					
Blue cod	· North and South Islands · Stewart Island · Chatham Islands	Rocky reef fringes, open reef and sand; can exist in marginal habitats (e.g. inner fiords of Fiordland, diet supported by chemosynthesis) · **Juveniles –** open reef and sandy areas, less than 15m · **Adults –** rocky reef fringes, open reef and sandy areas; habitat complexity is important	**Scale of m-km** · <100 m (~75% recaptures found within 100 m) · <1 km (60-65% recaptures found within 1 km) · 315 km (longest distance recorded, but most caught near site of tagging) (Mace & Johnston 1983, Cole et al. 2000 Carbines 2004, Carbines & McKenzie 2004, Dias-Guisado 2014)	Long distance connectivity by migrations (Carbines 2004, Carbines & McKenzie 2004) Genetic differentiation between Chatham Islands and mainland; no to little differentiation on mainland, but isolation by distance observed (Smith 2012, Gebbie 2014) Limited mixing between inner and outer fiord populations in Fiordland (Rodgers & Wing 2008, Beer et al. 2011, Wing et al. 2012, Beer 2014)	Tag-recapture Mitochondrial DNA, microsatellites Otolith microchem, size structure, stable isotope analysis

Snapper	· Northern half of North Island (east and west coasts) · Northern waters of South Island (rarely in southern South Island)	Estuaries, harbours, rocky reef environments, soft sediment substrate · **Larvae** – seagrass beds, horse mussel beds, sponge gardens – which support food (copepods) · **Juveniles** – estuaries, seagrasses, sand flats adjacent to reef (but close to shore); habitat complexity with no to moderate flow · **Adults** – wider range of habitats: estuaries, harbours, rocky reef, soft sediment, around islands and in channels; faster tidal currents	**Scale of m-km** · <500 m (recaptures within 500 m over 3 yr) · 700-900 m (total distance at reef sites) · 2.1-18.9 km (total distance at outer coastal sites) · <10 km (75% recaptures) · ~26 km (mean distance from tagging site) Movement differs between habitats; fish are more resident in reef sites Movements may be associated with spawning (Paul 1967, Crossland 1976, Will et al. 2001, Parsons et al. 2010,2011)	Larval subsidies from population within marine reserve contributed juveniles to populations within 40 km (Le Port et al. 2014, 2017) Migration between populations (Paul 1967, Crossland 1976) Genetic differentiation between west and east coast of North Island (with Hauraki Gulf being more closely related to the west coast) (Smith et al. 1978, Bernal Ramirez 2003) Different fishery stocks (Parsons et al. 2014a, Walsh et al. 2006, Walsh et al. 2011, Walsh et al. 2012, MPI 2013)	Oceanographic models, microsatellites Tag-recapture Allozymes, mitochondrial DNA, microsatellites Size structure
Seaweed					
Bladder kelp	· South and east coast of South Island · Cook Strait region (Marlborough Sounds and Wellington) · Stewart Island · Subantarctic Islands (but not Snares Island)	Intertidal, subtidal rocky reef, below 18-19°C (prolonged) Nutrient limited in winter, and sediment negatively affects growth and settlement Found mostly in sheltered areas, but water motion can increase nutrient uptake	<u>Dispersal</u> Two main ways: (1) Zoospores **Scale of m** · 5-150 m in calm · 4000 m in storm · 1000s m (model) (2) Kelp raft **Scale of km** · 1000s km (Anderson & North 1966, Reed et al. 1988, Gaylord et al. 2002,2006, Macaya et al. 2005, Macaya & Zuccarello 2010a,b)	Kelp rafts with long distance dispersal have viable reproductive entities (Macaya et al. 2005, Hernández-Carmona et al. 2006) No to very little genetic differentiation between populations around mainland New Zealand, Stewart Island and Subantarctic Islands (Macaya & Zucarello 2010a,b, Macaya 2010)	Examination of spore production from rafts Mitochondrial DNA, microsatellites

Marine Mammals					
NZ sea lion	· Otago · Stewart Island · Auckland Islands · Campbell Island	· **Land** – away from anthropogenic disturbance, close to beach/estuary, long forest areas behind beach for dispersion · **Sea** – Benthic foragers, use the continental shelf	**Land – scale of m-km** · 800 m – 1.5 km inland for dispersion · 10 km^2 (high site fidelity, remain in this area) **Sea -- scale of km** · ~100 km from shore (Subantarctic foraging) · ~ 5 km from shore (Otago foraging) (McNally et al. 2001, Chilvers et al. 2005a, 2011a,b, Chilvers 2008, 2009, Auge et al. 2011a)	Juvenile males move between colonies and sometimes juvenile females emigrate (McConkey et al. 2002, Chilvers & Wilkinson 2008) No genetic differentiation between mainland, Stewart Island or Subantarctic Islands	Tag-resight Mitochondrial DNA, microsatellites
Hector's dolphin	South Island (west coast, east coast, south coast)	Both subspecies– Warm, turbid, shallow coastal waters, remain in bays and frequent harbours	**Hector's -- scale of km** · ~60 km (longest distance between two sightings) · 50 km range along coast, most activity within 17 km · ~5-30 km offshore **Māui -- scale of km** · 140 km range along coast, most activity within 35 km · ~1-20 km offshore (Brager et al. 2002, Slooten et al. 2005,2010, Rayment 2008,2009, Oremus et al. 2012, McKenzie & Clement 2016)	Strong genetic differentiation between Māui and Hector's dolphins; strong genetic differentiation between populations of Hector's dolphins, with 3 populations (1) west coast, (2) east coast, (3) south coast (Pichler et al. 1998, Pichler 2001, 2002, Hamner et al. 2012) Evidence of inbreeding for Māui dolphins and loss of genetic diversity for Hector's dolphins (Hamner 2014, Hamner et al. 2017, Pichler & Baker 2000) Movement of Hector's dolphins outside of range (with some incorporating themselves in Māui range – potential for interbreed) (Hamner et al. 2013, Pichler 2002)	Mitochondrial DNA, microsatellites Mitochondrial DNA, microsatellites Genetic recapture (using microsatellites)
Māui dolphin	North Island (140 km stretch along west coast)				

Penguins					
Little blue penguin	· North and South Islands · Stewart Island · Chatham Islands	· **Land –** variable; grassy fields, herbfields, scrublands, woodland forests, rock screes, caves, urban areas · **Sea –** pelagic foragers, bathymetry and geographic features influence foraging; proximity to river mouth reduces foraging distance	**Scale of km** · 9-30 km (foraging ranges recorded from colonies in Hauraki Gulf, Chatham Islands, Oamaru, Wellington) · 102 km (mean foraging ranges in Marlborough Sounds during incubation) Foraging ranges influenced by location, colony size and stage of breeding (i.e. incubation, chick rearing) (Mattern 2001, Chiaradia et al. 2007, Agnew 2014, Poupart et al. 2017, Chilvers 2019)	Movement of individuals between colonies (Johannesen et al. 2002, Poupart et al. 2017) Two species exist in New Zealand: (1) colonies at Otago and Oamaru have Australian origin (*E. novaehollandiae*), (2) rest of colonies across NZ are same (*E. minor*) (Banks et al. 2002, Peucker et al. 2009, Grosser et al. 2015,2016) No genetic differentiation between populations of *E. minor* throughout New Zealand (Grosser et al. 2015)	Tag-resight Allozymes, mitochondrial DNA, microsatellites Mitochondrial DNA, microsatellites
Yellow-eyed penguin	· South Island (east coast) · Stewart Island · Auckland Islands · Campbell Island	· **Land** – low podocarp or hardwood forests, needed for thermal relief; require suitable landing sites (beach, rock platform) · **Sea** – benthic foragers, foraging on shelf, reef, oyster beds, horse mussel beds; rely on benthic features to navigate	**Scale of km** <60 km (foraging rage; generally 10-25 km) High site fidelity (Richdale 1957, Darby & Seddon 1990, Moore 1999, Ratz et al. 2004, Mattern et al. 2007, Parker 2009, 2010, Ellenberg & Mattern 2012, Mattern et al. 2013, Chilvers et al. 2014, Mattern & Wilson 2018)	Strong genetic differentiation between Subantarctic Islands and mainland (no gene flow between populations) (Boessenkool et al. 2009, 2010) Low rates of immigration between populations (Lopes & Bossenkool 2010) Only one individual recorded as ever moving between populations (DOC unpublished data, cited in Boessenkool et al. 2009 and Ellenberg & Mattern 2012)	Mitochondrial DNA, microsatellites Computational model Tag-resight

Fiordland crested penguin	· Southern South Island (South Westland and Fiordland) · Stewart Island (and outlying islands)	**Land –** dense podocarp-broadleaf forest and scrub, caves, boulder beach; colonies often near creeks or waterways to ocean	**Scale of km** · 50 km (foraging of breeding) · ~1000s km (total journeys 3500-6800 kms; foraging before moulting) (Mattern & Wilson 2018; Mattern et al. 2018)	Unknown

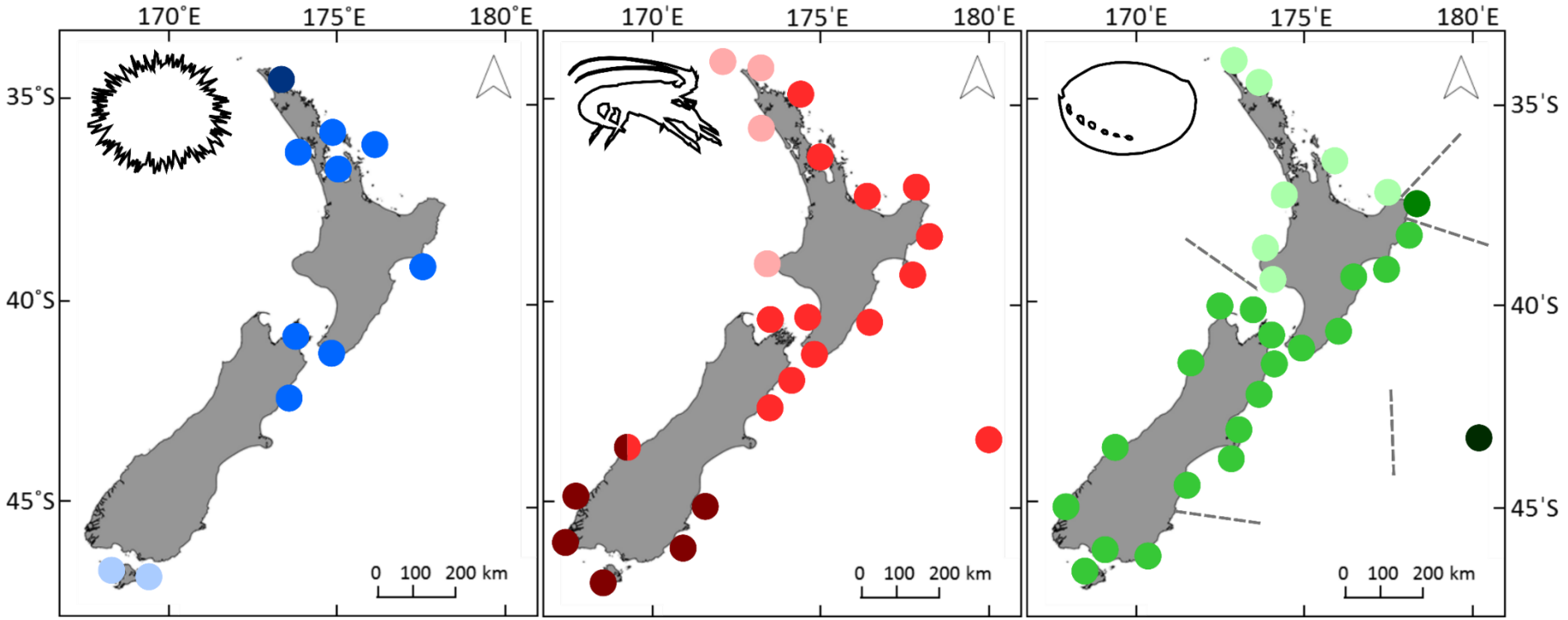

Figure 1. Population structure for invertebrates in New Zealand (L to R: kina, adapted from Nagel et al. 2015; spiny rock lobster, adapted from Thomas and Bell 2012, Ilyushkina 2018; pāua, adapted from Will et al. 2011, 2015). Each circle on the map indicates a sample location (i.e., population) from the associated study/studies, and the colours reveal the simplified population structure, where populations of the same colour are genetically similar, and populations of different colours showed some genetic differentiation. Circles split with two colours represent conflicting reports from different studies. Dashed line for pāua represent identified phylogenetic breaks (from Will et al. 2011). The Chatham Islands are represented by the circles to the east of New Zealand, and are not to scale (Chatham Island distance from east coast = ~850 km).

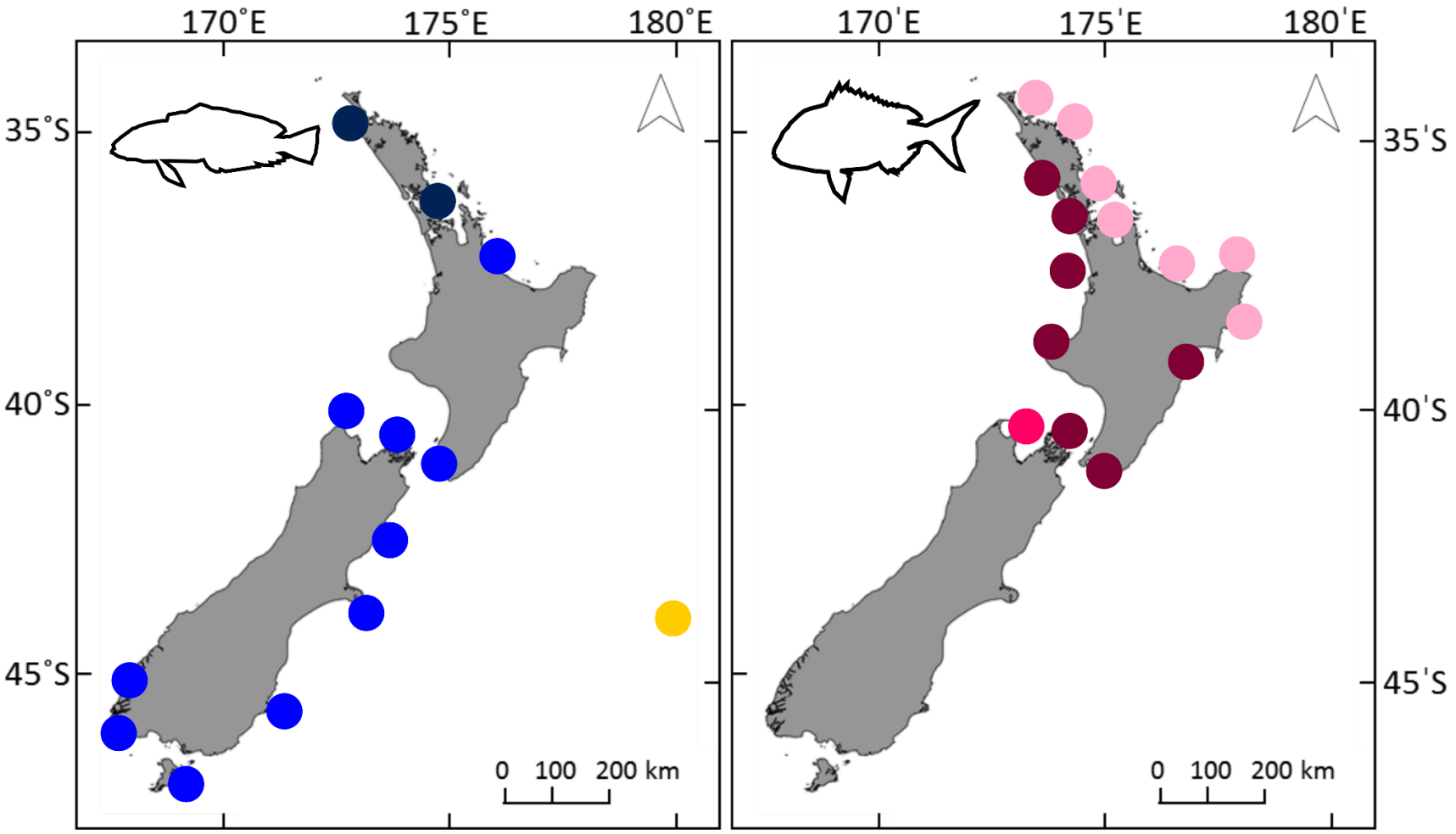

Figure 2. Population structure for fish in New Zealand (L to R: blue cod, adapted from Smith 2012, Gebbie 2014; snapper, adapted from Smith et al. 1978, Bernal Ramirez 2003). Each circle on the map indicates a sample location (i.e., population) from the associated study/studies, and the colours reveal the simplified population structure, where populations of the same colour are genetically similar, and populations of different colours showed some genetic differentiation. The Chatham Islands are represented by the circles to the east of New Zealand, and are not to scale (Chatham Island distance from east coast = ~850 km).

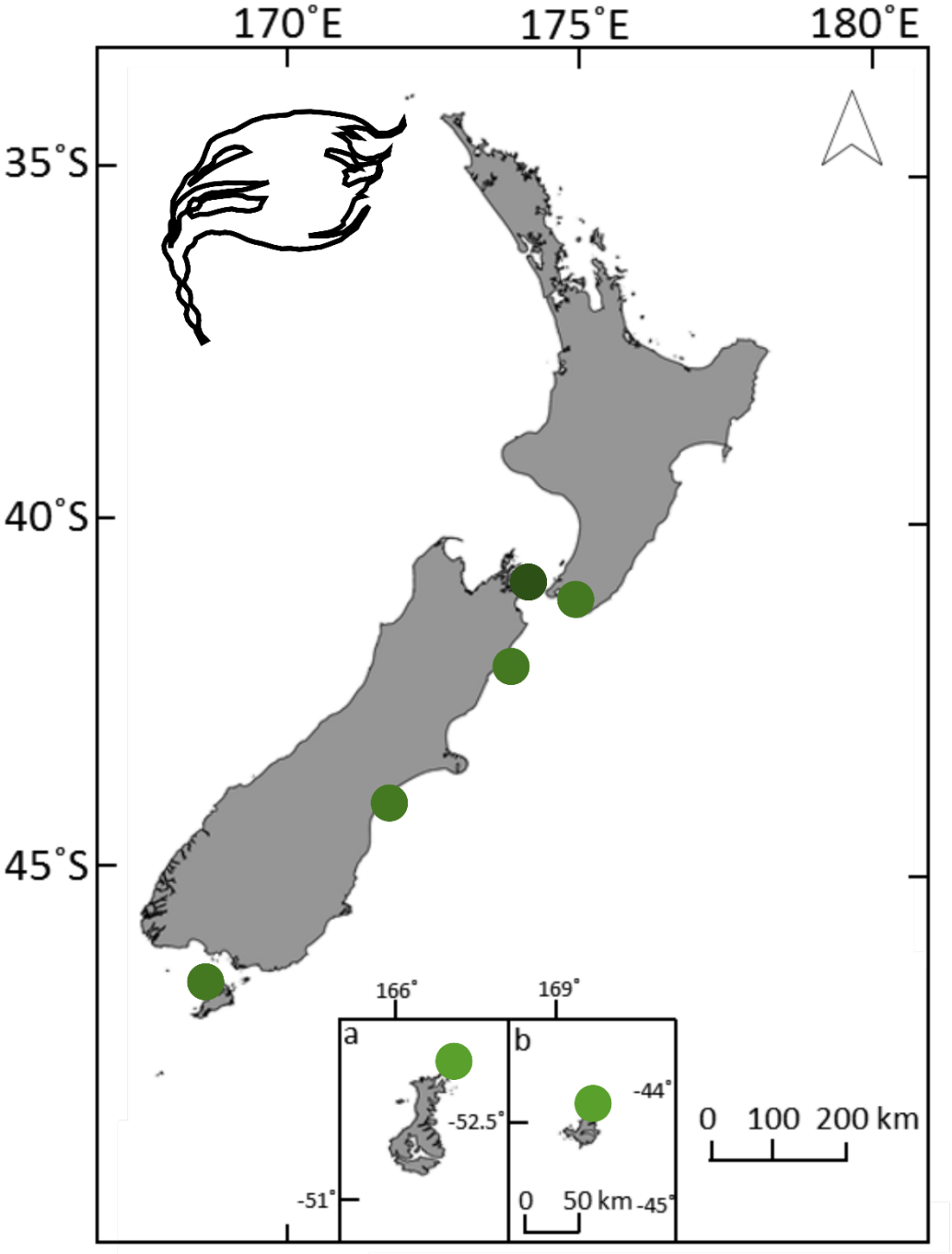

Figure 3. Population structure for giant kelp (Macrocystis) in New Zealand, including (a) Auckland Islands and (b) Campbell Island (adapted from Macaya 2010, Macaya and Zuccarello 2010a,b). Each circle on the map indicates a sample location (i.e., population) from the associated study/studies, and the similar shades of colour indicate genetic similarity between populations and high levels of gene flow. Picton and the Subantarctic Islands are a slightly different shades as they showed very minor genetic differentiation.

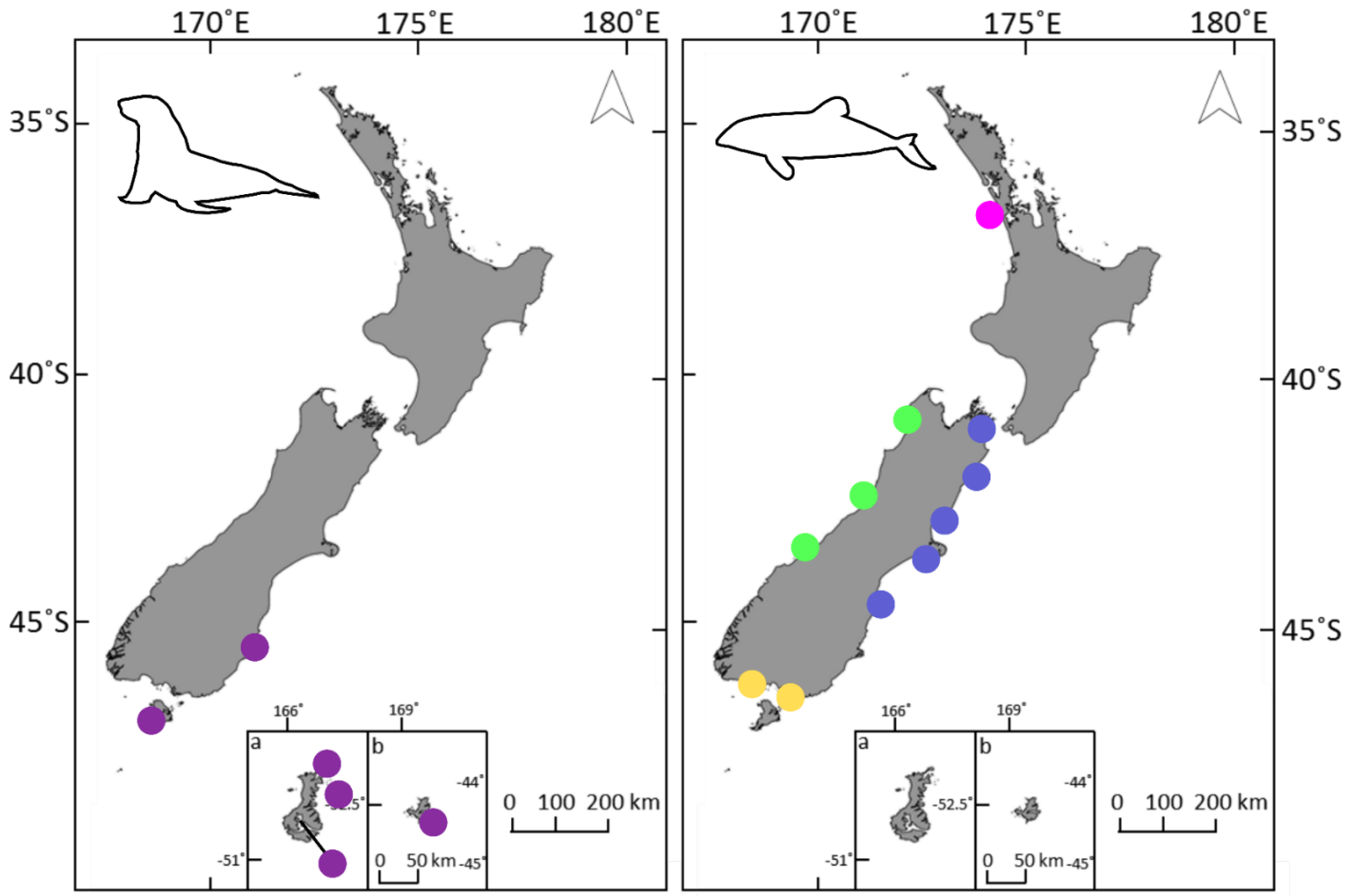

Figure 4. Population structure for marine mammals in New Zealand, including (a) Auckland Islands and (b) Campbell Island (L to R: sea lions, adapted from Osborne et al. 2016, Collins et al. 2017; Hector's and Māui dolphin, adapted from Hamner et al. 2012). Each circle on the map indicates a sample location (i.e., population) from the associated study/studies, and the colours reveal the simplified population structure, where populations of the same colour are genetically similar, and populations of different colours showed genetic differentiation.

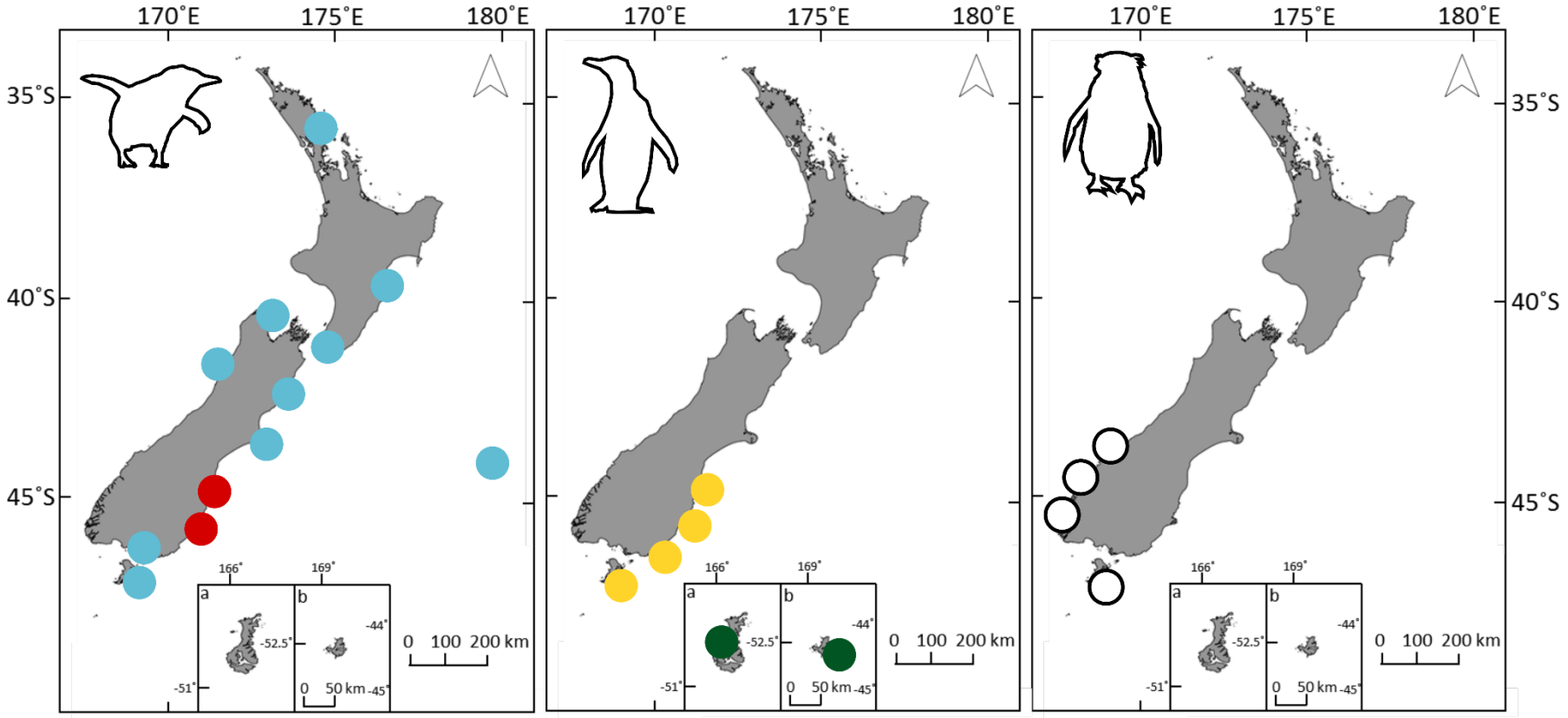

Figure 5. Population structure for penguins in New Zealand, including (a) Auckland Islands and (b) Campbell Island (L to R: little blue penguins, adapted from Grosser et al. 2015; yellow-eyed penguins, adapted from Triggs and Darby 1989, Boessenkool et al. 2009). Each circle on the map indicates a sample location (i.e., population) from the associated study/studies, and the colours reveal the simplified population structure, where populations of the same colour are genetically similar, and populations of different colours showed some genetic differentiation. Empty circles mean that population structure is unknown, but indicate species distribution.

5. Results

5.1. Commercially and culturally important invertebrates

5.1.1. Sea urchin (kina)

Habitat	• Rocky reef (cryptic or exposed) • Coarse/shell substrate • Sometimes sand or mud bottom (rarely)
Home range	• Small, on the scale of meters
Connectivity	• PLD = 1-2 months • Larval dispersal distance = 100s km • Differentiation between North Island and South Island (+ Wellington) populations • Genetic differentiation between inner and outer fiords • Differences in demographic dynamics between outer and inner fiords (with indirect evidence that outer fiords act as larval sources for inner fiords)

The sea urchin, *Evechinus chloroticus*, is a commercially and culturally important echinoderm in New Zealand, commonly referred to by its Māori name 'kina' (McShane et al. 1994a, Miller and Abraham 2011). Kina are found throughout New Zealand, having a wide distribution on both the North and South Islands. They have been reported as far south as Snares Island and Stewart Island, as far east as the Chatham Islands, and as far north as Three Kings Islands (Dix 1972a, Barker 2013). They are absent from the Auckland Islands and Campbell Island (Andrew 1988, Barker 2013), and there are contrasting reports of kina occurring in the Kermadec Islands. Dix (1972a) speculated that the few reports confirming its appearance in the Kermadec Islands likely originate from conjecture that has been continually repeated in conversation, but instead its absence from field surveys conducted in the Kermadec Islands (i.e., Keable and Reid 2015, Duffy and Ahyoung 2015) indicate that it does not likely exist there.

5.1.1.1. Habitat use of kina: exposed versus cryptic

Kina occur from the shallow subtidal to depths ~15 m, although have been found to 60 m (Barker 2013). Wing et al. (2003) documented that 90% of surveyed urchins in the Doubtful-Thompson Sound complex, Fiordland occurred between 3-9 m. In northern New Zealand, they have been found in the intertidal (Dix 1972a). They are

often found in aggregations or clumps, and sometimes form ‘kina barrens’ where they graze on available algae, leaving behind barren rock (Choat and Schiel 1982, Shane and Naylor 1991, Barker 2001). Kina barrens are more often observed in northern New Zealand (Shears and Babcock 2004, Miller and Abraham 2011, Barker 2013), but do occur to a lesser extent in other areas of New Zealand (Villouta et al. 2001, Barker 2001, Shears and Babcock 2004). Kina can occupy a range of different habitats, and its habitat use often depends on factors including: its life stage (i.e. size), food availability and/or the presence of predators (Andrew and Choat 1982, Andrew and MacDiarmid 1991, Cole and Keuskamp 1998, Barker 2013, Spysksma et al. 2017).

Larvae have been found to preferentially settle on to crustose coralline algae, followed by oyster shell, aged rock and finally aged plastic (Lamare and Barker 2001a). Juveniles and adults tend to occupy different habitats, where smaller urchins (juveniles <40 mm in test diameter) remain ‘cryptic’ until they grow larger and assimilate into the adult population (Andrew and MacDiarmid 1991, Barker 2013, Spysksma et al. 2017). Once reaching a larger size, adults become more exposed and occupy a range of habitats, including rocky reef, shell or coarse substrate, and sometimes, though to a lesser extent, fine sand and muddy substrate (Dix 1972a, Andrew 1988, Barker 2013, Glockner Fagetti and Phillips 2020).

Food availability can influence exposed versus cryptic habitat use in adult kina. For instance, kina have been found to be more exposed on the reef in environments that have low algal cover, but more cryptic (i.e., have higher crevice occupancy) in areas with high algal abundance (Cole and Keuskamp 1998, Shears and Babcock 2004, Spyskma et al. 2017). Availability of food likely drives this pattern, where kina become more exposed in those areas with little algae because they are out actively foraging and searching for food, whereas in areas where algae is plentiful, kina can take advantage of drift algae and feeding requires less movement (Andrew and Stocker 1986).

The role of predators also contributes to this inverse relationship of exposure and algal cover. Common predators of kina include blue cod, snapper and spiny rock lobster (Dix 1972a, Andrew and MacDiarmid 1991). In general, when predators are abundant, densities of kina are maintained through predation, resulting in less grazing by kina

and thus a higher abundance of algae; conversely, in environments with fewer predators present, kina populations tend to increase, and barrens may form from excessive grazing (Andrew and Choat 1982, Cole and Keuskamp 1998). Shears and Babcock (2004) compared the density and population structure of kina populations in relation to barren habitat and algal community structure in both reserve and non-reserve sites. These authors found that there was a significantly lower density of kina and urchin barrens for those of the reserves that have been protected for 15+ years (both CROP and Tawharanaui Marine Reserves), and suggested such differences were likely attributed to higher predation in reserves. However, this trend was not universal for all marine reserves (13 investigated reserve sites), and different environments had less noticeable trends between the predator-grazer-algal relationship. In fact, at the Long Bay-Okura, Kapiti and Te Tapuwea o Rongaokako Marine Reserves, kina did not play an important role in structuring algal communities (Shears and Babcock 2004).

Shears and Babcock (2004) also found that kina were more cryptic, especially larger individuals, in reserve sites. It has been speculated that crevice occupancy in high algae environments is a behavioural response to the presence of predators, rather than a response to food availability. For instance, experimental evidence from Spyskma et al. (2017) indicated that kina were more cryptic in the presence of dead urchins, but not in the presence of more food. Furthermore, observations taken overnight (when kina are generally active and emerge from crevices) in fished reefs at Leigh by Spyskma (2016) revealed that the presence of dead urchins resulted in ~80% of night-time crevice occupancy versus ~40% in the control location without dead urchins. Nonetheless, it is likely that both predator presence and food availability play a role in kina density and kina crevice occupancy. Other factors that have also been shown to affect kina density, including wave exposure (positively correlated to abundance; Choat and Schiel 1982, Walker 2007) and sediment (negatively correlated to larval survival; Phillips and Shima 2006, Walker 2007).

5.1.1.2. Home range of kina: stay close to home

The few studies that have examined kina movement have reported very small home ranges. Andrey and Stocker (1986) and Andrew and MacDiarmid (1991) both tagged kina at CROP Marine Reserve and found that kina moved an average of 34.2 cm over

a 24 hr period (Andrew and MacDiarmid 1991). In a separate study, Andrew and Stocker (1986) found that kina movement (measured as overnight displacement) was approximately 2x greater when occupying exposed habitat (80-180 cm) than when occupying cryptic habitat (20-70 cm), likely due to the greater need to forage and find food. In a field experiment examining movement in relation to predation, Spyskma (2016) found that over one hour, average kina movement was 48.1 cm in response to the addition of 'injured conspecifics', 17.6 cm in response to the addition of an 'extraneous cue' (crushed pilchard), and 5.7-7.4 cm in response to control treatments. Furthermore, movement of these kina was more likely if the addition of the cue was within 0.5 m of them.

Tag and recapture studies for kina in both Kaikoura and Kaiteriteri (Dix 1970a) and Fiordland (Lamare and Mladenov 2000) similarly reveal small home ranges. Dix (1970a) tagged 310 kina in Kaikoura with recovery rates of 57% after 3 months, 26% after 6 months, and 17% after 9 months and a maximum distance moved of 4.8 m. At Kaiteriteri, 27 kina were tagged and only 4 were recovered after a month, all within 5 m of the tagging site (Dix 1970a). Dix (1970a) speculated that the decrease in recovery rates over time was likely attributable to mortality rather than movement, as the fitness (measured by gonad indices and gut content) were lower for the tagged specimens and many dead tagged urchin tests were found at the sites. Lamare and Mladenov (2000) tagged urchins in Fiordland and found that after 1 year, retention rates were 23.5% and 37.7% (at two different sites) and after 4 years, was 30.12% (at one of the sites, no data for other). Thus, after long periods of time, kina are found to remain in the same area, indicating a small home range. This relatively high recapture rate over time, coupled with the observed low movements, suggests that after settlement, the home range of kina is fairly small (on the scale of meters).

5.1.1.3. Connectivity of kina: multiple 'stocks'

Movement patterns of kina have been examined through the use of genetic tools (Mladenov et al. 1997, Baker 2011, Nagel et al. 2015), demographic variability (Lamare and Barker 2001a, Wing et al. 2003, Wing 2009, Wing 2011), and plankton tows that identify movement of larvae (Lamare 1998). The genetic studies have investigated genetic differences between various populations in the North Island and South Island, whereas demographic variability and larval dispersal work has been

done primarily in Fiordland, in an attempt to understand how kina move around the fiords.

Due to the relatively long PLD of kina (1-2 months; Dix 1969, Walker 1984, Lamare and Barker 2001b, Oldman et al. 2006) and large distances (100s km) of dispersal, a single well-mixed stock of kina around New Zealand could be possible and was supported by earlier work by Mladenov et al. (1997). However, using recent genetic techniques, Nagel et al. (2015) instead found that kina are comprised of multiple genetic stocks within New Zealand when examining populations at eight main locations in both the North and South Islands: Northland, Haruaki Gulf, Piha, Mahia Peninsula, Wellington, Nelson, Kaikoura and Stewart Island (Fig. 1). Within the Haruaki Gulf, the authors also looked the genetic composition of populations at a smaller scale, examining genetic differentiation between the Whangaroa Peninsula, Great Barrier Island and Waiheke Island. Populations of kina in the North Island (+ Marlborough Sounds) were genetically different to those in the South Island, split by a hydrodynamic barrier in the Cook Strait that likely limits gene flow between these two regions. Across the small scale within the Hauraki Gulf, populations were generally well connected, but slight genetic differences were detected between the outer gulf (Great Barrier Island) and inner gulf (Whangaroa Peninsula and Waiheke Island).

Genetic structuring of populations over a small scale have also been observed in Fiordland. Perrin et al. (2003) found that not only was the Fiordland population genetically different than the rest of the New Zealand populations, but that small scale genetic differences also occurred between inner and outer fiord sites for all 14 fiords. Two distinctive genetic populations were evident in Fiordland: one comprised of outer fiord (coastal) populations, and the other comprised of the mid and inner fiord populations. Perrin et al. (2003) concluded that the high energy environment towards the outer fiords allows mixing of those populations, while either a recent and unique colonization or selection acting on the inner fiords (characterised by sparse resources, low algal cover, and freshwater input) produce genetically similar populations.

Wing et al. (2003) examined the abundance, growth, gonad development, larval settlement and size structure of inner and outer Fiordland populations in the Doubtful-Thompson Sound complex. The highest growth rate and gamete production occurred near fiord entrances, and kina were more abundant and had higher larval settlement

(determined through use of settlement collectors) in outer and mid-fiord sites. Wing et al. (2003) also constructed a hydrodynamic model to estimate larval dispersal and identify areas of concentrated larvae after 30 days of dispersion, finding different potential sink populations toward the mid and inner fiords.

In a subsequent study, Wing (2009) examined the size structure between 1998 and 2007 at outer and inner fiords across 22 sites and calculated recruitment indices based on the fraction of individuals <60 mm (i.e., newly emergent juveniles). Outer fiords were found to contain larger kina associated with higher densities of available food (*Ecklonia radiata*), while inner fiords contained smaller kina with lower densities of food. Furthermore, the recruitment index was significantly positively associated with distance from outer coast. This pattern was reported again by Wing (2011) across 53 Fiordland sites in 2002. Time series data (Wing 2009) revealed that inner fiord populations were subject to common adult mortality events (followed by recolonization of juveniles), as evidenced by absence of previously recorded larger individuals and appearance of new smaller individuals over the course of a year. Wing (2009) and Wing (2011) speculated that outer fiords likely act as a source for inner fiord populations, basing this on both findings of larval sinks in the Doubtful-Thompson Sound Complex (Wing et al. 2003) and previous work by Lamare (1998), which indicated (through use of plankton tows and hydrodynamic models) that larvae were retained in the fiords due to the estuarine circulation. While this pattern of movement may require more direct evidence to validify, it is apparent that differences in population dynamics between inner and outer fiords exist, where outer fiord populations showed more stability and inner fiord populations displayed more demographic variability over time.

Interestingly, Wing (2011) identified nine outer fiord populations containing higher frequencies of larger kina that are ‘likely productive source populations’ and highlighted that zero of these nine populations are currently within an existing marine reserve, suggesting that the source populations of kina are currently not adequately protected in the fiords. Protecting source populations that seed multiple populations is especially important due to the sporadic recruitment of this organism.

5.1.2. New Zealand spiny rock lobster

Habitat	• Rocky reef (crevices, holes, gaps) • Sandy patches, low lying reef, horse mussel beds important for inshore-offshore movements • Juveniles generally remain more cryptic than adults
Home range	• Small, less than 5 km • Inshore-offshore movements that coincide with mating, moulting and foraging (less than 5 km)
Connectivity	• PLD = 1-2 years • Larval dispersal distance = 100s-1000s km • Migrant dispersal distance = 100s km • High levels of gene flow due to juvenile migrants and long PLD • Likely different sources and sinks for larvae: (1) far north, (2) east coast North Island, (3) Chatham Islands, and (4) southern New Zealand • Low to moderate levels of genetic differentiation between: (1) northwest North Island, (2) northeast North Island and (3) southern New Zealand

There are two species of lobsters that exist in New Zealand waters: (1) the red or spiny rock lobster, also commonly referred to as crayfish (*Jasus edwardsii*); and (2) the packhorse lobster, also referred to as the green rock lobster (*Sagmariasus verreauxi*). The spiny rock lobster is found in southern Australia and Tasmania, as well as throughout New Zealand, extending its range as far north as the Three Kings Island, as far south as the Auckland Islands and as far east as the Chatham Islands (Kensler 1967). By contrast, the packhorse lobster is distributed mainly eastern in Australia, throughout the northeast coast of New Zealand and the Kermadec Islands, and has been found as far south as Bluff, though instances of the packhorse lobster in southern waters are rare (Kensler 1967). The two are distinguishable from one another in that the packhorse lobster generally grows larger than the spiny rock lobster and has a smooth tail. While both are fished in New Zealand, the spiny rock lobster fishery is among the most economically valuable commercial fisheries in New Zealand, and therefore has been the subject of extensive research examining different aspects of its ecology. In this report, we focus on the habitat requirements, home range and movement patterns of only the spiny rock lobster (*Jasus edwardsii*).

5.1.2.1. Habitat of spiny rock lobsters: rocky reef inhabitants

Spiny rock lobsters are found mainly in subtidal rocky reef habitat, though sometimes form aggregations on sand (see inshore-offshore movements in Section 5.1.2.2. for more information; Kelly et al. 1999). They require shelter from predators and are typically seen in complex habitats including shallow broken rock habitat, small and large boulder complexes, crevices, cracks, gaps and holes in the reef (Kensler 1967, Andrew and MacDiarmid 1991, Lucieer and Pederson 2008). Lobster abundance is often positively correlated with the availability of shelter habitats (MacDiarmid 1987). The inclusion of habitat complexity in marine reserve design is important in supporting lobster densities; for instance, the Fiordland Te Awaatu Channel Marine Reserve (est. 1993) contains a complex kelp forest and had the highest density of lobsters compared to the Taipari Roa Marine Reserve (est. 2005), which had no lobsters likely due to its degraded habitat (Jack and Wing 2010). Mussel bands in Fiordland have also been found to be positively correlated to lobster densities, and lobsters occurring in degraded habitats in Fiordland where mussels were absent relied on less nutritional food sources (Jack et al. 2009, Jack and Wing 2010).

Studies examining the influence of habitat and predation on spiny rock lobster in Tasmania have found lower predation in structurally complex kelp forests relative to low complexity barren habitats, with survival in kelp forests 40% versus 10% in barrens, likely due to the presence of shelters (Hinojosa et al. 2014). By contrast, Hesse et al. (2015) found no difference in predation rates between kelp forest and barren habitats in northeast New Zealand, with the authors concluding that while shelters may be more available in kelp forest habitats, lobster predators are also more abundant, indicating that factors other than habitat alone dictates lobster abundance.

Lobsters of different life stages prefer different habitats. Later-stage lobster larvae (puerulus) settle in crevices, holes and indentations, and sometimes though less frequently, on complex seaweeds and bryozoans (Lewis 1977, Booth and Phillips 1994, Booth 2001, Hinojosa et al. 2014), and sandy environments where they sometimes bury themselves (however, they are intolerant of deep silt, Booth 2001). Juveniles have more specificity in habitat use, preferring small holes similar to their size, which allows them to be tightly enclosed on all sides (Edmunds 1995, Booth and

Ayer 2005). The availability of substrate and habitats for puerulus and juveniles can affect the overall settlement and recruitment success in a population.

By contrast, adult lobsters tend to be more variable in habitat preferences, occupying larger holes, crevices and gaps on the reef. Adult lobsters typically form cohabitation groups in sheltered areas, where groups of more than 100 individuals can occur (MacDiarmid 1994). During monthly surveys from 1982 to 1985 in CROP Marine Reserve, MacDiarmid (1994) found that around 50% of the observed lobsters were associated with a cohabitation group of 7 individuals or more. These groups were more likely to consist of mature females and larger males, with juvenile lobsters leading more solitary lives.

Much of the research surrounding spiny rock lobsters has addressed the effect of marine reserves on lobster density, with consideration into how design and habitat features of reserves may benefit lobster populations. Generally (though not always), lobster abundance and size distributions have increased after the establishment of a marine reserve (Cole et al. 1990, Kelly et al. 2000, Davidson et al. 2002, Freeman et al. 2012a,b, Young et al. 2016). In examining the effects of reserve age, reserve size, length of coastline protected, and minimum distance to the offshore boundary on the rate of increase and recovery of lobster populations in five North Island marine reserves and three South Island marine reserves, Freeman et al. (2012a) found that age of the reserve was the most important factor determining lobster recovery, and size did not influence the initial recovery rate of lobsters. Similarly, Diaz-Guisado et al. (2012) examined 13 New Zealand marine reserves and found that size of reserve had no effect on lobster density and size, but rather age did. Although MPA size has not been found to directly correlate with lobster abundance and/or size, size of certain habitats within the reserve is likely more important in influencing such metrics, and (while not investigated in these studies) may provide a more thorough understanding of size dependency (especially in relation to cross-boundary movements and buffer zones).

Freeman et al. (2009) examined lobster populations on three reefs in the Te Tapuwae o Rongokako Marine Reserve, one that was fully encompassed in the marine reserve (100%) and two reefs that were only partly protected (40% and 9% protection), with the reefs separated by muddy sediment. Of the 5225 lobsters tagged on the three

reefs over 3 years, 921 lobsters were recaptured at least once, recording 1114 lobster movements. Of these, 98% moved within a reef and only 1.5% of individuals moved between two reefs. Only 1% of lobsters from the fully protected reef were found outside of the reserve, whereas 29% of lobsters tagged from the reef with only 9% protection were found outside the reef. This study demonstrates that varying protection of habitats within reserves can have different outcomes, which can have important considerations in MPA planning and design. For instance, an entire reef may be encompassed in a marine reserve in order to protect an entire population, whereas boundaries that intersect reefs may allow for greater spill over effects (e.g., Kelly 1999, Kelly and MacDiarmid 2003, Freeman et al. 2009). Similarly, Rojas-Nazar et al. (2019) found that the Taputeranga and Kapiti Marine Reserves had higher catch per unit effort at reefs that were fully protected than partially protected. Significant edge effects overtime may lead to population declines and collapses, but this depends on a number of factors including the rate of immigration from the protected site and the proportion of the population that is protected (Roberts et al. 2001).

5.1.2.2. Home range of spiny rock lobsters: depends on size and sex

Spiny rock lobsters generally have high site fidelity with a small home range once settled (i.e., less than 5 km), but they have small scale seasonal inshore-offshore movement patterns (Booth 1997). They are crepuscular and nocturnal (41 m [median] at night reported in CROP Marine Reserve), but are active during the day during mating season (MacDiarmid et al. 1991). During the mating period in CROP Marine Reserve, females were found to active moving between shelters to find suitable shelter and mates at night (MacDiarmid et al. 1991). By contrast, males were found searching for females both day and night, with the total distance covered by males inversely related to the size of the male (MacDiarmid et al. 1991). Observations made using acoustic tracking of lobsters in CROP Marine Reserve revealed that movement ranged from 29 m/day to 1 km/day, and that lobsters spend 84% of their time at their home site (Kelly 2001).

Tag and recapture studies also reveal a small home range. Annala (1981) tagged 4613 lobsters between 1975-1978 near Gisborne and found that of only 3.5% of the recaptures (2131 returns) were recovered further than 5 km of the original tagging site. Similarly, Kelly and MacDiarmid (2003) found that 70% of tagged and recaptured

lobsters moved less than 250 m (and 87% within 2.5 km) in CROP Marine Reserve, finding that site association increased with lobster size. In the Te Tapuwea o Rongokako Marine Reserve, Freeman et al. (2009) found that all of the tagged and recaptured lobsters remained within 4 km of the initial release location, and most movements were 1-2 km for males and 100-200 m for females. For settled adult lobsters, home range is therefore small, generally less than 5 km. Less frequently reported, some lobsters have been found to spend their time between two locations. Kelly (1999) found that five of the 32 lobsters with acoustic tags in CROP Marine Reserve travelled between two sites within 200 m-1.3 km of each other, spending anywhere from 1-93 days between each site.

Spiny rock lobsters make seasonal inshore-offshore movements (within 5 km), and these have been found to be associated with moulting, foraging and reproductive cycles (Booth 1997, Kelly 2001, MacDiarmid 1991), rather than environmental factors (MacDiarmid 1987, MacDiarmid et al. 1991, MacDiarmid 1991). In northeast New Zealand (CROP and Tawharanui Marine Reserves), 32 lobsters were fitted with acoustic tags for 14-355 days in order to track lobster movements (Kelly 2001). Over the year, 21% of the lobsters did not leave the home site, and for the ones that did, 56% of them returned. It has been reported that lobsters go offshore to forage nocturnally on bivalves and other prey items (MacDiarmid 1987, Kelly 2001, Kelly and MacDiarmid 2003). Shifts in depth distribution have also been found throughout the year for each sex. Males increased their movement activity twice throughout the year in the summer and in the winter, where movements into the shallows (<10 m) have coincided with moulting and also the mating season (which occurs from April – July; MacDiarmid 1987, Kelly 2001, Kelly and MacDiarmid 2003). Female movement was associated with the reproductive cycle. For females, mating and moulting has been shown to be synchronized, where females moult in the shallows in the winter (MacDiarmid 1991, Kelly et al. 1999). Females mate and carry eggs for 3-4 months (Kelly et al. 1999), and then egg-bearing lobsters increase their movement activity and head offshore (>25 m depth) just prior to releasing eggs (September – October; MacDiarmid 1987, MacDiarmid 1991, Kelly 2001). It is thought that females travel to the edge of coastal reefs where strong currents can transport and allow the rapid dispersal of larvae (McKoy and Leachman 1982, MacDiarmid 1987).

When lobsters go offshore, they typically form aggregations of hundreds of individuals on sandflats, horse mussel beds or low-profile reefs, with individuals on the edges of aggregations facing outward and protecting the group (Kelly et al. 1999, Kelly 1999). At CROP Marine Reserve, aggregations were found to exist offshore (with different sex ratios depending on the time of year) for 7 months of the year, but remained inshore for 3 months over winter during mating (April – July; Kelly et al. 1999).

5.1.2.3. Connectivity of spiny rock lobsters: high gene flow but low levels of genetic differentiation

Spiny rock lobster larvae are among the longest-lived larvae for any marine organism, where larvae can last 12-24 months in the water column (Booth 1994, Bradford et al. 2014). Larvae (first stage larvae called phyllosoma phase) drift with oceanographic currents until they undergo metamorphosis into the later stage puerulus, which can swim from about 200 km offshore toward the shore to settle (Booth and Phillips 1994, Jeffs et al. 1999, Jeffs et al. 2002, Chiswell and Booth 2008). While it remains unknown how exactly puerulus navigate to the shore, possible mechanisms include using sound, water chemistry, and magnetic fields as directional cues, among other things (see Jeffs et al. 2005 for review). The main methods for investigating connectivity patterns for spiny rock lobsters include examining settlement data (i.e. from collectors, as in Booth and Tarring 1986), tracing larvae using oceanographic models, tagging and recapturing lobsters, and examining genetic differences of populations. The movement and connectivity patterns of lobsters are a product of oceanographic currents/barriers, long PLD, settlement success and migrations (of both juveniles and adults).

Using collector data, settlement patterns have been found to vary both spatially and temporally in New Zealand, where densities of settlers were related to different environmental factors (i.e., La Niña corresponding to settlement in southern NZ; Hinojosa et al. 2017). Oceanographic models tracing larvae have revealed that 9-14% of larvae from southeast Australia disperse to the west coast of New Zealand (Chiswell et al. 2003). Furthermore, within New Zealand, four main areas of dispersal (i.e., sources and sinks) have been identified by Chiswell and Booth (2008). The first area is the far north, which receives settlers from the west coast and supplies larvae to the east coast of the North Island. The second area is the east coast of the North Island,

which entrains a large amount of locally produced (and southernly produced) larvae in the Wairarapa Eddy (Chiswell and Booth 1999). The third area is south New Zealand, which has high levels of self-recruitment and supplies some larvae to northern parts of New Zealand. Lastly, the Chatham Islands act as a sink for larvae originating from mainland New Zealand (over half settled larvae are from the mainland), and supply larvae locally and to the east coast of the North Island. Importantly, Chiswell and Booth (2008) found that larval flow occurs from the South Island to the North Island, but with little flow occurring in the opposite direction, which has implications when identifying important source populations to protect.

Tagging and recapture studies have revealed that a small proportion of the lobster population travel larger distances, some as nomads (i.e., no directionality in movements) and others as migrants (i.e., directionality of movement, often against prevailing current; Booth 1997). The lobsters undergoing longer journeys are generally immature females and small males (McKoy 1983, Annala and Bycroft 1993). For instance, in CROP Marine Reserve, MacDiarmid (1987) found that the larger number of post settlement juveniles were not correlated with numbers of pre-settlement puerulus in larval collectors, suggesting increases in the number of juveniles was via immigration rather than settlement. Migrations over 100 km from original tagging sites have been reported, with a maximum distance of 460 km observed in Otago (Street 1971, Booth 1997). In the South Island, movement generally occurs during spring and summer (Booth 1997). Recaptures have also revealed that lobsters tend to remain within the shelf, within the 100 m contour (Street 1971, McKoy 1983, Booth 1997). McKoy (1983) examined movements of spiny rock lobsters in Stewart Island by tagging 4393 small female and male lobsters between 1974-1978, finding that 16% underwent migrations along the southeast coast of Stewart Island, with 16 lobsters recaptured in Fiordland.

In a review by Booth (1997) on long-distance movement in *Jasus edwardsii*, details are given for pooled tag data of 31,000 lobsters from 32 locations around New Zealand, and recapture rates reported (but not total distance moved) for those lobsters found greater than 5 km from the original tag site, from 1947-1993. From these studies, the maximum percent of far-travelling recaptures occurred on the Otago Peninsula in 1970, where 100% of the recaptured lobsters (63 of 220 originally tagged) were

recaptured further than 5 km (Street 1971, 1973). For more detail, see Table 1 in Booth (1997), which demonstrates that recapture rates varied across environments and across time.

There have been a number of genetic studies examining gene flow in spiny rock lobster populations within New Zealand, and between New Zealand and Australia. Early studies all indicated the existence of one genetic stock, with high levels of gene flow between New Zealand populations, and between Australia and New Zealand (Smith et al. 1980, Booth et al. 1990, Ovenden et al. 1992). The recognition of one genetic stock across New Zealand was reconsidered after a study using microsatellite loci by Thomas and Bell (2013). In this study, authors examined lobsters from six populations around New Zealand (and two in Australia) and found three significantly genetic clusters in New Zealand, with low to moderate differentiation: (1) northern sites (Hauraki Gulf), (2) central sites (Wellington, Kaikoura, Chatham Islands and Southwest Coast of New Zealand), and (3) southern site (Stewart Island) (Fig. 1). These were also genetically different from Southern Australia and Tasmania, which was further supported by Morgan et al. (2013), who also used microsatellites and found significant differentiation between southeast New Zealand and Australia.

Thomas and Bell (2013) compared their genetic findings to oceanographic models (Chiswell et al. 2003, Chiswell and Booth 2008). Both genetic data and oceanographic models supported dispersal from southeast Australia to New Zealand (where differences in magnitude between both methods were likely due to mortality or temporal variability); genetic data predicted about 2% of New Zealand spiny rock lobster were from Australia (Thomas and Bell 2013), and oceanographic models predicted 8-14% (Chiswell et al. 2003). The four areas of larval recruitment identified by Chiswell and Booth (2008) (described above) were not distinguished as genetically discrete areas by Thomas and Bell (2013). Genetic data supported larval exchange among all regions (except the far north and far south). Both oceanographic models and genetic data support the southern population is restricted from other locations and has high larval retention. The Chatham Islands population was found to be genetically the same as mainland New Zealand, which is supported by the Chiswell and Booth (2008) findings that over half of the settled larvae originated from the mainland. It is likely that although Chiswell and Booth (2008) identified discrete larval recruitment

areas, the exchange of larvae between areas (sources and sinks identified by Chiswell and Booth 2008) is enough to allow populations to remain genetically similar.

The most recent genetic study examining connectivity of lobsters in New Zealand uses high resolution single nucleotide polymorphisms (SNPs), and examined genetic differentiation in adult and juvenile populations (Ilyushkina 2018). In this study, high levels of gene flow were found for both adults and juveniles of all populations, but genetic markers revealed that three populations in New Zealand have different selective pressures (i.e., adaptive potential). These populations include northwest New Zealand, northeast New Zealand and southern New Zealand (Fig. 1), which is consistent with the findings of Thomas and Bell (2013). Local adaptations were found to be driven by sea surface temperature in these populations (Ilyushkina 2018). Thus, gene flow is high between populations, but some limitations appear to result in slight genetic differences between populations. Furthermore, different sources and sinks for populations likely exist.

5.1.3. Abalone (pāua)

Habitat	• Juveniles in intertidal, shallow (2-5 m) cobble, barren environments • Adults in wave exposed, deeper (5-20 m) rocky reef
Home range	• Small, less than 150 m
Connectivity	• PLD = ~72 hr but up to 8 days • Larval dispersal distance = 0.2-4 km (calm conditions); ~50-80 km (high energy environments) • Three to four phylogenetic breaks identified: (1) Chatham Islands break, (2) Cook Strait break, (3) East Cape Break, (4) break in southeast coast of South Island

Abalone are molluscs that have important cultural and economic value in New Zealand, commonly referred to by their Māori name pāua. Pāua contribute to customary, recreational and commercial fisheries in New Zealand. There are three species of pāua in New Zealand: the yellow-foot pāua (*Haliotis australis*), the white-foot pāua (*H. virginea*) and the black-foot pāua (*H. iris*). In this report, we consider the ecology of only the black-foot pāua (hereafter referred to as pāua), which is most desired by fisheries. Pāua is distributed on both the North Island and South Island, as

well as Stewart Island, Snares Island and the Chatham Islands (Poore 1969, Sainsbury 1977).

5.1.3.1. Habitat use of pāua: different for juveniles and adults

Pāua occupy intertidal and subtidal rocky reefs, occurring up to 100 m depth, but are mainly in the intertidal to depths of about 20 m (Poore 1969, Sainsbury 1977). Different life stages of pāua have different habitat preferences. Larvae (PLD of ~ 72 hr but up to 8 days; Tong et al. 1992, Moss and Tong 1992) are negatively buoyant before becoming planktonic, and settle on coralline algae such as *Pnophyllum coronatum* and *Hydrolithon rupestris* (McShane 1992, Roberts et al. 2004). Settlement success often depends on depth. For instance, an *in situ* experiment investigating growth and survival of post settlers found that settlement was greater in deeper waters compared to shallow waters, where <1% pāua survived after 16 weeks in the shallow waters (1-2 m depth), but 10% in the deep waters (6-8 m depth) (McShane and Naylor 1995a). The difference in survival was attributed to greater water movement and accumulation of finer sediments in the shallows, which caused dislodgment and smothering. Similarly, sedimentation has been shown to result in increased mortality of pāua larvae (Phillips and Shima 2006).

Juvenile pāua tend to prefer habitats sheltered from wave exposure, and have been found in high densities in environments containing cobbles and boulder fields (Laferriere 2016). Aguirre and McNaught (2011) conducted an *in situ* experiment investigating habitat-dependent effects on recruitment on pāua, comparing low complexity habitats (barren habitats) and high complexity habitats (algal habitats), at depths of 2-3 m versus 5-6 m. Juvenile pāua density was greater at the barren and shallow habitats; however, recruits were larger in algal habitats and had greater survival in algal habitats at depth. Aguirre and McNaught (2011) discussed that density-dependent growth and survival may be potential mechanisms driving this observed pattern. Increased habitat complexity may be associated with increased survival due to both increased available food and increased available shelter, and Aguirre and McNaught (2013) demonstrated that habitat complexity offered refugia for juvenile pāua by decreasing the chance of predation by starfish.

By contrast, adult pāua are often associated with areas of high wave exposure and dense macroalgal cover (Laferriere 2016). They generally occupy areas deeper than juveniles (i.e., >5 m, subtidal) and their abundance has been found to be positively correlated with crustose coralline algae and canopy cover (but negatively correlated to articulated corralling algae and understorey algal cover; Aguirre and McNaught 2012).

Wave exposure is linked to growth in pāua. Stunted populations have been observed to occur in areas that are sheltered from wave action (Schiel and Breen 1991, McShane et al. 1994b, McShane and Naylor 1995b). For instance, the exposed headlands of D'Urville Island were found to contain bigger and faster growing pāua than adjacent sheltered bays (McShane and Naylor 1995b). Furthermore, translocation experiments reveal that pāua moved from sheltered locations to exposed locations grew significantly more than those transplanted the opposite way (Laferriere 2016). Because the diet of pāua depends heavily on drift algae, food limitation is thought to drive the reduction of growth in stunted populations, where calmer waters result in less movement of drift algae. Thus, while calmer waters may support juveniles, they may also impair adult populations. It is therefore important to consider all life stages and habitat requirements for pāua when considering their protection.

5.1.3.2. Home range of pāua: small due to their sedentary nature

When transitioning from juvenile to adult stages, pāua move between depth strata. Settled larvae move from deep to shallow habitats (i.e., subtidal to intertidal), and juveniles tend to stay intertidal until reaching a certain size. Aguirre and McNaught (2012) found that juveniles remained cryptic between 67 – 75 mm shell length, with differences in shell length at different sites; and Poore (1972a) report that juveniles under 100 mm long inhabit more cryptic habitats. Once adulthood is reached, transition back from shallow to deep habitat occurs, as well as from more cryptic to open, exposed reef (Poore 1972a, Aguirre and McNaught 2012). As adults, the home range of sedentary pāua is small, on the scale of meters (Poore 1972a). Poore (1972a) examined movements and home range of pāua in New Zealand using recapture data, where individuals were tagged and observed "low water" (i.e., intertidal) versus "subtidal" colonies. This study found that intertidal colonies had more movement in the autumn and winter (lower recapture rates), where more disturbed seas likely resulted

in increased movements. Tagged individuals from the subtidal colonies dispersed more slowly (higher recapture rates). This study did not document distances moved for each tagged pāua over time. However, twelve (of the 101) tagged pāua were found away from the original tagging site, and the maximum recorded distance moved of 150 m. Pāua were thought to move in response to disturbance and/or to food availability.

Poore (1972b) found that pāua that feed on drift algae were more sedentary than those in calmer environments, that had to actively search for food (feeding more on attached algae than drift algae). During observations in a 42 hr period of 15 pāua (observations every 3 hr), pāua moved more at night, but overall most movement was within one meter radius of the colony, with some individuals not moving at all (Poore 1972a). One individual moved beyond a 5 m radius, and another individual moved 2 m outside of the colony but returned to the colony after 3 hr. Homing behaviours (i.e., movement recorded in individual, but with returns to a single location) is reported in some *Haliotis* species in other parts of the world, and it is thought to be important for spawning and successful fertilization (McShane 1992). There is little information available of homing for the black-foot pāua.

5.1.3.3. Connectivity of pāua: multiple phylogenetic breaks exist

Movement between pāua populations have been inferred through both oceanographic models and genetic studies. The PLD of pāua is ~72 hr (but up to 8 days; Tong et al. 1992). Stephens et al. (2006) used oceanographic models and predicted that in calm conditions, larvae are most likely to be transported 200 m from parents, having a maximum dispersal of 4 km. In higher energy seas with prolonged winds, dispersal was found to occur up to ~50 km from parents, with a maximum dispersal of ~80 km. Pāua often spawn during increased wave turbulence (associated with storms), which assists in dispersal (McShane 1992, Poore 1973). Despite these larger distance dispersal trajectories, negatively buoyant larvae can become entrapped in crevices, beneath kelp, or in localized small eddies, resulting in local settlement and recruitment to the parental population (McShane 1992, Shepherd et al. 1992). Furthermore, while high energy environments may promote long-distance dispersal of pāua, high energy environments are not conducive for both settlement or settlers; therefore, the requirements for settlement can be quite specific and result in sporadic recruitment (Sainsbury 1982, Poore 1973).

Genetic studies employing an array of methods, including use of allozymes, mitochondrial and nuclear genes, and microsatellite markers, have been used to examine the structure of pāua populations across New Zealand. Although early studies examining genetic differentiation between pāua populations found little evidence for population structuring (e.g., Dollimore 1977, Frusin 1982), more recent studies have identified distinct genetic populations structured by both hydrodynamic forcing and geographic isolation (Smith 2008; Smith and McVeagh 2006). For example, Smith and McVeagh (2006) found genetic differences in mitochondrial DNA between populations in the Chatham Islands, Stewart Island, Great Barrier Island and South Taranaki, attributing structure to both hydrographic currents (the east Auckland current, Southland current, Taranaki – West Auckland / Tasman current) and large distances too far for larvae to travel (as in the Chatham Islands; Smith 2008).

The most recent studies examining genetic structure of pāua use a combination of mitochondrial DNA and microsatellite markers and have revealed a north-south split in New Zealand (Will 2009, Will et al. 2011, Will et al. 2015). Analysis of mitochondrial DNA between 25 populations from New Zealand (North Island, South Island, Stewart Island, Chatham Islands) has identified four main populations: (1) Chatham Islands, (2) western Cook Strait region, (3) southeast coast of South Island, and (4) East Cape of North Island (Will et al. 2011) (Fig. 1). The phylogenetic breaks for these are due to either isolation by distance (i.e., populations 1) or complex hydrographic features such as currents (i.e., populations 2-4). This was further corroborated with microsatellite markers, where population structure was detected in examining mitochondrial DNA from 485 pāua from 27 locations. Three phylogenetic breaks were identified: (1) between the Chatham Islands and the mainland, (2) the Cook Strait break (where the southern part of North Island was genetically the same as the South Island), and (3) East Cape Break. On a smaller scale, McCowan (2013) looked at 10 reef sites in the Tory Channel and found minimal structure on a scale of 200 km. Overall, there is weak but biologically significant genetic structuring of pāua populations within New Zealand, with gene flow likely higher than expected due to the large and/or historic population size of pāua (Will et al. 2015).

5.1.4. Blue cod

Habitat	• Larvae settle in deep waters before coming inshore • Juveniles more typical in shallow (<15 m) open reef and sandy areas • Adults on fringes of rocky reef and seafloor structures (such as biogenic reefs) • Abundance positively associated with coarse sediment, cobble habitat, depth, and negatively associated with distance from rocky/biogenic reef
Home range	• Small, less than 1 km
Connectivity	• PLD = 10 days • Larval dispersal distance = unknown, but likely less than 850 km (inferred from differentiation between mainland and Chatham Islands) • Migrant dispersal distance = 100s km • Some migration likely occurs, allowing some mixing of populations • Mainland New Zealand is genetically different than the Chatham Islands • Little genetic differentiation among populations on mainland New Zealand, but an isolation by distance pattern occurs • Likely limited movement between inner and outer fiords in Fiordland

Blue cod (*Parapercis colias*) make up an important recreational and commercial fishery in New Zealand. They are demersal fish and are distributed around both the North and South Island, Stewart Island, and the Chatham Islands (Leach et al. 1999). There is a greater abundance of blue cod in the southern waters, which is where the bulk of commercial fishing occurs (Bradford 1998, Carbines and McKenzie 2001). While habitat use, home range and connectivity are important aspects to consider in the protection of this species, the reproductive behaviour of blue cod also warrants consideration. Blue cod are protogynous hermaphrodites, meaning they change sex from females to males during their life (Carbines 2004, Brandt et al. 2017), though cues for this are not well known. It is thought that because sex changes can happen over a wide range of sizes and ages, the cues are not size specific, but rather related to demographic features of the population (Carbines 2004). For some fish, inversion can be influenced by the presence or ratio of large males (Cole and Robertson 1988), and the lack of specific requirements for sex inversion in blue cod suggest this might be the case for this species as well.

Brandt (2016) found that density had effect on blue cod sex ratio and that large males influenced the local sex ratios in the Marlborough Sounds. Sex inversion has implications from a conservation and fisheries perspective, because the removal of large males from the population can result in a skewed sex ratio and affect the reproductive capability of a population (Alonzo and Mangel 2004). Male-biased sex ratios have been reported for heavily fished populations of blue cod in the Marlborough Sounds and Banks Peninsula, whereas offshore areas with reduced fishing pressure showed a more female-biased ratio (Beentjes and Carbines 2005, Beentjes and Carbines 2011). Designing MPAs for the protection of organisms that undergo sex inversion like blue cod requires extra consideration; for instance, more and larger reserves may be required to adequately protect populations of sequential hermaphrodites that have both low flexibility in their ability to change sexes and a larger number of males needed for fertilization (Easter and White 2016, Brandl et al. 2018).

5.1.4.1. Habitat of blue cod: on rocky and biogenic reef fringes

Blue cod inhabit coastal habitats near rocky reefs, occupying depths up to 150 m and have even been recovered from trawling surveys up to 350m (Warren et al. 1997). Settlement and early life stages of blue cod remain poorly understood, but it is thought that larvae settle into deep (>120 m) offshore waters before coming inshore closer to reefs (Rapson 1956). Juveniles generally occur more frequently in shallow (<15 m) open reef and sandy areas, whereas adults remain on the edge of rocky reefs near sand (Carbines 2004). In baited underwater video (BUV) surveys in the Pōhatu Marine Reserve and Akaroa Marine Reserve, blue cod abundance was found to be positively associated with coarse sediment, cobble habitat and depth, and negatively associated with distance from reef structure (Brough et al. 2018).

Habitat has been shown to affect blue cod diet and growth. There have been a number of studies looking at population structure in terms of feeding and growth in different fiords in Fiordland (Carbines and Beentjes 2003, Rodgers and Wing 2008, Wing et al. 2012, Beer and Wing 2013, Beer 2014). Gut content and stable isotope analysis of blue cod in inner fiord and outer fiord habitats have revealed that these populations rely on different sources of organic matter (Rodgers and Wing 2008, Wing et al. 2012, Beer 2014). Populations in the inner fiord had a diet that contained diverse benthic

prey, with a significant input of recycled carbon via chemosynthesis. By contrast, outer fiord diet consisted of pelagic prey, was of a higher nutritional value, and was supported mainly by primary production from macroalgae and phytoplankton (Rodgers and Wing 2008, Wing et al. 2012, Beer 2014). Sizes and growth also differed between inner and outer fiord (Beer and Wing 2013, Beer 2014). It was found that the inner fiords had a female-bias sex ratio, with a high proportion of large, old, slow-growing females. Conversely, the outer fiords contained a sex ratio closer to 1:1 or was male dominated (Carbines and Beentjes 2003), with fish generally smaller, younger and of better condition (Beer and Wing 2013, Beer 2014). Alternative food sources in the marginal inner fiord habitats can still support blue cod, which have adapted their feeding strategies (Wing et al. 2012). Blue cod can exist in a variety of habitats, but often benefit from more complex, algal-dominated environments.

Habitat complexity has proven important when observing the effects of dredging on blue cod populations (Cranfield et al. 2001, Jiang 2002, Jiang and Carbines 2002, Carbines and Cole 2009). When examining the differences between a dredged environment versus a recovering adjacent reef via underwater video transects, Carbines and Cole (2009) found that topographic complexity, epifauna (like sponges) cover and macroalgal cover were all positively associated with blue cod abundance (and it is likely that these patterns were also driven by the difference in fishing effort in both environments). Similarly, differences in diet between both habitats were observed, where those in the recovering biogenic reef had a more diverse diet (Jiang 2002, Jiang and Carbines 2002). The recovery of blue cod during the period when the oyster fishery was closed (and thus dredging stopped) from 1993-1996 further illustrates that habitat modification can have effects on the population (Cranfield et al. 2001).

Marine reserves have been shown to have a positive effect on the size and abundance of blue cod. For instance, in the Long Island-Kokomohua Marine Reserve, Davidson (2001) found that 35% of blue cod caught in the reserve were >330 mm versus <1% caught outside of the reserve, and Davidson et al. (2014) found that blue cod were 3x more abundant in the reserve than outside. In the Tonga Island Marine Reserve, legal sized blue cod were 40x more abundant in reserves and 48% of blue cod were > 300 mm within the reserve versus 5% outside for the reserve (Davidson et al. 2013a).

Similarly, in the Horoirangi Marine Reserve, monitoring from 2006-2013 revealed that the abundance of legal sized blue cod increased over time in the reserve, and in 2013, that 35% were greater than 300 mm compared to 1.7% outside the reserve (Davidson et al. 2013b). Brough et al. (2018) found that in the Pōhatu and Akaroa Marine Reserves, the abundance of legal size blue cod (> 300 mm) 3.6 and 2.1 times greater, respectively, than in non-reserve control areas. While the trend has been marine reserves benefit blue cod, marine reserve size has not been found to affect the size or density of blue cod, although marine reserve age has been shown to be important (Diaz-Guisado et al. 2012).

5.1.4.2. Home range of blue cod: high site fidelity

Blue cod have small home ranges. Males are territorial, often defending a small group of females (Carbines and McKenzie 2001), and the area that they defend is positively correlated to male size (Mutch 1983). The movements of blue cod have been inferred using tag and recapture methods. Mace and Johnston (1983) tagged 2430 blue cod from 1973-1976 in the Marlborough Sounds, and of the recaptured fish (84 fish after a mean 138 days at liberty), 71.6% were caught at the same headland or reef they were originally tagged in. The remaining ~30% were found within 41.7 km of the original tagging site (mean distance travelled 7.6 km). In this study, all of the blue cod over 30 cm in tail length were recaptured at their original tagging site, suggesting large fish do not migrate, but instead smaller blue cod tend to be more migratory. Similarly, Cole et al. (2000) found that in reserves, large blue cod (> 35 m length) did not travel farther than 150 m of the tagging site. However, Rapson (1956) reports migration for some fish over 30 cm tail length (migration distance ~50 km), challenging this notion. Other movements have been postulated, including inshore-offshore movement and congregations associated with spawning and temperature changes (Graham 1953, Robertson 1980). However, these movements are likely site specific and rare (Mace and Johnston 1983).

Cole et al. (2000) tagged 90 blue cod each at four sites in the Marlborough Sounds, two inside the Long Island-Kokomohua Marine Reserve and two outside the marine reserve in fished sites. The authors used two methods of resighting tags (depth-stratified timed counts and longshore transect counts). For depth-stratified timed counts, 89 resights were recorded over a year (Jan 1998 – Jan 1999), and 84% of all

resights occurred between 8-17 m depth. For longshore transects, 238 tagged fish were recorded 377 days after initial tagging, and mean distances travelled for each site ranged from 50-73 m. Most of these tagged fish were found within 100 m of the original tagging site, with 75% and 73% of tagged blue cod found within 100 m of the tagging site in fished sites and reserve sites, respectively. Seven fish (of the 238) travelled farther than 200 m. Carbines (2004) and Carbines and McKenzie (2004) found similar patterns, with 60% of recaptured blue cod within 1 km of the original tagging site in the Foveaux Strait (over 20 months) and 65% of recaptured adults moving less than 1 km of original tagging site in Dusky Sound (over 17 months), respectively. In the Foveaux Strait, the largest distance moved was 156 km, but median movement was 800 m (Carbines 2004). On the Wellington south coast, Diaz-Guisado (2014) tagged a total of 539 fish at sites both inside and outside of the Taputeranga Marine Reserve from October 2010 to May 2012. Of the 48 fish recaptured, 40 were recaptured inside of the study area, with distances travelled ranging from 1 m (fish that were 97-191 days at liberty) to 2 km (a fish that was 85 days at liberty). The remaining 8 fish were recaptured northward of the study area, with distances ranging from 45 km (173 days at liberty) to 315 km (244 days at liberty).

5.1.4.3. Connectivity of blue cod: gene flow but isolated by distance

Connectivity patterns of blue cod have been largely inferred using tag-recapture, genetic, otolith microchemistry, stable isotope and size structure data. Despite having high site fidelity, some larger-scale movement and/or migrations for blue cod has been reported. For instance, tagging and recapture in Fiordland has shown that some movement from outer fiord habitats to inner fiord habitats occurred, where it has been estimated that the open coast populations supply ~10% annually to the inner fiord sink (Carbines and McKenzie 2004). Further, residency within the inner fiord habitats has been shown to be 100%, indicating that this movement in unidirectional (Carbines and McKenzie 2004). Blue cod have also been found travelling long distances from their original tagging site (see Section 5.1.4.2.), with distances up to 315 km reported (Diaz-Guisado 2014). Thus, a small portion of the population may leave their home site and migrate further.

The pelagic duration of blue cod is short, with eggs are in the water column for approximately 5 days before hatching into a pelagic larva for another 5 days

(Robertson 1973). Genetic studies have employed mitochondrial DNA and microsatellites to investigate genetic differentiation between 14 locations around the North Island, South Island, Stewart Island and Chatham Islands (Smith 2012, Gebbie 2014). Smith (2012) examined the mitochondrial region of 475 blue cod from 13 locations and found that the mainland and Stewart Island populations were genetically different from the Chatham Islands. While the mainland and Stewart Island populations were genetically similar, there was an isolation by distance pattern observed, meaning that while the populations are still well mixed, there is a subtle genetic difference between furthest away populations. Gebbie (2014) found the same pattern as Smith (2012) using both mitochondrial DNA and microsatellites (Fig. 2). Some populations were found to have a weak but significant genetic difference, particularly noteworthy the Otago and Kaikoura populations, which are both contained within the same fishery unit (i.e., called BCO3). While levels of weak genetic differentiation suggested mixing of populations, an isolation by distance pattern indicates that there are likely biological differences between populations (Gebbie 2014).

Otolith microchemistry, which provides a water chemistry signature of the environment that a fish has occupied, allows inference about the location and movements of individual fish (Beer et al. 2011, Beer 2014). Differences in the otolith microchemistry was found between inner and outer fiord blue cods from the Bradshaw-Thompson, Breaksea and Dusky Sounds (Beer et al. 2011, Beer 2014). In Dusky Sound, three discrete groups were identified as belonging to inner, mid and outer fiord environments, implying that there is limited mixing between these populations over months to years (Beer et al. 2011, Beer 2014). Limited mixing is further supported through the studies examining population structure in the fiords based on size structure and diet composition (see Section 5.1.4.1.; Beentjes and Carbines 2005, Rodgers and Wing 2008, Wing et al. 2012, Beer and Wing 2013, Beer 2014).

5.1.5. Snapper

Habitat	• Larvae and juveniles in estuaries, seagrass beds or sand flats next to reef; prefer habitat complexity and low levels of flow • Adults exhibit a wider range of habitats, including estuaries, harbours, rocky reef, soft sediments; prefer faster tidal currents • Habitat influences movement and residency
Home range	• Small, less than 30 km from tag site, but most less than 10 km • Home ranges <1000 m (linear distance) in complex reef environments, versus 2-20 km (linear distance) in open and offshore environments • Higher residency in complex reef environments • Inshore-offshore movements may be associated with spawning
Connectivity	• PLD = 18-32 days • Larval dispersal distance = up to ~40 km • Migrant dispersal distance = 100s km • Some migration between populations found through tagging, allowing mixing of populations • East coast of North Island is genetically different from west coast of North Island, with Hauraki Gulf being more similar to the west than east coast • Size structure differences exist throughout their distribution

Snapper (*Pagrus* or *Chrysophrys auratus*) is one of the most abundant finfish species in inshore waters in New Zealand, and makes up an important recreational and commercial fishery (see Parsons et al. 2014a for review of life-history traits of snapper). They are distributed mainly in the North Island, inhabiting the northern half of the North Island; and are also found in the northern waters of the South Island, but are rarely in the southern South Island (Graham 1953, Crossland 1981). They are protogynous hermaphrodites, starting life as females and maturing into males (although some remain female; Easter and White 2016). While they are important economically in New Zealand, they also have ecological importance, being identified as a keystone species that have the ability to drastically change the surrounding environment (Babcock et al. 1999, Shears and Babcock 2002). For instance, predation by snapper on urchins can keep the urchin population in check, allowing macroalgae to grow (Babcock et al. 1999, Shears et al. 2002). Because of their economic and ecologic importance, there are numerous studies examining the ecology and fishery science of snapper in New Zealand (and worldwide).

5.1.5.1. Habitat of snapper: depends on life stage

Different life stages of snapper (larvae, juvenile and adult) have different habitat preferences. Larvae are rarely seen in coastal waters and instead settle in sheltered estuaries in areas with seagrass, horse mussel beds or sponge gardens (Parsons et al. 2014a). Larval survival is highly dependent on food availability and therefore, abundance of larvae is often associated with areas that have high densities of prey (copepods; Pankhurst 1991, Zeldis et al. 2005).

Juvenile snapper (10-230 mm standard length, Parsons et al. 2014a) generally inhabit estuarine environments. Francis (1995) collected snapper juveniles by trawling in Kawau Bay and found that they preferred environments with little to no topography, such as mud substrate over sand/shell bottoms. While mud substrate would appear not to support habitat complexity, Thrush et al. (2002) found that juveniles were associated with habitat structure on soft sediment benthos, where abundance of snapper were positively correlated to habitat features including depressions, burrows, shells, boulders, cobbles and sand waves. In later studies, habitat complexity has been shown to be important for juvenile snapper because it allows predator avoidance and supports prey items, with abundance of juvenile snapper often higher in structured habitats (Ross et al. 2007, Parsons et al. 2014b, 2015). For instance, experiments have revealed that in the presence of predators, juveniles sought out shelter (Ross et al. 2007). Furthermore, juvenile abundance was highest in environments with intermediate water velocities with structural complexity, as these conditions allow prey items to be suspended while reducing energetic costs associated with swimming (i.e., structural complexity provides refuge from flow; Parsons et al. 2014b). Juvenile snapper also exist in rocky reef habitats, where Ross et al. (2007) recorded a high abundance of juvenile snapper over sand flats adjacent to rocky reef habitat in CROP Marine Reserve. Because juveniles rely on some level of habitat complexity, modifications to the benthos (e.g., through dredging) or loss of habitat (e.g., seagrass) can have negative consequences for these fish.

Adults occupy a wider range of environments than juveniles, occurring depths of up to 200 m (Crossland 1981), though are generally found shallower than 50 m (Kendrick and Francis 2002). They can inhabit estuaries, harbours, rocky reef environments, and soft sediment environments (Crossland 1981, Parsons et al. 2014a). Compton et al.

(2012) observed 1190 adult snapper using video and correlated their presence to various environmental factors. These authors found that larger snapper were associated with faster tidal currents (water with higher orbital velocities) and occurred in channels and waters around small islands, compared to 844 juvenile observations which were in slower moving waters closer to the shore. The habitat that an adult snapper inhabits generally influences its movement patterns, where the establishments of marine reserves have resulted in higher residency and less movement of adult snapper (see Section 5.1.5.2.; Parsons and Egli 2005, Parsons et al. 2010).

5.1.5.2. Home range of snapper: depends on habitat

Snapper generally show high site fidelity and have a small home range, though variability in the movement patterns between fish and locations exist. Larvae move from coastal or deeper waters towards estuaries, likely guided by river plumes (Parsons et al. 2014a). Juveniles tend to stay within estuaries or sheltered bays, moving to coastal environments as they become adults. Movement out of the estuaries is evident through the seasonal cycles in snapper abundance in estuaries, where abundance is high in the spring but low in the autumn, when adult snapper leave nursery habitats (Francis 1995). This has been further confirmed through the use of otolith microchemistry, where adult otolith signatures from multiple locations indicate origin from a single estuarine environment (Parsons et al. 2014a).

Home range and movement of snapper has been recorded through an array of tagging and recapturing methods, acoustic telemetry and baited underwater video (BUV). Paul (1967) reviewed movement patterns based on tagging information from 1952 to 1963 across New Zealand, and found that of the 43 fish recaptured (from 8000 tagged), 33 fish moved less than 9.5 km from their tagging site. Crossland (1976) tagged 5045 individuals at multiple locations in the Hauraki Gulf (23 locations) and Northland (4 locations), finding that most movement was local, with the distance between tag and recapture sites being on average 25.7 km. Will et al. (2001) implanted fluorescent elastomer tags and 907 snapper in 1996 and an additional 117 in 1999 with individual ID codes. From 1997-2000, 71 individuals were recovered within 500 m of the tagging site and were observed up to three years later. Of the individually coded snapper, 42% were resighted, often repeatedly, over several months near the original tag site.

Tagging methods therefore have revealed that snapper have high site fidelity over short time periods, and likely small home ranges (100 ms-10s kms).

Because some snapper show greater variability in movements, acoustic telemetry has been employed to determine differences in migration and residency. In a study conducted in the Mahurangi Harbour (northeast New Zealand), Hartill et al. (2003) found that 20 (of the 28 tagged fish) remained in the tagging area throughout the observation period (Nov – Jan), and most movement was on the scale of hundreds of meters. Movement patterns have also been observed for snapper in CROP Marine Reserve (Parsons et al. 2003, Egli and Babcock 2004). Here, fish were found to have high site fidelity with home ranges of 650 m in diameter or less, where home ranges of fish overlapped indicating snapper were not territorial (Parsons et al. 2003). Furthermore, some fish were found to remain resident, others left permanently, and others left and returned (up to 83 days later; Egli and Babcock 2004). Snapper movements can be variable intra-specifically and seasonally. In fact, fisherman tend to identify snapper as two types: the “schooling” fish, which tend to congregate, migrate and move onshore-offshore seasonally likely associated with spawning, and the “resident” or “kelpy” fish which stay put in their home location in the rocky reefs (Parsons et al. 2011). Morphological differences in the head of schooling versus resident fish have even been observed (Parsons et al. 2014a).

An examination of habitat in relation to movement patterns may help to elucidate some of the variability in movement patterns. Denny et al. (2004) used baited underwater video (BUV) and found a significant increase in the abundance (7.4x) and biomass (818%) after the establishment of the Poor Knights Marine Reserve, where a seasonal trend in abundance was observed, with higher numbers in the autumn versus spring. Interestingly, the increase in density occurred too fast for it to be due to self-recruitment; that is, adult snapper immigrated to the Poor Knights and became residents. Willis et al. (2003) also used BUV to examine the effects of CROP, Hahei and Tawharanui Marine Reserves and found seasonal differences in abundances, supporting seasonal onshore-offshore migrations that may be related to spawning. However, some resident snapper have also been found to spawn without migrating (Parsons et al. 2003, Parsons et al. 2010).

Parsons et al. (2010) also looked at the movement patterns of fish inside and outside of CROP Marine Reserve, where ~40 fish were tagged using acoustic telemetry (half inside the reserve and half outside). All of the fish in the marine reserve remained associated with one area, which spanned an average of ~900 m linear distance. For the fish outside of the reserve, half displayed similar home range behaviour (i.e., ~900 m linear distance), while the other half were associated with two areas with larger home ranges, encompassing ~2100 m linear distances. From these findings, Parsons et al. (2010) concluded that marine reserve environments to some extent promote residency, and these patterns were likely driven by either changes in fish behaviour and/or selective removal (by fishing) of 'reserve fish' that had larger movements beyond the reserve boundary. Parsons et al. (2011) investigated this further by tagging 5983 fish at three different strata at Hauraki Gulf: coastal mainland reef (structurally complex), inner gulf, and mid gulf (later two dominated by soft sediment and some sponges, horse mussels and cobbles). Coastal reef snapper were found to remain the most resident (median 0.7 km distance moved), followed by inner (median 3.6 km) and mid reef snapper (median 18.9 km). This study concluded that because reef habitats are generally associated with higher invertebrate abundance and available prey items, it is likely that these habitats encourage a higher degree of residency.

5.1.5.3. Connectivity patterns of snapper: east versus west coast

Movement and connectivity patterns for snapper have been investigated using tag-recapture data, genetic analyses and length and age composition (Smith et al. 1978, Walsh et al. 2006, 2011, 2012, Bernal Ramirez et al. 2003, LePort et al. 2017). Tagging and recapturing fish have revealed that some fish move large distances. For instance, Crossland (1976) found a small proportion of the population in the Hauraki Gulf moved greater than 92 km, with the longest movement recorded as 169 km. Similarly, Paul (1967) found that ~15% of the recaptures in the Hauraki Gulf had moved between 16-418 km (with days at liberty ranging from 1 to 1127). Thus, it is likely that some individuals migrate or move between populations, promoting gene flow. Le Port et al. (2017) used genetic parentage and relatedness analysis to measure how larval subsidies from CROP Marine Reserve contributed to the surrounding fisheries. Fourteen juveniles were caught outside of the reserve and identified as being offspring from an adult caught inside of the reserve. Overall, adult snapper from within the reserve contributed about 10% of newly settled juveniles to the surrounding areas

(area of 400 km^2), and this 10% trend in contribution was consistent up to 40 km away. Le Port et al. (2017) discussed that these results indicate that reserves can provide recruitment subsidies to areas outside of the reserve, and have implications for species protection and fisheries management. This study supported findings of a 3D biophysical model that predicted snapper in CROP Marine Reserve provided significant larval subsidies within 40 km from the reserve, though also dependent on ENSO cycles and larval behaviour (Le Port et al. 2014).

Snapper have a short PLD (18-32 days; Francis 1994), and therefore it may be expected that populations are genetically different over distances. Smith et al. (1978) used allozymes to identify genetic differences between twelve locations in New Zealand, using three polymorphic loci. Two genetically distinct groups (or 'stocks') were identified: (1) the east coast of the North Island (Bay of Islands, Bream Bay, Hauraki Gulf, Bay of Plenty, East Cape), which was different from (2) the west coast of the North Island (Tasman Bay, Marlborough Sounds, North Taranaki, Mankau-Kaipara, Ninety Mile Beach, Wellington Harbour). Interestingly, the Hawke Bay population was more genetically similar to the west coast samples than the east coast samples, perhaps due to similar hydrological conditions and thus selective pressures. Thus, the Hawke Bay population may comprise a different stock than the rest of the east coast populations. Smith et al. (1978) identified Ninety Mile Beach, Bay of Plenty and Hawke Bay as boundary areas between different stocks, and possible grounds for stock mixing.

Bernal Ramirez (2003) examined genetic structure again two decades after Smith et al. (1978) and found similar patterns, suggesting temporal stability in population structure over time. Snapper (n = 291) were collected from six locations in New Zealand: Hauraki Gulf, Hawke Bay, Tasman Bay, Doubtless Bay, one site on the east coast of the North Island (East Coast), and one site on the west coast of the North Island (West Coast). Differentiation between the northeast and southern populations were found using microsatellite markers. The Tasman Bay population was significantly different to all other locations. Furthermore, the Hauraki Gulf population was different to the West Coast population; and Hawke Bay was different from the Hauraki Gulf and East Coast populations (Fig. 2). This population structure is mostly likely due to oceanographic features, where the Tasman Bay populations are isolated by the

D'Urville current, and the Hawke Bay population isolated from the rest of the east coast due to the Wairarapa Eddy. In another microsatellite analysis by Hauser et al. (2002) using ancient DNA in historical samples of fish scales, a significant decline in genetic diversity from 1950-1986 was reported for the Tasman Bay population, which supports either that this population has lower gene exchange with other populations or that this population has overgone declines and/or been overfished.

The geographic structuring of snapper populations into 'stocks' or different biological populations is reviewed in Parsons et al. (2014a). Authors summarize various New Zealand Fisheries Assessment Reports from different snapper commercial areas (i.e. SNA 1-3, 7-8, 10) on length and age composition (i.e., Walsh et al. 2006, Walsh et al. 2011, Walsh et al. 2012, MPI 2013). The frequencies of fish in each year-class on the west coast on the North Island were different from those on the east Northland location (Walsh et al. 2006). There are also differences in year-class structure between the east Northland, Hauraki Gulf and Bay of Plenty locations (Walsh et al. 2011). On the east coast of the North Island, below East Cape, the Mahia Peninsula separate two populations that differ in age structure, growth and year-class frequencies (i.e., Hawke Bay versus Gisborne waters, which later fish are more similar to Bay of Plenty; Walsh et al. 2012). And lastly, on the South Island, two distinct populations exist: the Marlborough Sounds and Tasman/Golden Bays (MPI 2013).

5.2. Kelp

5.2.1. Bladder kelp (*Macrocystis*)

Habitat	• Rocky reef substrate • Below 40° latitude, in waters where water temperatures do not reach above 18-19°C for extended periods of time • Generally in sheltered areas, but water motion can increase nutrient uptake in nutrient depleted waters
Dispersal	• Zoospores disperse on the scale of meters (5-150m, but can be 1000s of meters in high energy environments or storms) • Kelp rafts (with reproductive propagules) disperse on the scale of kilometres (100s-1000s km)
Connectivity	• High levels of gene flow around New Zealand, likely due to kelp rafts

Bladder kelp (also called giant kelp), or *Macrocystis pyifera*, form dense forests in temperate oceans and support diverse and productive ecosystems (Schiel and Foster

2006, Graham et al. 2007). These complex habitats provide an area for feeding, serve as nursery and spawning grounds, and provide refuge from predators for many organisms (Vasquez et al. 1998, Graham et al. 2007, Villegas et al. 2008). They form mutualistic relationships with many reef organisms, playing key roles in the exchange of nutrients and in trophic interactions (Hepburn et al. 2005, 2006, Perez-Matus and Shima 2010). A major worldwide concern is the decline of kelp forests from climate change and the negative cascading effects their disappearance may have on the surrounding environment (Krumhansl et al. 2016, Filbee-Dexter and Wernberg 2018).

In New Zealand, bladder kelp has a southern distribution, below 40° latitude (Hay 1990, Schiel and Hickford 2001). It occurs mainly on the southern and eastern coasts of the South Island, and is generally absent from the west coast of the South Island. For instance, there are no reports of bladder kelp north of Milford Sound (Schiel and Hickford 2001), and following the west coast around, it only reappears again in the Marlborough Sounds (Hay 1990). It is commonly found around protected areas of Fiordland and around Stewart Island (Schiel and Hickford 2001), is patchy around the Catlins (which contains more sandy areas compared to preferable rocky reef; Hay 1990), and occurs in Otago. It occurs patchily along the east coast, but large populations occur in Kaikoura and the Banks Peninsula, with the largest kelp beds reported in Motunau Island and Cape Campbell (Hay 1990, Shiel and Hickford 2001). Bladder kelp also occurs on the southern part the North Island, found along the Wellington South Coast, Kapiti Island, Cape Palliser and Castle Point (Hay 1990). Off of the mainland, large densities occur on the Chatham Islands (Schiel et al. 1995, Schiel and Hickford 2001), as well as on the Subantarctic Islands (Hay 1990). While it is abundant around the Auckland Islands, Campbell Island, Antipodes Island and the Bounty Islands, it is absent from the Snares Islands (Hay 1990).

In order to discuss the habitat, home range (dispersal), and connectivity patterns for bladder kelp, it is important to understand its life cycle (see North 1994, Schiel and Foster 2006 for more detail). Bladder kelp exists as two stages: the macroscopic ‘conspicuous’ stage (called the sporophyte) and the microscopic stage (called the gametophytes). The sporophyte is the life-history stage that forms the large kelp we are most familiar with, and produces microscopic zoospores. Zoospores either fall next to the plant or are carried away by currents and settle onto substrate, and then develop

into gametophytes. The gametophytes develop into males or females and produce either eggs or sperm (gametes). The gametes fuse to produce a sporophyte, thus completing the cycle. While some bladder kelp in New Zealand has been reported to live approximately one year (Pirker 2002), they are short-lived perennials and can live up to 4-8 years (Lobban 1978, Schiel and Foster 2006). Its growth is seasonal and declines in the summer due to nutrient limitations (Pirker 2002, Brown et al. 1997).

5.2.1.1. Habitat of bladder kelp: wide range due to high environmental plasticity

Bladder kelp grows on rocky reef substrate where temperatures do not exceed 18-19°C for long periods of time (Hay 1990). They exhibit a high degree of plasticity, allowing them to exist in a wide range of habitat, from intertidal to subtidal habitats (Graham et al. 2007). Schiel and Hickford (2001) found high densities (2-4 plants per m^2, canopy cover 85%) at 3-6 m depth on the east coast of the South Island, and Hay (1990) reported kelp occurring up to 16 m depth. In the Chatham Islands, bladder kelp has been found in at depths greater than 15 m, where although only a few individuals were present, their large size made them a dominant feature of the environment (Schiel et al. 1995). While generally occurring less than 20 m in New Zealand, reports of bladder kelp occurring up to 68 m have been recorded for other parts of the world (i.e., Prince Edward Island; Perissinoto and McQuaid 1992).

Abundance and habitat use of bladder kelp is constrained by physical factors, including sedimentation, nutrient availability and storms. For instance, sedimentation has been shown to negatively affect establishment of spores (Geange et al. 2014) and recruitment (Pirker 2002). In a study examining kelp forests in the Akaroa Harbour and Tory Channel, a high sedimentation event likely caused a reduction in the biomass of bladder kelp due to the smothering of the canopy and substrate, prohibiting successful recruitment for over a year (Pirker 2002). The seasonal flux of nutrients often dictates the growth of bladder kelp, with growth declining in the summer with the associated depletion of nutrients (Pirker 2002, Brown et al. 1997). Storms can also reduce the abundance of bladder. Reed (1987) found that the removal of vegetative biomass (fronds) decreased zoospore production; thus, the removal of and damage to plants that occur during storms may reduce the ability of plants to produce zoospores, which may have consequences for reproduction and dispersal.

Although bladder kelp is often found in protected and sheltered areas (as in the Chatham Islands; Schiel et al. 1995, Schiel and Hickford 2001), research has shown that increased water motion may increase nutrient uptake (by decreasing the diffusion boundary layer between water and frond). Increased nutrient uptake can be associated with increased growth and productivity, which may be especially important during periods (like summer) of low nutrient availability (Hepburn et al. 2007, Hurd and Pilditch 2011, Stephens and Hepburn. 2014). For instance, Hepburn et al. (2007) found that sites with higher amounts of flow in the Paterson Inlet (Stewart Island) also had higher frond growth rates than those at sheltered sites. Furthermore, this study reported constant growth rates year round in wave-exposed sites, but decreased growth rate during the nutrient poor summer and autumn in wave-sheltered sites, which indicated water motion may allow nutrients to be better absorbed. Too much water motion, however, may cause damage to the sporophyte.

5.2.1.2. Dispersal of bladder kelp: zoospores and kelp rafts

Dispersal of bladder kelp can occur two main ways: (1) through zoospores / gametes, and (2) through kelp rafts (Schiel and Foster 2006, Macaya 2010). The former is generally restricted to short ranges, whereas the kelp rafts allow long distance dispersal. While there has been extensive research examining dispersal of bladder kelp in other parts of the world, dispersal in New Zealand remains poorly understood. In California, USA, zoospores have been found to generally remain close to the sporophyte, and *in situ* observations of juveniles surrounding adult ranged from 5-150 m (Anderson and North 1966, Reed et al. 1988, Reed et al. 2006). Also in North America, water motion has been found to be positively associated with dispersal, where in calmer waters zoospores stayed closer to the parental sporophyte, but in high velocities and during storms, spores were found to disperse much further, up to 4000 m (Reed et al. 1988). Further, oceanographic models have estimated that dispersal in California can occur on the scale of 1000s of meters (Gaylord et al. 2002, 2006). For the most part, however, spores are generally restricted within a relatively small range, particularly in calm water conditions. After the development of the zoospore into the gametophytes, the egg releases a pheromone to attract sperm which swim about 1 mm to the egg (Maier and Muller 1986, Schiel and Foster 2006)

Kelp rafts are the main way by which long distance dispersal occurs. When sporophytes become detached from the surface, they can form floating rafts that can travel across long distances. Data from both North America and Chile have indicated that kelp raft dispersal is approximately 100 km (Chile; Macaya et al. 2005) to 890 km and greater (North America; Harrold and Lisin 1989, Hobday 2000, Hernández-Carmona et al. 2006). In Chile, Macaya et al. (2005) have found that approximately one fourth of samples from floating rafts of bladder kelp contained sporophylls and that rafts were able to release viable zoospores (although rates of reproduction were depressed compared to attached states). Sporophyte rafts have found to remain reproductively active for more than 100 days in Monterey Bay, where this long life of kelp rafts allowed dispersal to and reproduction with plants existing 100s of meters away (Hernández-Carmona et al. 2006). Because floating states remain functionally reproductive, they may facilitate dispersal and be an alternative mechanism for long distance dispersal, and are therefore thought to be an important way that gene flow in maintained across large distances (Macaya 2010).

5.2.1.3. Connectivity of bladder kelp: high levels of gene flow resulting in one global species

The population structure of bladder kelp has been examined worldwide, revealing that only one species exists across both Northern and Southern Hemispheres (contradictory to previous descriptions of four species), which is likely a product of the long dispersing kelp rafts (Macaya and Zuccarello 2010a). Genetic analyses of kelp rafts versus kelp attached to substrate in the Chilean fiords revealed that genetic similarities were found between sites 200 km apart, suggesting rafts can promote the mixture of sporophytes from multiple locations (Macaya 2010).

Using mitochondrial DNA and microsatellites, Macaya (2010) and Macaya and Zuccarello (2010b) found high levels of gene flow across the Southern Ocean (South Africa, Subantarctic Islands, Chile, Australia, New Zealand). Within New Zealand, little to no genetic differences were found between Stewart Island, Wellington, Picton, Kaikoura, and Timaru. Furthermore, Antipodes Island, Enderby Island and Campbell Island were closely related (Fig. 3). While small-scale studies examining population structure have not been published for New Zealand, Alberto et al. (2010) mapped habitat continuity and distances of samples in the Santa Barbara Channel in California

(across ~100 km), and compared their genetic differences using microsatellites. This study found that habitat continuity was negatively correlated to genetic differentiation, but distance was positively correlated to it. Thus, fragmentated populations of bladder kelp have the potential to result in genetically diverse subpopulations. However, it is likely that kelp rafts promote high levels of gene flow and mixing, and offer a route of connectivity if populations become fragmented and diverse.

5.3. Marine mammals

5.3.1. New Zealand sea lion

Habitat	• On land, require land away from anthropogenic threats, close to beaches and estuaries and near flat terrain (forest, dune) for dispersion phase • At sea, benthic foragers and feed at depth on continental shelves
Home range	• On land, travel up to 2 km inland for dispersion • At sea, travel ~100 km from coast in the Subantarctic Islands, but ~5km from coast at Otago
Connectivity	• Limited movement between colonies, but some individuals emigrate from colonies • Genetic studies reveal no genetic differentiation between any colonies, where Subantarctic Islands, Otago and Stewart Islands are all the same

The New Zealand sea lion (*Phocarctos hookeri*) is one of the rarest otariid (eared seals) species, and is currently classified as 'endangered' by the IUCN and 'nationally vulnerable' by the NZTCS (Gales and Fletcher 1999, Campbell et al. 2006, Baker et al. 2019). In order to discuss the current habitat requirements, home range and movement patterns in a relevant context, it is necessary to understand of the historical and current day distribution of the New Zealand sea lion. Historically, the New Zealand sea lion was distributed along the entire coast of the North and South Islands, Stewart Island, the Subantarctic Islands, and the Chatham Islands (Childerhouse and Gales 1998, Rawlence et al. 2016). However, subsistence hunting by Polynesian settlers extirpated the North Island, and then the onset of commercial sealing from European colonisation extirpated the South Island, Stewart Island and Chatham Island populations (Childerhouse and Gales 1998, Rawlence et al. 2016).

Today, the New Zealand sea lion exists predominately on the Auckland Islands and Campbell Island, which contribute to the majority of pup production (98%; DOC and MPI 2017). There are three breeding colonies on the Auckland Islands (Enderby Island, Dundas Island, and Figure of Eight Island) and two breeding colonies on Campbell Island (Davis Point and Paradise Point; Childerhouse et al. 2015a,b). Sea lion haul-outs, where they go onto land from the water, have been found at many other locations, including mainland New Zealand (Otago, Catlins), Stewart Island, the Snares Island and even as far south as the Macquarie Island (Crawley 1972, Childerhouse and Gales 1998, McNally 2001, McConkey et al. 2002, Campbell et al. 2006).

On Stewart Island, recolonization has also occurred from the Subantarctic Islands (Rawlence et al. 2016) and in 2018, Stewart Island was declared a breeding colony as pup production was at least 35 pups per year for over five years in a row (DOC 2018). By contrast, the Snares Island has seen a few pups produced from the 1970s, but it remains largely a male dominated non-breeding colony (Crawley 1972, Childerhouse and Gales 1998, McNally 2001). There has also been recolonization on the Otago coast, and today there are around 70 male and female sea lions that make up the Otago colony, with hopes that in the future Otago will also become a breeding colony (McConkey et al. 2002). While the Catlins does receive sea lions from the Subantarctic waters, it remains a non-breeding colony, comprised mainly of males (McNally 2001).

The current day population estimates (from ~9,880-11,767 sea lions; Collins et al. 2015, Chilvers and Meyer 2017) are much lower than the historical population estimates (17,300-205,000 sea lions from pre-sealing times; Collins et al. 2015). Population growth models have indicated that sea lions on the Auckland Islands have declined from 1998 to 2012 (Meyer et al. 2015a), with major threats being epizootics and pressure from fisheries (both competition for resources and bycatch; Chilvers et al. 2007, Robertson and Chilvers 2011, Chilvers 2012). Using age-structured models, Robertson and Chilvers (2011) report that sustained fishery pressure over the next 100 years will continue to lead to population declines and may even lead to the population becoming functionally extinct. However, a recent population viability analysis modelling by Hamilton and Baker (2014) demonstrate decline is not related

to bycatch, and slow growth would occur with current bycatch levels in the Auckland Islands. While there remains much debate around the effect of fisheries on the sea lion population (Hamilton and Baker 2014, Hamilton and Baker 2016, Meyer et al. 2015b, Meyer et al. 2017, Roberts et al. 2018a, Meyer et al. 2018), there appear to be threats (whether known or not) that have caused overall declines in the New Zealand sea lion population. In the New Zealand Sea Lion Threat Management Plan 2017-2022, the Department of Conservation and Ministry of Prime Industries have identified main threats in which future research will be targeted, including: (1) disease research, (2) research on female nutritional stress and diet, (3) research interaction with fisheries, (4) examination of efficacy of sea lion exclusion devices (SLEDs) in fisheries, and (5) review of impact of aquaculture (especially in relation to Port Pegasus) (DOC and MPI 2017); with the overall goal of moving the New Zealand sea lion to a 'not threatened' status.

5.3.1.1. Habitat of sea lions: on land (breeding, dispersal) and at sea (foraging)

New Zealand sea lions have habitat requirements on land and at sea. Sea lions have a breeding phase, which occurs generally on land close to shore, and a dispersion phase, in which females and pups travel inland to avoid aggressive males (Auge et al. 2009). This dispersion phase is unique to sea lions, and no other pinniped species have been recorded to travel as far inland (Auge et al. 2009). In order to identify areas in which recolonization by sea lions may occur, MacMilllian et al. (2016) conducted a GIS-based multi-criteria analysis of breeding habitat. Areas that were most suitable included those that were far away from anthropogenic disturbances (urban areas, roads), close to desirable features (beaches, estuaries) and had forest or flat areas behind beaches for the dispersion phase. Similarly, Auge et al. (2011b) identified that the most suitable habitats for sea lions on the Auckland Islands were sandy beaches with a wide area above high tide and moderate intertidal zone for breeding. Furthermore, for the dispersion period, beaches with flat terrain behind them with both vegetated sand dunes and forest were most preferred. The Auckland Island colonies have been found to be more social breeders and disperse inland after breeding, while females on Campbell Island have been found to be solitary and give birth farther inland (McNally et al. 2001).

At sea, sea lions are benthic foragers (Meyneir et al. 2009, Chilvers et al. 2011a,b) and are of the deepest diving otariids, also holding the record for longest dives (Gales and Matting 1997, Costa and Gales 2000). Sea lions display sexual dimorphism, and male sea lions have been found to dive deeper than females (Meyneir et al. 2008). New Zealand sea lions in the Auckland Islands utilize the entire Auckland Island shelf for foraging (Chilvers 2009, Chilvers et al. 2005a, Chilvers et al. 2011a,b). While generally different colonies of pinnipeds partition their habitats for foraging, satellite telemetry has revealed that colonies from Enderby Island and Dundas Island (both in the Auckland Islands) have been found to have partial overlap in their foraging rages (Chilvers et al. 2011b), which may be indicative of low prey availability for these sea lions.

There have been several studies that indicate that sea lions are diving to their physiological limits because they currently exist in marginal habitats. The Subantarctic Islands are at the edge of the historical range of the New Zealand sea lion, and as such, many studies suggest these sea lions may already be functioning outside (or near) the biological capacity for the species (Gales and Matting 1997, Costa and Gales 2000, Chilvers et al. 2005b, Chilvers et al. 2011a,b). Gales and Costa (1997) tagged 14 lactating females in the Subantarctic Islands in the summer 1995, and found that sea lions dove to an average of 123 m, with a maximum depth of 474 m recorded. Costa and Gales (2000) found similar mean dive depths to 124 m, but recorded a dive to 550 m. Depth durations were on average 3.4 minutes, but up to 11.5 minutes. Calculated field metabolic rates were found to be 5.8x that of metabolic rates of similar sized terrestrial animals (Costa and Gales 2000). Chilvers et al. (2011a) and Chilvers et al. (2005b) both found similar depth profiles, with respective averages of 118 m and 129.5 m and 4.6 min and 4.0 min. They reported that sea lions were diving beyond their aerobic dive limit on 65% of the dives, meaning that: (1) either the aerobic limits were miscalculated, (2) sea lions have adapted to function anaerobically, or (3) they are stretched to their physiological limits. These studies all suggest that the sea lions may be existing in marginal habitats on the edge of their range (see Section 5.3.1.2. for more information), and that management plans may want to consider that the baseline may be shifted for Subantarctic sea lions when assessing how other threats impact them.

In an effort to examine factors contributing to the nutritional stress recorded for the Auckland Island sea lion population, surveys of prey distribution (spatial and bathymetric) was conducted in areas where lactating females forage in both the Auckland Islands and the Snares Shelf, Stewart Island (Roberts et al. 2018b). Authors found a limited diversity of prey species in demersal trawl surveys in the Auckland Islands, stating this may explain the extreme diving depths recorded for sea lions here. Benthic camera surveys found that prey including the southern arrow squid, red cod, and yellow octopus are present at depths >100 m and likely overlap the foraging depths of sea lions. Furthermore, both trawl and benthic surveys found diurnal migrators hoki and southern blue whiting are likely available as prey for sea lions. On the Snares Shelf, a high abundance of potential prey shallower than 200 m suggests this is an optimal trophic habitat for sea lions.

5.3.1.2. Home range of sea lions: forage far from home, but depends on location

The home range of sea lions includes area needed for breeding and dispersal, as well as foraging areas. Both female and male sea lions from the Auckland Islands have shown high degree of philopatry, but females tend to show higher site fidelity and males tend to move more between colonies (Chilvers and Wilkinson 2008). Females that have been resighted away from their natal site are generally within an area of 10 km^2 (Chilvers and Wilkinson 2008). The range of dispersion females and pups following the breeding season can occur up to 2 km. Sea lions have been found inland from as far as 800 m-1.5 km from the shore, and as high as 250 m above sea level (McNally et al. 2001).

Foraging ranges have been recorded using satellite telemetry for lactating female sea lions and reveal large foraging ranges in the Subantarctic Islands, where sea lions generally foraged ~100 km from the colony and travelled ~200-400 km per trip (Chilvers et al. 2005a, Chilvers 2008, Chilvers 2009, Chilvers et al. 2011a,b). These distances and areas used by New Zealand sea lions recorded were the highest and largest of any sea lion species (Chilvers et al. 2005a).

For all the colonies (Enderby Island, Dundas Island, Figure of Eight Island) that forage across the Auckland Island shelf, foraging ranges overlapped with commercial fishing areas (Chilvers et al. 2005b, Chilvers 2008, Chilvers 2009, Chilvers et al. 2011b),

which increased competition for prey and increased risk of mortality by bycatch. In a study examining foraging ranges at the Figure of Eight Islands, three out of the four sea lions that were tracked foraged in areas that were also used by the squid and scampi fishery (Chilvers 2009). Large et al. (2019) conducted a spatial analysis for fisheries risk for New Zealand sea lions from all available spatial tracking data of sea lions on the Auckland Islands between 1996 and 2012. Using data from 2014-2017, this model indicated that estimates of annual death were highest for scampi trawls (3 deaths per year), then squid trawls (2.33 deaths per year), and finally other Auckland Islands fisheries (0.33 deaths per year). Large et al. (2019) concluded that commercial trawls are unlikely to have significantly suppressed the Auckland Islands population (without consideration to other anthropogenic threats), and that model estimates would be further improved with data from squid fisheries prior to 1980s when trawling effort was greater. Additional models have constructed to examine the impact of fisheries on sea lions, including ones examining Auckland Islands sea lion interactions with the arrow squid fishery (Roberts 2019), and with SLEDs on trawl nets (Middleton 2019).

Foraging ranges can differ between sexes, as expected since sea lions exhibit sexual dimorphism. Leung et al. (2012) examined size dimorphism and niche divergence between sexes for foraging, by tracking juveniles (19 females and 14 males) at Enderby Island (Auckland Islands). It was found that males travelled about twice as far (males versus females: 183.3 km versus 98.7 km for total trip distance; 35.8 km versus 68.4 km for mean distance from colony; 50.9 km versus 92.7 km for max distance from colony). Sex differences in foraging is thought to reduce competition. However, the foraging range of the females had twice as much overlap with fisheries than males, and Leung et al. (2012) suggest female juveniles at the highest risk of mortality from starvation (from increased competition) or bycatch. Mortality of juvenile females has the potential to lead to reduced fecundity and breeding success of the colony.

Foraging also differs between Subantarctic colonies and mainland colonies. A study conducted by Auge et al. (2011a) compares diving and foraging at the ‘edge of historic range’ Auckland Islands population versus the mainland Otago population. It was found that the Otago population had significantly smaller foraging ranges, shorter foraging trips and less time at sea than the Auckland Island population. For instance,

Otago populations travelled a max distance of 4.7 km from the colony (total travel distance 26.4 km), whereas Enderby Island populations travelled 102 km from the colony (total travel distance 423 km). Furthermore, because foraging occurred closer to the shore, juveniles had access to foraging grounds in Otago, whereas in the Auckland Islands, ranges were out of reach of juveniles.

5.3.1.3. Connectivity of sea lions: different colonies but genetically the same

Connectivity patterns of New Zealand sea lions have been made through the use of tagging and genetic studies. Emigration of individuals is often encouraged as population size grows (Chilvers and Wilkinson 2008), and male sea lions in particular have been found to move from 700 m away to as far as mainland New Zealand from the Auckland Islands (Chilvers and Wilkinson 2008). This corroborates sighting of sea lions in Otago, where most immigrants were males younger than 2 years old originating from the Auckland Islands (McConkey et al. 2002). Females are more likely to stay philopatric, and Chilvers and Wilkinson (2008) reported that limited movement of females happens between the Auckland and Campbell islands, and thus they are considered two separate management units (DOC 2009, MPI 2015). However, emigration of females from colonies has occurred (i.e., Otago colonisation by one female; McConkey et al. 2002). Tagging studies have therefore revealed that while the colony generally shows high site fidelity, a small proportion move between colonies.

Genetic studies have been employed to determine whether genetic differences reflect the high site fidelity and lack of movements between colonies observed for sea lions, and studies have revealed that there is no genetic differentiation between populations in New Zealand (Osborne et al. 2016, Collins et al. 2017). Osborne et al. (2016) used microsatellite markers to examine genetic variation from 1205 samples of live and dead pups collected over 2000-2007 from the following Auckland Island locations: Enderby Island (both Sandy Point and South East Point), Dundas Island, and Figure of Eight Islands. Genetic data revealed that this population went through a population bottleneck and exhibited signs of inbreeding, but there was no genetic differentiation between populations on the Auckland Islands. Collins et al. (2017) also examined population structure using microsatellite and mitochondrial DNA data for 271 individuals from the Otago Peninsula, Stewart Island, the Auckland Islands (Enderby Island, Dundas Island, Figure of Eight Islands) and Campbell Island (Paradise Point,

Davis Point). Both markers revealed high levels of gene flow and no structure between populations (Fig. 4). Authors concluded that the New Zealand sea lion is therefore one genetic stock and genetically speaking, could be considered one management unit. However, because threats and biological traits may vary between locations, management strategies may be different across colonies.

5.3.2. Hector's and Māui dolphin

Habitat	• Warm, turbid, shallow coastal waters • Likely prohibited by depth (remain within 100 m depth contour)
Home range	• Hector's dolphins: most movement within ~60 km, populations remain within 50 km of coast (most activity along 17 km); farthest offshore ~30 km • Māui dolphins: occupy 140 km stretch of coast (most activity within 35 km stretch of coast); farthest offshore ~20 km
Connectivity	• Māui and Hector's dolphins genetically distinct populations • Within Hector's dolphins, three distinct populations: (1) east coast of South Island, (2) west coast of South Island, (3) south coast of South Island

Hector's dolphins (*Cephalorhynchus hectori*) are the smallest members of the Delphinidae family (Perrin et al. 2008), endemic to New Zealand and recognizable by their rounded dorsal fin and black, white and grey colours. There are two subspecies, which are referred to as Hector's dolphin (*Cephalorhynchus hectori hectori*) and Māui dolphin (*Cephalorhynchus hectori māui)* (Baker et al. 2002). From here, we will refer to each subspecies separately, with Hector's dolphin referring to the subspecies *C. hectori hectori*.

Hector's dolphins are distributed on the north, east, west and south coasts of the South Island, occurring only along certain parts of the coast (Brager and Schneider 1998, Pichler 2001, Hamner et al. 2012). Population abundances have been estimated through photo identification capture and recapture, genotype biopsies and aerial transects (Gormley et al. 2005, Slooten et al. 2005, 2006, Hamner et al. 2017). Recent aerial surveys conducted on the east, west and south coasts together estimate the current population to be 14,849 individuals (95% confidence interval [CI]: 11,923-18,492; Clement et al. 2011, MacKenzie and Clement 2014, McKenzie and Clement 2016). Hector's dolphins are classified as 'endangered' by the IUCN and 'nationally vulnerable' by the NZTCS (Baker et al. 2019).

By contrast, the slightly larger Māui dolphins are distributed only on the west coast of North Island, occupying ~140 km of coastline from Maunganui Bluff to New Plymouth, but mostly remaining between Manukau Harbour and Port Waikato (Russell 1999, Slooten et al. 2005, Oremus et al. 2012). Recent studies have estimated that the population size of the Māui is 55 individuals (95% CI: 48-69; Hamner 2014) and 63 individuals (95% CI: 57-75; Baker et al. 2016). Because of their small numbers, Māui dolphins have been classified as 'critically endangered' by the IUCN and 'nationally critical' by the NZTCS (Baker et al. 2019).

Threats to Hector's and Māui dolphins include impacts from fisheries (as dolphins are often caught in gillnets and as bycatch in trawls), disease (toxoplasmosis), seismic surveying, seabed mining and vessel-based tourism (Dawson and Slooten 1993, Slooten 2013, DOC Fisheries 2019). Life-history traits of these dolphins make them particularly vulnerable to anthropogenic threats, namely their slow rate of reproduction and short generation time, small geographic range, and small population size (Brager et al. 2002, Clement et al. 2011, Hamner et al. 2012, Baker et al. 2012, MacKenzie and Clement 2014, McKenzie and Clement 2016, Hamner et al. 2017). Both Hector's and Māui dolphin populations have experienced declines over the past decades (Cooke et al. 2019, Slooten and Dawson 2020). Because these dolphins are at risk of extinction, understanding their habitat, home range and movement patterns is critical, and ongoing spatial risk assessments of threats are being conducted to inform threat management plans (Roberts et al. 2019).

5.3.2.1. Habitat of Hector's and Māui dolphins: warm, shallow and turbid waters

Hector's and Māui dolphins have coastal distributions, staying generally nearshore (Bejder 1997, Brager et al. 2003, Oremus et al. 2012, Rayment et al. 2010). Hector's dolphins have been found to prefer shallow (0-20 m depth), turbid and warm nearshore waters (Brager et al. 2003, Rayment et al. 2010, Weir and Sagnol 2015, Roberts et al. 2019). For instance, on the east coast of the South Island, dolphins were mostly found in depths less than 39 m, in water with less than 4 m visibility, and in temperatures above 14°C (Brager et al. 2003). Sightings of dolphins in Banks Peninsula suggest that they do not inhabit deeper waters, as all of the sightings were within the 90 m isobath (Rayment 2008). Furthermore, individuals have been sighted either north or south of Kaikoura Canyon, suggesting that they do not inhabit deep waters, and that

the deep waters associated with the canyon area could act as natural barrier dividing dolphins into two groups in Kaikoura (Weir and Sagnol 2015).

On the south coast of the South Island in Porpoise Bay, dolphins were found to remain in the small bay in the surf zone, near the reef (Beider 1997). Dolphins have also been found to utilize low visibility harbours, where Māui dolphins were found to use three of the five harbours on the west coast of the North Island (Slooten et al. 2005), and Hector's dolphins have been reported in the Akaroa Harbour (Brager et al. 2002). While both Hector's and Māui dolphins generally stay inshore, they can also move further offshore, and in some cases have been reported beyond boundaries of marine mammal sanctuaries (i.e. Banks Peninsula Marine Mammal Sanctuary) and outside of areas where net restrictions have been set (see Section 5.3.2.2. for more information; Du Frense 2010, Rayment et al. 2010, Slooten et al. 2010, Dawson et al. 2013, Slooten 2013, Nelson and Radford 2019).

5.3.2.2. Home range of Hector's and Māui dolphins: close to shore, but seasonal

The home ranges of both Hector's and Māui dolphins are small (less than 100 km from shore), and dolphins show strong site fidelity (Brager et al. 2002, Rayment et al. 2009, Oremus et al. 2012). Their range is not expected to extend beyond the 100 m isobath (Rayment 2008). Photo identification over 12 years of Hector's Dolphins on the east coast of the South Island revealed that all but one individual remained within a distance of 60 km, with the largest distance from the initial and final resight was 106 km (Brager et al. 2002). Similarly, Rayment et al. (2009) found that the mean linear distance between the two extremes of sightings at the Banks Peninsula was 36 km, ranging from 9-107 km. Kernel densities (i.e., estimates of home range) revealed a home range of ~50 km along the coast, with most activity centred around a stretch of 17 km (Rayment et al. 2009). In aerial surveys along the west coast of the South Island, McKenzie and Clement (2016) observed Hector's dolphins mostly close to shore (>5.5 km) and at depth less than 40 m, but up to 17.7 km away and in waters up to 200 m deep.

For Māui dolphins, sightings from boat surveys and genotype recaptures from biopsy samples revealed that the mean along-shore range of Māui dolphins was 35.5 km (Oremus et al. 2012). While the Māui dolphin range extended 139 km of coastline,

they showed clumped distribution (likely due to patchy food resources) and generally stayed within a smaller area from the Manukau Harbour and Port of Waikato (Oremus et al. 2012). In the most recent acoustic monitoring of dolphin populations along the west coast of the North Island, Nelson and Radford (2019) used click detector devices (called C-PODs) to determine dolphin distribution and found that clicks decreased with increasing distance from shore. These authors found that the most clicks were recorded 0.91 km (from Hamilton's Gap) in the summer, and that a large number of clicks were also detected at 8 km from shore.

Seasonal inshore-offshore movements for Hector's dolphins have been recorded for the population on the east coast of the South Island (Brager 1998, Rayment et al. 2010, Slooten et al. 2010). In the summer in the Banks Peninsula population, dolphins remained more aggregated near the shore, whereas in the winter they move further offshore and had a more dispersed distribution (Slooten et al. 2005, Slooten et al. 2010, Rayment et al. 2010). Aerial surveys revealed that 79% of dolphins remained within the 7.4 km boundary of the Banks Peninsula Marine Mammal Sanctuary during the summer, whereas only 35% did over the winter, where ranges extended beyond 28 km (Slooten et al. 2010). Similarly, Rayment et al. (2010) found that in the summer, 19% of dolphins went beyond the 7.4 km boundary whereas in the winter, 56% went beyond the boundary. It is thought that seasonal changes in dolphin abundance and inshore-offshore movements are likely a result of prey distribution as well as movements associated with birthing (i.e., inshore provides refuge for birth and calves; Rayment et al. 2010). On the west coast of the South Island, McKenzie and Clement (2016) found that Hector's dolphins were observed further offshore and deeper in the winter (17.7 km and 200 m depth) than summer months (12 km and 160 m depth). In Porpoise Bay, photo identification of Hector's dolphins during 79 boat surveys revealed that ~50-65 dolphins were resident in the bay during the summer, with abundance unknown in winter (Bejder 1997, Bejder and Dawson 2001). Furthermore, Dawson et al. (2013) found diurnal movements for Hector's dolphins within the Akaroa Harbour in the Banks Peninsula.

Māui dolphins have also been found to exhibit season inshore-offshore movements, where in winter they move to deeper waters and become more dispersed (Slooten et al. 2005). Their movements offshore have been recorded between ~5-13 km (Slooten

et al. 2005, Du Frense 2010), and more recent studies have recorded dolphins 18.2 km from the shore in November (Nelson and Radford 2019). Furthermore, using C-PODs, Nelson and Radford (2019) detected dolphins at moorings 8 km and 10.1 km offshore the Manukau Harbour mainly at night, indicating diurnal inshore-offshore movements similar to movements recorded for Hector's dolphins.

5.3.2.3. Connectivity of Hector's and Māui dolphins: distinct populations

Genetic and morphological differences support species differentiation between Hector's and Māui dolphin (Russell 1999, Pichler and Baker 2000, Baker et al. 2002, Pichler 2002, Hamner et al. 2012). Baker et al. (2002) was the first to suggest the recognition of a new subspecies *C. hectori māui* based on combined genetic and morphological data. Within Hector's dolphins, three populations (and suggested management units) have been identified from the west coast, east coast and south coast of the South Island (Picher and Baker 2000, Pichler 2001, Pichler 2002, Hamner et al. 2012).

Pichler et al. (1998) was the first to examine the genetic structure of Hector's dolphins, examining mitochondrial DNA from beachcast or gillnet caught specimens, and found regional genetic differences. Pichler (2001) and Pichler (2002) did a more extensive population structure study and examined samples from the North Island (n = 29) and South Island (n = 251), where South Island populations included: Cloudy Bay, Kaikoura, Pegasus Bay, Akaroa, Timaru, Jackson Bay, Greymouth, Westport, Te Waewae. Mitochondrial DNA and microsatellite data revealed four strongly genetically different groups: the North Island (Māui dolphin), (2) the west coast of the South Island (Jackson Bay, Greymouth, Westport), (3) the east coast of the South Island (Cloudy Bay, Kaikoura, Pegasus Bay, Akaroa, Timaru), and (4) the south coast of the South Island (Te Waewae Bay). Populations within each of these regions, however, were strongly mixed and not different. Gene flow was modelled to occur in a stepping-stone fashion, as in dispersal only occurs to the immediate adjacent population (Pichler 2001, 2002). Thus, population fragmentation resulting from the reduction in population size and/or range or the loss of one population can puts other populations at risk of losing genetic diversity.

Hamner et al. (2012) expanded on this study and examined tissue from 438 dolphins (342 Hector's dolphins and 96 Māui dolphins), collected from 1988 to 2007 from either dead specimen or by using a biopsy dart or skin swab for live dolphins. Genetic differences were examined using microsatellites and mitochondrial DNA from ten populations on the South Coast, from the east coast (Cloudy Bay, Kaikoura, Pegasus Bay, Banks Peninsula, Timaru), from the west coast (Westport, Greymouth, Jackson Bay), and from the south coast (Te Waewae Bay, Toetoe Bay). Results from this study agreed with previous studies, identifying 4 strongly genetically different groups of dolphins: North Island (Māui dolphin), east coast of South Island, west coast of South Island, and south coast of South Island (Fig. 4). Because distances between these regions are larger than the home range of these dolphins, distance may be acting as a barrier to gene flow between populations. Interestingly, within the South Island, 4 migrants were identified, which had a parent from another region. Thus, evidence for limited dispersal and gene flow exists, which has implications for the protection of 'corridors' outside of home ranges.

Additional sightings of Hector's dolphins in other areas suggest that dispersal and emigration does sometimes occur. The higher proportion of males caught in gillnets on the South Island, many outside of the marine mammal sanctuaries, is thought to perhaps indicate that juvenile males move more between populations (Pichler and Baker 2000, Hamner et al. 2012). Hector's dolphins have been genetically identified in the southern North Island (the Wellington Harbour, Peka Peka Beach) and among the North Island Māui dolphin population (Hamner et al. 2013, Hamner 2014). Additional sightings of Hector's dolphins (information available on the DOC sightings database: https://www.doc.govt.nz/mauisightings) have been made in around the North Island, including Auckland, Coromandel, Bay of Plenty, Bay of Islands, Gisborne, Hawke Bay, Manawatu-Wanganui, Cook Strait, Waikato, Wellington, and Palliser Bay; and also within the fiords of Fiordland (Pichler 2002). Māui dolphins have been sighted outside of their range in Auckland, Waikato, Manawatu-Wanganui and Taranaki. Acoustic monitoring has revealed dolphins along the Tapuae coastal area of Taranaki region, but because clicks cannot be distinguished between Hector's and Māui dolphins, it is unclear if they are Hector's dolphins moving northward or Māui dolphins moving southward (Nelson and Radford 2019). Such sightings indicate there is potential for migration of dolphin populations and potential for unidentified

populations existing in New Zealand. In Porpoise Bay, Bejder (1997) reported that resident individuals were visited occasionally by either neighbouring populations, indicating potential population mixing; however, authors state that these visitors could instead be individuals within the Porpoise Bay population that had larger home ranges (Bejder 1997).

Genetic data reveal that these populations are at risk due to low genetic diversity. Pichler and Baker (2000) examined historical and contemporary samples of Hector's and Māui dolphins and found that the Māui dolphin once consisted of three different maternal lineages, but today comprise of only one. Furthermore, based on current trends of genetic variation loss, the east coast of the South Island population is predicted to lose all of its mitochondrial genetic diversity within the next 20 years (Pichler and Baker 2000). It has already been suggested that the Māui dolphins are at risk of, if not already, suffering from inbreeding depression (Hamner 2014, Hamner et al. 2017). Beachcast Māui dolphin on the North Island were 78% female, consisting of many neonatal or pregnant dolphins (Pichler and Baker 2000, Hamner et al. 2012). Birth defects and pregnancy related complications can arise from inbreeding, and while this warrants further investigation, it could be a sign of inbreeding within Māui dolphin populations (Hamner et al. 2012).

5.4. Penguins

There are six species of penguins that breed in New Zealand: the little blue penguin (*Eudyptula minor*, called by the Māori name kororā); the yellow-eyed penguin (*Megadyptes antipodes*, called hoiho); and four species of crested penguins, which are the Fiordland crested penguin (*Eudyptes pachyrhynchus*, called tawai), the Snares penguin (*Eudyptes robustus*), the Eastern rockhopper penguin *(Eudyptyes fiholi*) and the erect-crested penguin (*Eudyptes sclateri*). The yellow-eyed penguin, the Fiordland crested penguin, the Snares penguin and the erect-crested penguin are endemic to New Zealand. In this report, we consider habitat requirements, home ranges and movement patterns for only the little blue penguin, the yellow-eyed penguin and the Fiordland crested penguin, which are the only penguins that breed on mainland New Zealand. However, a comprehensive review of the current information about the ecology of all six penguins can be found in a recent report by Mattern and Wilson (2018), complied for Birds New Zealand.

5.4.1. Little blue penguin

Habitat	• On land, highly variable (including grassy fields, forests, caves, rock screes, and even urban areas) • At sea, pelagic foragers where river proximity appears to enhance foraging
Home range	• High site fidelity to natal colonies • Variable foraging ranges, from approximately 10 to 100 km from shore
Connectivity	• Two species exist in New Zealand: *Eudyptula novaehollandiae* in Otago and Oamaru (originated from Australia) and *E. minor* existing in the rest of New Zealand • High levels of gene flow between remaining populations of *E. minor* throughout New Zealand, supporting observations of movement between colonies

The little blue penguin (*Eudyptula minor* and *E. novaehollandiae*) is the smallest penguin in the world and is found throughout mainland New Zealand (both North and South Islands), the Chatham Islands, and Stewart Island, as well as southern Australia and Tasmania. Grosser et al. (2015) identified two genetically distinct species of little blue penguin: the Australian species (*E. novaehollandiae*, that also exists in Otago) and the New Zealand species (*E. minor*; for more explanation see Section 5.4.3.). The white-flippered penguin (*Eudyptula minor albosignata,* see Challies and Burleigh 2004 and Allen et al. 2011) has been identified as a separate species of little blue penguin that is endemic only to the Banks Peninsula and Motunau Island, morphologically distinguishable by its paler coloured flippers. The Pohatu Marine Reserve was established in 1999 with an objective to protect the white flippered penguin, among other seabirds that frequent this area. Grosser et al. (2015) reported that the white-flippered penguin is not genetically distinct from *E. minor* and should be considered the same, yet the white-flippered penguin is still recognized as a separate taxon when classifying threats in New Zealand (Robertson et al. 2016). The little blue penguin is classified as 'least concern' by the IUCN and 'at risk – declining ' by the NZTCS (Robertson et al. 2016).

5.4.1.1. Habitat requirements of little blue penguins: not too picky

On land, little blue penguins nest in a wide variety of environments, including grassy fields, herbfields, scrublands, woodland forests, rock screes, caves and even in urban areas (Marchant and Higgins 1990, Dan 1994, Braidwood et al. 2011). They often nest

in burrows, under trees, in rock crevices, under rocks, in rabbit holes, in pipes and in driftwood (Waas 1990, Perriman and McKinlay 1995, Davis and Renner 2003, Bull 2000a,b, Heber et al. 2008, Dann 1994, Braidwood et al. 2011). Nest boxes have been put in place as a conservation measure in some areas and have proven successful for little blue penguins (i.e., Tairaroa Head, Perriman and McKinlay 1995). Braidwood et al. (2011) found that differences in nesting environment can differ between locations, where 97% of penguins nested in coastal forest in Buller, while only 55% of penguins nested in coastal forest (and the rest in scrubland) in South Westland (Braidwood et al. 2001). In Buller, nests were under rocks (72%), in caves (6%), in soil (7%), or in artificial nest boxes (15%); whereas in South Westland, nests were in soil (43%) or sand (23.3%). Colonies from both of these locations nested within 25 m of the sea (Braidwood et al. 2011). Exposure, elevation and soil type can all affect breeding success, with elevation important in reducing the risk of flooding and sand providing better drainage (Bull 2000a,b, Perriman and McKinlay 1995).

At sea, little blue penguins are pelagic foragers that typically dive to depths of up to 50 m (van Heezik 1990, Chiaradia et al. 2007). Bathymetry and geographical features have been reported to influence foraging behaviour for little blue penguins (Mattern et al. 2001, Chiaradia et al. 2007). Mattern (2001) found that little blue penguins in the Marlborough Sounds tended to dive deeper, for longer and more frequently than that of other colonies, where bathymetry and surrounding islands in the sounds restricted penguins and caused an increase in diving effort to find prey. Chilvers (2017, 2019) examined diving behaviour of little blue penguins in the Marlborough Sounds and compared it to other colonies (Stewart Island, Abel Tasman, Tauranga, Wellington). Surprisingly, although the Stewart Island population sits next to a 100 m deep trench, the little blue penguins there performed the shallowest dives. In contrast, in the shallower Marlborough Sounds, penguins dived deeper. Similarly, the Wellington Harbour was the shallowest site, but had the deepest dives (Chilvers 2017). Chilvers (2019) argued that bathymetry and geography alone do not explain diving behaviour, but that prey availability, water and wind movements (eddies, currents, upwellings, etc.) are also important. Increased diving effort has been shown to have consequences on breeding, where increased effort resulted in lower body condition and a higher chance of egg desertion (Numata et al. 2000). Nonetheless, as pelagic foragers, little blue penguins seem to be able to adapt to various environments and

adopt different foraging behaviours, allowing them to be flexible in terms of habitat needs at sea. However, productive seas within 50 km of the colony seem to best support little blue penguins.

Interestingly, distance of a colony to a river mouth seemed to result in penguins having to travel less distances to forage, thereby increasing reproductive success and overall population viability (Zhang et al. 2015, Poupart et al. 2017). River mouths are often associated with increased productivity, where phytoplankton blooms associated with river plumes attract other higher trophic organisms, which include prey items for little blue penguins. Therefore, because the presence of river appears to influence foraging behaviour, this feature could be considered when designating areas for protection for little blue penguins.

5.4.1.2. Home range of little blue penguins: variable

Banding and recapture studies have revealed that little blue penguins tend to remain where they were first banded (i.e., their colony), with only few penguins moving between colonies. For instance, Johannesen et al. (2002) surveyed 268 penguins on the Otago Peninsula and found 258 were originally tagged on the Otago Peninsula, revealing high site fidelity. Similarly, Kinsky (1958, 1960) examined little blue penguins in the Wellington Harbour and only found three of 435 banded penguins outside of the Harbour over a four-year period. While it is generally thought that penguins remain close to home, recent data from penguins tagged with GPS loggers reveal that they are also capable of travelling quite far, up to 215 km from their colony (Poupart et al. 2017). Foraging range can vary between locations (also supported by differences in diet composition reported between different colonies; Chilvers 2019), and vary throughout stages of chick breeding and rearing (adults tend to stay closer to nests during chick rearing; Agnew 2014). Colony size has also been shown to affect foraging range, with foraging areas increasing with colony size (Chiaradia et al. 2007), perhaps due to competition and the need to search for prey.

In a study examining foraging ranges, little blue penguins in the Hauraki Gulf (Motu Muka) were found to have a mean maximum range of 18.9 km and a mean total distance of 60.4 km (K. Lukies, unpublished data). Furthermore, GPS-tracking in 2014 of a little blue penguin from Rangatira Island, Chatham Islands revealed that maximum

distance travelled from the colony was 18.4 km (H. Schultz, pers. comm.). Agnew (2014) and Chiaradia et al. (2007) both found that in Oamaru, little blue penguins stayed within 20 km of the shore. Mattern (2001) compared foraging between the Marlborough Sounds (Motuara Island) colony and an Oamaru colony. The Marlborough Sounds penguins had a foraging range within a 9 km radius of their nesting site (with a mean total trip distance of 24.4 km) versus the Oamaru colony, which remained with a 30 km radius (with a mean total trip distance of 57.4 km). However, diving effort was found to be higher for those penguins in the Marlborough Sounds, which dived more often, deeper and for longer. It was speculated that in the Marlborough Sounds, penguins were restricted due to the surrounding bathymetry and geographical features, making them have to search longer for prey.

Poupart et al. (2017) similarly examined foraging ranges of three colonies of little blue penguins at Wellington, Marlborough Sounds (Motuara Island), and the Buller region and found differences in foraging ranges. At Wellington, penguins stayed within 12 km (mean) of their colony and journeyed between 1-3 days. This was consistent throughout the year, independent of breeding stage. In the Marlborough Sounds, during incubation, penguins travelled further within 102 km (mean; range 1-214 km), with trips lasting 1-16 days. Some birds travelled as far as across the Cook Strait. During chick rearing, little blue penguins stayed much closer to nests (within 10 km) to tend to chicks. Little blue penguins in Buller also showed the same pattern of longer and further trips during incubation than chick rearing. Differences in travel distances were attributed to prey availability.

5.4.1.3. Connectivity of little blue penguins: two species exist in New Zealand

Kinsky and Falla (1976) were the first to suggest multiple species of little blue penguins existing in New Zealand. They looked at morphometrics and plumage and described six subspecies based on differences in these traits. Meredith and Sin (1988) then used allozyme analysis to examine the genetic divergence of four little blue penguin populations from Motaunau Island, Onawe Island, Poor Knights and Maud Island. Low to moderate divergence was observed between these populations, with Poor Knights being the most diverged population (but still closely related, referring to intraspecific differences). Divergence values (based on number of differences of nucleotides in sequences) between these populations were less than half than those of interspecific

divergence values between the little blue penguin and the yellow eyed penguin (i.e. 0.001-0.087 versus 0.189-0.213). This suggests that while populations may have diverged slightly, they likely consist of the same species, refuting the morphology work done by Kinsky and Falla (1976).

Mixing between populations is likely, as tag-resightings and GPS tracking has revealed large movements and mixing between colonies (Johannesen et al. 2002, Poupart et al. 2017). For instance, penguin surveys on the Otago Peninsula reveal that nine (of 268) penguins were originally tagged at Oamaru (80 km away) and one was from Penguin Beach (2 km away). Therefore, a small proportion of the penguin population likely moves between populations and promotes gene flow.

Recent genetic studies have revealed that two species of little blue penguin exist in New Zealand (Banks et al. 2002, Peucker et al. 2009, Grosser et al. 2015, Grosser et al. 2016). In the most recent study, Grosser et al. (2015) used mitochondrial, nuclear and microsatellite markers and described one species from Australia and south eastern New Zealand (*Eudyptula novaehollandiae*) and another species (*E. minor*) from the rest of New Zealand (Fig. 5). This study surveyed a large number of locations, including: (1) the North Island (Northland [3 sites], Bay of Plenty, Hawke's Bay [3 sites], Wellington [2 sites]); (2) the South Island (Golden Bay, West Coast, Kaikoura, Banks Peninsula [3 sites], Oamaru, Katiki Point, Otago Peninsula, Porpoise Bay); (3) the Chatham Islands (2 sites); and (4) Stewart Island; as well as four locations in southern Australia. Microsatellite analysis revealed all locations in New Zealand except for Otago and Oamaru had high gene flow, suggesting *E. minor* is comprised of one species that mixes throughout the country (including the Chatham Islands). Furthermore, in Otago and Oamaru where both species exist, instances of hybridisation have been documented between both species (Grosser et al. 2015). Coalescent modelling revealed that the Otago and Oamaru populations are a result of the arrival and colonization of *E. novaehollandiae* in New Zealand (Grosser et al. 2016).

In relation to the management of the little blue penguin, the lack of gene flow between both species should be considered because species exhibit some different life-history traits. For instance, *E. novaehollandiae* generally broods twice versus once as in *E. minor*. Further, *E. novaehollandiae* forms social groups called rafts when returning to

sea, whereas *E. minor* does not, likely evolved as a predator avoidance strategy which would be needed in Australia (Daniel et al. 2007, Grosser et al. 2016).

5.4.2. Yellow-eyed penguin

Habitat	• On land, low podocarp or hardwood forests (for thermal relief) • At sea, benthic foragers on the continental shelf (seeking reefs, oyster beds, horse mussel beds)
Home range	• High site fidelity to natal colonies • Relatively small foraging ranges, <60 km, but generally within 10-25 km
Connectivity	• Little to no gene flow between mainland and Subantarctic Islands, as they are genetically distinct populations

Yellow-eyed penguins (*Megadyptes antipodes*) are distributed along the southeast coast of the South Island, Stewart Island (and its outlying islands), Campbell Island and the Auckland Islands (68-79% of the population breeding in the latter two Subantarctic Islands, with 38-50% breeding in the Auckland Islands; Muller et al. 2020). Genetic and morphological analyses of historic samples of yellow-eyed penguins revealed that the yellow-eyed penguin expanded their range from the Subantarctic Islands to mainland New Zealand within the last few hundred years (after the extinction of their sister species *M. waitaha* sp. nov.; Boessenkool et al. 2008). The low abundance (1700 breeding pairs; Mattern and Wilson 2018) and highly specialized foraging strategy of the yellow-eyed penguin has resulted in the species being particularly vulnerable to threats, leading to fluctuations in the population size with many quick declines over recent decades (van Heezik 1989, Gill and Darby 1993, Moore 2001, Mattern et al. 2007). The yellow-eyed penguin is classified as 'endangered' by the IUCN and 'nationally endangered' by the NZTCS (Robertson et al. 2016), and the efforts towards the conservation of this species has resulted in it being one of the most studied penguin species in New Zealand.

5.4.2.1. Habitat of yellow-eyed penguins: specific requirements above and below sea

Yellow-eyed penguins have habitat requirements on land and at sea, and a loss of either of these habitats has major consequences for the reproductive success and overall population viability of these penguins (Darby and Seddon 1990, Browne et al. 2011, Ellenberg and Mattern 2012). On land, yellow-eyed penguins are surface

nesters that gather materials (twigs, grasses, leaves) from areas within 40 m of their nesting sites (Darby and Seddon 1990). They nest isolated from one another and can travel up to 700 m inland to find a suitable nest site (Seddon and Davis 1989, Darby and Seddon 1990). They breed in low podocarp or hardwood forests, where cover allows penguins to shelter in the cool forest and avoid thermal stress (Darby and Seddon 1990). On the Auckland Islands, breeding habitat was found to be predominately southern rata forest and scrub vegetation (Ellenberg and Mattern 2012).

Habitat loss of coastal forests throughout mainland New Zealand has resulted in yellow-eyed penguins having to breed in less than optimal areas, which involves often nesting in dense vegetation of flax, gorse and other native shrubs like ngaio, *Hebe*, and tree nettle (Richdale 1957, Roberts and Roberts 1973, Ellenberg and Mattern 2012, Chilvers et al. 2014, Mattern and Wilson 2018). Nests have even been observed in open grassland without cover (McKay et al. 1999), resulting in yellow-eyed penguins being more prone to thermal stress. It is thought that habitat loss and predator-induced injuries and/or fatalities (among other terrestrial and marine threats) has led to population declines, and therefore the reservation of breeding areas and revegetation have been of focus when trying to reduce anthropogenic impacts and protect the yellow-eyed penguin (Moore 2001; see: https://www.doc.govt.nz/globalassets/documents/conservation/native-animals/birds/sea-and-shore/draft-te-mahere-rima-tau-2019.pdf).

Yellow-eyed penguins also require suitable landing sites when returning from the sea, which include sandy and/or pebble beaches or rock platforms (Mattern and Wilson 2018). Moore (1992) found that on Campbell Island, 61% of landing sites for yellow-eyed penguins were shingle or small boulder beaches and 39% were rocky wave-cut platforms, ramps or promontories. On the Auckland Islands, 64% of landing sites were rocky shores, 31% were boulder beaches and 4% were sandy beaches (Moore 1992).

At sea, yellow-eyed penguins are mainly benthic foragers that rely on a constant food source, often travelling along consistent paths and revisiting the same feeding locations (Moore 1999, Mattern 2007, Mattern et al. 2007). When examining diving behaviour, Mattern et al. (2007) found that 87% of yellow-eyed penguin dives were benthic. Yellow-eyed penguins have U-shaped dive profiles and also remain close to

the benthos when travel to and from foraging grounds (Mattern et al. 2007, Chilvers et al. 2014). It is thought that yellow-eyed penguins use benthic features like reefs, shingle patches and flora to navigate while foraging (Mattern et al. 2007). Their foraging sites generally include sites containing horse mussel fields, oyster beds and reefs, which support demersal and benthic invertebrates and fish (Ellenberg and Mattern 2012).

The continental shelf surrounding the southeast coast of the South Island has proven important for yellow-eyed penguins, where dive depths generally are confined by ocean depths (Moore 1999, Ellenberg and Mattern 2012). For instance, dives in Otago (shelf from 40-80 m) were up to 66 m versus dives in the Catlins (shelf from 80-150 m), which were up to 128 m (Seddon and van Heezik 1990, Moore et al. 1995). Dive depths in Stewart Island are on the same order of magnitude, averaging 61 m, with a maximum of 116 m (with 63% of dives between 3-20 m and 16% of dives between 80-100 m; Chilvers et al. 2014). The yellow-eyed penguins are the only benthic feeders of the New Zealand penguins (which are pelagic), and this strategy is thought to reduce competition with penguins and other seabirds (Ellenberg and Mattern 2012). While primarily benthic foragers, yellow-eyed penguins sometimes forage pelagically; for instance, in the Auckland Islands they employ both benthic and pelagic foraging (Mattern and Ellenberg 2018).

Diet and prey composition of yellow-eyed penguins varies with seafloor composition, with higher abundances of opalfish (desired prey) on coarse and gravel substrate, versus a higher abundance of blue cod and red banded perch (alternative prey items) on well-defined benthic substrate like oyster beds and reef have been reported (Mattern and Ellenberg 2018). Changes to the benthic habitat and associated available prey has been shown to affect reproduction of yellow-eyed penguins. Browne et al. (2011) examined the diet of two populations of yellow-eyed penguins on Stewart Island and Codfish Island, where the former had a reduced reproductive status (0.38-0.67 chicks per pair) than the latter (0.96-1.51 chicks per pair). Though these populations were only 30 km apart, their diets were markedly different, where Stewart Island consisted of 99% prey biomass of blue cod as prey versus Codfish Island which had 70% blue cod and 27% opalfish. These authors link these differences in diet and lower reproductive success with recent oyster dredging in the Foveaux Strait, where oyster

dredging resulted in reduced abundance of opalfish and increased availability of alternative prey items (e.g., blue cod) at Stewart Island. Blue cod were thought to be too big to be regurgitated and fed to young, explaining chick starvation observed at Stewart Island. Thus, as selective feeders that rely on specific benthic habitats, yellow-eyed penguins are vulnerable to changes in habitat (van Heezik 1989).

5.4.2.2. Home range of yellow-eyed penguins: stay close to home

Yellow-eyed penguins have high nest fidelity, where adults tend to remain in a single breeding area and return to the same site in consecutive years (Darby and Seddon 1990, Mattern and Wilson 2018). Strong philopatry has been observed, with 98% of breeders returning to their original nesting location (Richdale 1957, Ratz et al. 2004) and 90% of penguins staying within their breeding area (Richdale 1957). Non-breeders and juveniles tend to travel further and have been seen in Canterbury, Kaikoura and Cape Campbell, usually going to shore to moult (Mattern and Wilson 2018). There have been reports of yellow-eyed penguins breeding as far north as the Banks Peninsula, but with little success and instead recruitment is likely from southern populations (Parker 2009, Parker 2010, Mattern and Wilson 2018).

Foraging ranges of yellow-eyed penguins are relatively small (compared to other penguins), classifying them as near-foragers (Mattern and Wilson 2018). For the most part yellow-eyed penguins follow consistent foraging patterns, and during breeding stay within 10-25 km of the coast, which was been reported in Oamaru, Boulder Beach (Otago) and Long Point (Catlins; Moore 1999, Mattern et al. 2007, Ellenberg and Mattern 2012, Mattern et al. 2013, Chilvers et al. 2014, Mattern and Wilson 2018). The maximum distance recorded from Boulder Beach (Otago) was 57 km from nesting site (Moore et al. 1995, Moore 1999). Penguins from Codfish Island and the Auckland Islands have been found to forage up to 50 km away (Mattern 2007, Ellenberg and Mattern 2012, Mattern and Wilson 2018). At the Otago Peninsula, non-breeders and juveniles travelled further for longer, but ultimately these penguins are constrained by the continental shelf (Ellenberg and Mattern 2012). A summary of foraging ranges for different stages of breeding for different years and locations can be found in Table 4 of Ellenberg and Mattern (2012).

5.4.2.3. Connectivity of yellow-eyed penguins: two to three subpopulations

Connectivity patterns for yellow-eyed penguins have been determined largely from tagging and genetic data. Unpublished data from DOC has revealed that exchange between mainland New Zealand and the Subantarctic Islands is rare. From the ~550 tagged sub-Antarctic penguins and the ~10,000 tagged mainland penguins, only one penguin was found to have exchanged locations, where one penguin from the Subantarctic waters was found dead on Stewart Island (DOC unpublished data in Boessenkool et al. 2009, Ellenberg and Mattern 2012). The first study to examine the genetic makeup and gene flow between populations of yellow-eyed penguins was performed by Triggs and Darby (1989). These authors examine allozymes between populations on the South Island and Subantarctic Islands and found that the yellow-eyed penguins consisted of three genetically isolated subpopulations (mainland, Auckland Islands, Campbell Islands), with significant moderate genetic differentiation between the Auckland Islands and Campbell Island. This study also revealed that there is relatively low genetic diversity within the yellow-eyed penguin, making them vulnerable to population declines and collapses due to bottlenecks and the founder's effect.

This low exchange rate was unexpected as the recent range expansion of yellow-eyed penguins from the sub-Antarctic islands to mainland New Zealand would suggest high dispersal potential (Boessenkool et al. 2009). However, low exchange was confirmed using mitochondrial DNA and microsatellite genetic analyses by Boessenkool et al. (2009) and Boessenkool et al. (2010), who found strong genetic differentiation between mainland New Zealand and the Subantarctic Islands (Fig. 5). An immigration rate between the Subantarctic Islands and mainland New Zealand was found to be 0.003 individuals per generation, which was further confirmed through computational models (Lopes and Boessenkool 2010). It is possible that the convergence of three fronts between the mainland and sub-Antarctic islands act as a barrier for these penguins (Mackintosh 1960). Virtually no gene flow or exchange between populations means that neither population can seed the other if one declines or collapses, but also means that disease is not likely to be spread between populations. Due to the high genetic differentiation and negligible immigration rate between mainland New Zealand and the Subantarctic Islands, it is suggested that these populations be considered separate management units (Boessenkool et al. 2009).

5.4.3. Fiordland crested penguin

Habitat	• On land, dense podocarp-broadleaf forests and scrub, caves, boulder beaches • At sea, little information available
Home range	• During pre-moult, travel to Subtropical and Subantarctic Fronts for 2-3 months, for total trip distances of approximately 3500-6800 km • During breeding, stay close to shore, within 50 km
Connectivity	• Unknown

The Fiordland crested penguin (*Eudyptes pachyrhynchus*) is the only crested penguin that breeds on mainland New Zealand (estimated 2500-3000 breeding pairs; Mattern and Wilson 2018). It is classified as 'vulnerable' by the IUCN and 'nationally vulnerable' by the NZTCS (Robertson et al. 2016). Because they live in dense forests, they are often difficult to survey and as a result, are among the least studied penguins in the world (Mattern 2013, Long 2017, Mattern and Wilson 2018). They currently only exist on the southwest coast of the South Island (South Westland and Fiordland) as well as Stewart Island (and its outlying islands), though historically their range expanded much further (but genetic diversity has remained stable over time; Cole et al. 2019). Some penguins have been seen moulting in Otago, Snares Island, Auckland Islands and Campbell Island (Young et al. 2015, Mattern and Wilson 2018). Furthermore, due to the difficulty in observing these penguins, past estimates of populations have been said to be underestimates (Mattern 2017, Long 2017). Fiordland crested penguins were originally considered the same species with the Snares penguin and the erect-crested penguin (Kinsky 1970), but recent studies have confirmed that these are in fact three separate species, confirmed through the use of morphology (Davis and Renner 2003) and genetic analyses (Baker et al. 2006, Ksepka et al. 2006, Cole et al. 2017, Pan et al. 2019). As such, they should be considered as separate units for management purposes.

5.4.3.1. Habitat of Fiordland crested penguins: dense forests

Fiordland crested penguins nest in small scattered groups, primarily on steep slopes in dense podocarp-broadleaf rainforests and scrub, but also in caves and along rocky shorelines and boulder beaches (Warham 1974, Long et al. 2010, Long et al. 2011, Mattern 2013, Long 2017). Nests are often found along small creeks and gullies that allow entry to and from the beach (Long 2017). Areas with high flax coverage as well

as flat beaches have been identified as unsuitable for nesting, though rarely a few pairs of penguins have been found nesting among flax (Long 2017). In Fiordland, penguins have been found nesting in caves and under rock overhangs, as well as in dugouts under trees or small ledges under rocky overhangs (Russ et al. 1991, McLean and Russ 1991).

5.4.3.2. Home range of Fiordland crested penguins: venture far from home

Fiordland crested penguins are philopatric, where both males and females return to the same site annually to breed (St. Clair et al. 1999). In South Westland, 175 adults were monitored from 1988 to 1995 and a return rate of 53-83% was recorded (mean of 71% for both sexes; St. Clair et al. 1999). Fiordland crested penguins leave their nest site annually to feed before they moult, which requires large amounts of energy (Warham 1974). During this pre-moulting period following breeding (breeding from July – November), penguins travel thousands of kilometres for days to months (Mattern et al. 2018). Mattern et al. (2018) found that penguins travelled from 66-77 days, making roundtrip journeys from 3505-6801 km long. These tagged penguins went to one of two places: (1) the Subtropical Front or (2) the Subantarctic Front. Penguins that did not breed left earlier and went to the Subtropical Front, where movement was driven by chlorophyll-a concentration (proxy for productivity; Mattern et al. 2018). In contrast, penguins that bred left later and went to the Subantarctic Front, where movement was driven by increased surface current, lower water depths and increased slope gradients (Mattern et al. 2018).

During the breeding season and chick rearing period, Fiordland crested penguins forage close to their nests. For instance, the Jackson Head colony penguins were found to forage 10-50 km from their nest, while penguins from Codfish Island (off Stewart Island) foraged close to shore or 20-30 km away in the Foveaux Strait (Mattern and Wilson 2018). By contrast, penguins in Fiordland foraged 1-4 km from their nest (with only one penguin ever recorded as leaving the fiords over 3 years), spending most of their time within Piopiotahi Marine Reserve (Mattern and Wilson 2018).

5.4.3.3. Connectivity of Fiordland crested penguins: unknown

The movement patterns and exchange between colonies of Fiordland crested penguins remains largely unknown (Fig. 5). As colonies return to the same nesting site

annually, it may be expected that there is limited gene flow between colonies. However, penguins may also travel between colonies, allowing genetic continuity. Connectivity of Fiordland crested penguins warrants further investigation, where genetic tools may shed light into movement patterns.

6. References

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Appendix 1. Glossary of genetic terms

Table A1. Glossary of genetic terms useful for interpreting genetic connectivity results presented in this report.

Term	Definition
Sequence	A **sequence** is the ordering of bases (i.e., four different nucleotides) that make up a DNA strand. A specific sequence corresponds to a gene, and sequences ultimately comprise the genetic makeup of an organism.
Allele	An **allele** is a variant form of a gene. A gene is coded by a certain DNA sequence, and variations (due to differences in bases) of that sequence are called alleles. Genetic differentiation can be determined by looking at the frequency of alleles in a population.
Allozyme	**Allozymes** are forms of enzyme. DNA sequences fold certain ways to form enzymes. Differences in allozymes between populations are determined by examining their structural differences (caused by differences in alleles). Because these enzymes code for proteins which are important for cell functioning, they are often highly conserved across organisms. This means that they often lack variability and can fail to detect genetic differences between populations. Furthermore, changes in an enzyme sequence can occur without changing the structure of an allozyme, which means that differences that exist can be missed.
Mitochondrial DNA	**Mitochondrial DNA** makes up genes that are found in the cellular mitochondria. Differences in the sequences of the mitochondrial DNA between populations means populations have diverged. Like allozymes, the mitochondrial DNA is often highly conserved and thus it can also lack variability needed to detect fine-scale genetic differences. Furthermore, mitochondrial DNA is inherited maternally, so only provides information about differences in the maternal lineages.
Microsatellites	**Microsatellites** are pieces of DNA that contain repeated sequences. When the DNA copies itself in the cell, it often makes mistakes when copying repeat sequences. As a result, microsatellites are highly variable between populations (unlike allozymes and mitochondrial DNA). Because of this, comparing differences in microsatellites has become a preferred method for population structure studies.
Single nucleotide polymorphism (SNP)	A **single nucleotide polymorphisms (SNPs)** is a difference of a single nucleotide in a sequence. By comparing differences between entire sequences belonging to individuals across different populations, genetic differentiation can be determined. SNPs provide large amounts of data and can be used to determined very fine scale differences between populations.
F_{ST}	The fixation index (**F_{ST}**) of a population is a measure of population differentiation based on variation in allele frequencies between populations, and is generally calculated using microsatellite or SNP data. **F_{ST}** ranges from 0 to 1, and ranges from no genetic differentiation and complete panmixis (0) to complete genetic differentiation and isolation (1). Interpreting **F_{ST}** values can be arbitrary and depend on the taxa being investigated. Hartl and Clark (1997) have suggested: - Little genetic differentiation: **F_{ST}** < 0.05 - Moderate genetic differentiation: 0.05 < **F_{ST}** < 0.15 - Great genetic differentiation: 0.15 < **F_{ST}** < 0.25 - Very great genetic differentiation: **F_{ST}** > 0.25

Divergence	Genetic **divergence** occurs when two populations accumulate genetic changes over time, and is measured by calculating the percent difference in nucleotides in sequences. It is generally calculated in phylogenetic studies that employ mitochondrial or nuclear DNA. Larger values indicate larger divergence and many discuss an appropriate 'threshold' value to constitute a species, because (like F_{ST} measures) divergence values can be arbitrary and depend on the taxa and question being investigated. Some suggest 3% difference is enough to cluster groups into separate operational taxonomic units (i.e., Sogin et al. 2006), though intraspecific diversity can also exceed 3% (Brown et al. 2015).

While a complete understanding of genetics is not required to interpret the trends presented in this report, it is noteworthy that the choice of a genetic marker in a study has implications for the results (e.g., Brown 1996). For instance, many earlier studies examining population structure used allozymes and failed to capture any differentiation between populations. However, more recent studies that employ microsatellite markers have found significant population structure for populations once thought to be well connected (i.e., for abalone, allozymes used in Dollimore 1997, Frusin 1982; versus microsatellites used in Will et al. 2011, Will et al. 2015). This is due to the fact that differences in allozyme frequencies between populations are determined by differences in structure of the allozyme; however, sequences that make up the allozyme may be different but result in no change to the allozyme structure. Therefore, some variability may be missed. Furthermore, allozymes (and mitochondrial DNA) are often highly conserved because they are important (and thus evolutionarily selected for), and thus few differences may exist between them across populations (Meyer 1994, Waugh 2007). Microsatellites and SNPs, by contrast, are generally non-conserved and detecting variation using these markers results in more detailed data. Therefore, it may be better to choose allozymes and/or mitochondrial DNA for looking at genetic differences between more distantly related organisms (i.e., different species), while microsatellites and SNPs may be better for determine variability within a species (i.e., different populations of a species).

Appendix 2. References used for literature review

Table S2. List of references consulted for literature review sorted by species, and indicating study location and information was extracted for the paper. Information was not extracted from papers highlighted in grey as they did not contain relevant information for this report, but these studies may be of interest in further reading on life-history traits and ecology for species. For the Hector's dolphin section, WC, EC, SC refer to west coast, east coast and south coast, respectively.

Reference	Location	Information extracted
Sea urchin (kina) – *Evechinus chloroticus*		
Andrew 1988	Leigh	Habitat
Andrew & Choat 1982	Leigh (CROP)	Grazer-predator-algae relationship
Andrew & MacDiarmid 1991	Leigh (CROP)	Habitat, home range; grazer-predator-algae relationship
Andrew & Stocker 1986	Leigh (CROP)	Habitat, home range
Barker 2001	Review	Review
Baker 2011	North and South Island (Northland, Hauraki Gulf, Piha, Mahai Peninsula, Wellington, Nelson, Kaikoura); Stewart Island	Genetic population structure
Barker 2013	Review	Review
Choat & Schiel 1982	North Island (CROP, Poor Knights)	Grazer-predator-algae relationship
Cole et al. 1990	Leigh (CROP)	Effects of marine reserves
Cole & Keuskamp 1998	Northeast NZ (CROP, Tawharanui, Poor Knights)	Habitat; effects of marine reserves
Delorme & Sewell 2013	Leigh, Hauraki Gulf	Habitat
Delorme & Sewell 2014	Leigh	Habitat
Dix TG 1969	Kaikoura	Larval information
Dix TG 1970a	Kaikoura, Kaiteriteri	Home range
Dix TG 1970b	Kaikoura, Kaiteriteri	Reproduction
Dix TG 1972b	Kaikoura, Kaiteriteri	Growth
Dix TG 1972a	Kaikoura, Kaiteriteri, Tasman Bay, Queen Charlotte Sound	Habitat
Duffy & Ahyong 2015	Kermadec Islands	Distribution
Glockner Fagetti & Phillips 2020	Wellington	Habitat
Keable & Reid 2015	Kermadec Islands	Distribution
Lamare 1998	Fiordland	Larval information
Lamare & Barker 1999	Fiordland	Larval information
Lamare & Barker 2001a	Tory Channel, Marlborough Sound; Doubtful Sound, Fiordland	Habitat
Lamare & Barker 2001b	Fiordland	Larval information
Lamare & Mladenov 2000	Fiordland	Home range

Lamare & Stewart 1998	Fiordland	Reproduction
McRae 1958	Wellington	Morphology
McShane et al. 1994a	Review	Review
McShane & Anderson 1997	Fiordland	Growth
McShane & Naylor 1991	Fiordland	Habitat
McShane et al. 1996	Wellington, Fiordland	Reproduction
McShane et al. 1993	Fiordland	
Miller & Abraham 2011	Report on fisheries	Report on fisheries
Mills et al. 2014	Field guide	Habitat
Mladenov et al. 1997	North and South Island (Leigh, Gisborne, Kaikoura, Dunedin, Fiordland); Steward Island	Genetic population structure
Nagel et al. 2015	North and South Island (Northland, Hauraki Gulf, Piha, Mahai Peninsula, Wellington, Nelson, Kaikoura); Stewart Island	Genetic population structure
Oldman et al. 2006	Hawke's Bay (Te Taonga O Ngati Kere, Te Angiangi Marine Reserve)	Larval dispersal
Perrin et al. 2003	Fiordland (14 fiords)	Genetic population structure
Phillips & Shima 2006	Wellington	Larval information
Shears & Babcock 2004	NZ Marine Reserves (CROP, Tawharanui, Long Bay-Okura, Te Whanganui A Hei, Poor Knights, Mayor Island-Tuhua, Te Tapuwae o Rongokako, Sugarloaf, Kapiti, Long Island, Tonga Island, Flea Bay-Pohatu, Te Awaatu Channel)	Effects of marine reserves
Spyksma 2016	Northeast NZ (CROP, Tawharanui)	Habitat
Spyksma et al. 2017	Northeast NZ (CROP, Tawharanui)	Habitat
Villouta et al. 2001	Fiordland	Habitat; grazer-predator-algae relationship
Walker 2007	Hauraki Gulf	Habitat
Walker 1982	Hauraki Gulf	Reproduction
Walker 1984	Hauraki Gulf (Goat Island)	Larval information
Wing 2009	Fiordland (14 fiords)	Habitat, discussion of source-sink dynamics
Wing 2011	Fiordland (14 fiords)	Habitat, discussion of source-sink dynamics
Wing et al. 2003	Fiordland	Habitat, discussion of source-sink dynamics
Spiny rock lobster – *Jasus edwardsii*		
Andrew & MacDiarmid 1991	Leigh (CROP)	Habitat
Annala 1981	Gisborne	Home range
Annala & Bycroft 1993	Fiordland	Home range

Booth 2001	Gisborne	Habitat
Booth 1997	Review	Home range and movement
Booth 1994	East coast NZ	Larval information
Booth 1989	Fiordland	Larval information
Booth & Ayers 2004	Gisborne	Habitat
Booth & Phillips 1994	Review	Habitat
Booth et al. 1990	North and South Island; Stewart Island	
Booth & Tarring 1986	Gisborne	Larval information
Bradford et al. 2014	Australia	Larval information
Bradstock et al. 1948	Wellington	Home range
Bradstock et al. 1953	Wellington	Home range
Chiswell & Booth 2008	North and South Island, Chatham Islands	Larval information in relation to source-sink dynamics
Chiswell & Booth 1999	East coast North Island (Wairarapa Eddy)	Larval information in relation to source-sink dynamics
Chiswell et al. 2003	New Zealand, Australia	Larval dispersal
Cobb 1997	Review	Review
Cole et al. 1990	Goat Island	Effects of marine reserves
Crear et al. 2000	Australia	
Davidson et al. 2002	Tonga Island Marine Reserve	Effects of marine reserves
Diaz Guisado et al. 2012	NZ Marine Reserves (Poor Knights Islands, CROP, Te Whanganui a Hei, Tahua, Te Tapuwae o Rongokako, Te Angiangi, Kapiti, Tonga Island, Horoirangi, Long Island, Flea Bay, Milford Sounds, The Gut)	Effects of marine reserves
Edmunds 1995	Tasmania	Habitat
Freeman 2008	Gisborne, Napier (Te Tapuwea o Rongokako, Te Angiangi)	Habitat, home range, effects of marine reserves
Freeman et al. 2012b	East Cape to Wairoa River (CRA3; Te Tapuwae o Rongokako)	Effects of marine reserves
Freeman et al. 2009	Te Tapuwea o Rongokako Marine Reserve	Habitat, home range, effects of marine reserves
Freeman et al 2012a	NZ Marine Reserves (Te Tapuwea o Rongokako, Te Angiangi, Long Island-Kokomohua, Kapiti Island, Tonga Island, CROP; Te Whanganui-a-Hei, Horoirangi)	Habitat, home range, effects of marine reserves
Freeman & MacDiarmid 2009	Te Tapuwea o Rongokako Marine Reserve	Effects of marine reserves

Haist et al. 2007	New Zealand	
Hayakawa et al. 1990	Castle Point	Larval information
Hesse et a. 2015	Leigh	Habitat
Hinojosa et al. 2017	Moeraki, Kaikoura, Castle Point, Napier, Gisborne; Stewart Island (plus Australia)	Larval information (settlement)
Hinojosa et al. 2014	Australia	Habitat
Ilyushkina 2018	North and South Island, Stewart Island, Chatham Islands	Genetic population structure
Jack & Wing 2010	Fiordland (Te Awaatu Channel, Kutu Parera, Taipari Roa)	Habitat, effects of marine reserves
Jack & Wing 2011	Fiordland	Habitat
Jack et al. 2009	Fiordland (Te Awaatu Channel, Kutu Parera, Taipari Roa)	Habitat, effects of marine reserves
Jeffs et al. 2005	Review	Larval information
Jeffs et al. 2002	Southeast coast North Island	Larval information
Jeffs and Holland 2000	Port of Gisborne	Larval information
Jeffs et al. 2001	Castle Point	Larval information
Jeffs et al. 1999	Castle Point	Larval information
Kelly 2001	Northeast NZ (CROP, Tawharanui)	Home range
Kelly 1999	Leigh (CROP)	Home range
Kelly & MacDiarmid 2003	Leigh (CROP)	Home range
Kelly et al. 1999	Leigh (CROP)	Habitat
Kelly et al. 2000	NZ Marine Reserves (CROP, Tawharanui, Tuhua Marine Reserve, Cathedral Cove Marine Reserve)	Effects of marine reserves
Kensler 1967	Review	Review
Langlois et al. 2006	Northeast NZ (CROP, Tawharanui)	Effects of marine reserves
Lucieer & Pederson 2008	Tasmania	Habitat
MacDiarmid 1994	Leigh (CROP)	Habitat
MacDiarmid 1991	Leigh (CROP)	Home range
MacDiarmid 1987	Leigh (CROP)	Habitat
MacDiarmid et al. 1991	Leigh (CROP)	Home range
McKoy 1983	Stewart Island, eastern Foveaux Strait	Home range
McKoy & Leachman 1982	Marlborough Sounds, D'Urville Island, Kapiti Island, Wellington	Larval dispersal
Mislan & Babcock 2008	Northeast NZ (CROP, Tawharanui)	Habitat
Morgan et al. 2013	Southeast South Island (and Australia)	Larval dispersal
O'Rorke et al. 2014	East coast New Zealand	

Ovenden et al. 1992	Gisborne, Moeraki (and 11 sites in Australia)	Genetic population structure
Rojas-Nazar et al. 2019	Central NZ (Taputeranga, Kapiti)	Effects of marine reserves
Smith et al. 1980	Gisborne, Wellington, Stewart Island (also Tasmania)	Genetic population structure
Street 1969	New Zealand	Report
Street 1971	Otago	Home range
Street 1973	Southland	Home range
Thomas 2012	North and South Island (Hauraki Gulf, Wellington, Kaikoura, Southwest Coast); Stewart Island; Chatham Islands (and southern Australia, Tasmania)	Genetic population structure
Thomas & Bell 2013	North and South Island (Hauraki Gulf, Wellington, Kaikoura, Southwest Coast); Stewart Island; Chatham Islands (and southern Australia, Tasmania)	Genetic population structure
Villacorta-Rath et al. 2016	Hauraki Gulf, Tonga Island, Chatham Islands, Stewart Island	
Abalone (pāua) – *Haliotis iris*		
Aguirre & McNaught 2013	Wellington	Habitat
Aguirre & McNaught 2012	Wellington	Habitat
Aguirre & McNaught 2011	Wellington	Habitat
Clarke 2001	Northern NZ	Growth
Coates et al. 2013	North American (Southern California)	Movement
Cornwall et al. 2009	Wellington	Habitat (feeding)
Dollimore 1977	North (3 sites) and South Island (2 sites)	Genetic population structure
Frusin 1982	Chatham Islands, Wellington, Kaikoura	Genetic population structure
Hooker & Creese 1995	Leigh (CROP)	Reproduction
Laferriere 2016	Central NZ Marine Reserves (Kapiti, Long Island, Tonga Island, Horoirangi, Taputeranga)	Habitat
McCowan 2013	Tory Channel, Marlborough Sounds	Genetic population structure
McShane 1995	Review	Review
McShane et al. 1994b	South Island (D'Urville, North Faces, Perano, Stair, Cascade, Waituna, Kahuragni, Catlins)	Habitat, juvenile vs. adult abundance
McShane & Naylor 1995a	D'Urville Island	Habitat
McShane & Naylor 1995b	Wellington	Habitat

McShane et al. 1994c	61 sites from North and South Island, Chatham Islands, Stewart Island	Habitat
Moss 1999	Wellington	Settlement information
Naylor et al. 2006	30 sites from mainly South Island and south of North Island	Demography
Oldman et al. 2006	Hawke's Bay (Te Taonga O Ngati Kere, Te Angiangi Marine Reserve)	Larval dispersal
Phillips & Shima 2006	Wellington Harbour	Habitat
Poore 1969	Kaikoura, Taylors Mistake	General ecology
Poore 1973	Kaikoura	Reproduction
Poore 1972b	Kaikoura, Taylors Mistake	Home range (feeding and movement)
Poore 1972c	Kaikoura	Growth
Poore 1972a	Kaikoura, Taylors Mistake	Home range
Roberts et al. 2004	Experiment	Habitat
Sainsbury 1982	Banks Peninsula	Population structure, growth, reproduction, and mortality
Schiel & Breen 1991	Stewart Island, Marlborough Sounds, Karori Rock	
Shepherd & Brown 1993	Southern Australia	
Smith 2008	Report	Connectivity
Smith & Conroy 1992	Wellington, Chatham Islands	Population structure
Smith & Mcveagh 2006	East Northland, Stewart Island, Taranaki/West Auckland, Chatham Islands	Genetic population structure
Stephens et al. 2006	East coast North Island	Larval dispersal
Will 2009	North (13 sites) and South (13 sites) Island; Stewart Island, Chatham Islands	Genetic population structure
Will et al. 2011	North (13 sites) and South (13 sites) Island; Stewart Island, Chatham Islands	Genetic population structure
Will et al. 2015	North (13 sites) and South (13 sites) Island; Stewart Island, Chatham Islands	Genetic population structure
Wilson & Schiel 1995	Dunedin	Reproduction
Wing et al. 2015	Stewart Island	Regime shift
Blue cod – *Parapercis colias*		
Beentjes & Carbines 2005	Banks Peninsula, Fiordland	Habitat
Beentjes & Carbines 2011	Otago	Habitat, abundance
Beentjes & Sutton 2017	Motunau	Abundance, size
Beentjes et al. 2019	Fouveaux Strait	Abundance, size
Beer 2011	Fiordland	Habitat, connectivity
Beer & Wing 2012	Fiordland	Habitat
Beer et al. 2013	Fiordland	Habitat

Beer et al. 2011	Fiordland	Connectivity
Brandt 2016	Queen Charlotte Sound, Pelorus Sound, D'Urville Island, Cook Strait	Reproduction, sex inversion
Brandt et al. 2017	Queen Charlotte Sound, Pelorus Sound, D'Urville Island, Cook Strait	Reproduction
Brough et al. 2018	Banks Peninsula	Effects of marine reserves
Carbines 2007	Stewart Island	Abundance, size
Carbines 2004	Marlborough Sounds, Foveaux Strait	Home range
Carbines & Cole 2009	Foveaux Strait	Habitat
Carbines & Beentjes 2009	Kaikoura, Motunau	Abundance, size
Carbines& Beentjes 2006	Kaikoura, Motunau	Abundance, size
Carbines & Beentjes 2003	Fiordland	Habitat, abundance, size
Carbines & McKenzie 2001	Southland	Home range, movement
Carbines & McKenzie 2004	Fiordland	Home range, movement
Cole et al. 1990	Goat Island	Effects of marine reserves
Cole et al. 2000	Marlborough Sounds	Home range
Cranfield et al. 2001	Foveaux Strait	Habitat
Davidson 2001	Marlborough Sounds (Long Island - Kokomohua Marine Reserve)	Effects of marine reserves
Davidson 2014	Marlborough Sounds (Long Island - Kokomohua Marine Reserve)	Effects of marine reserves
Davidson et al. 2013a	Abel Tasman (Tonga Island Marine Reserve)	Effects of marine reserves
Davidson et al. 2013b	Nelson (Horoirangi Marine Reserve)	Effects of marine reserves
Diaz-Guisado 2014	Wellington	Home range, effects of marine reserves
Diaz-Guisado et al. 2012	NZ Marine Reserves (CROP, Poor Knights, Kapiti, Tuhua, Te Whanganui A Hei, Te Awaatu Channel, Piopiotahi, Long Island-Kokomohua, Tonga Island, Te Angiangi, Pohatu, Te Tapuwae o Rongokako, Horoirangi)	Effects of marine reserves
Gebbie 2014	North and South Island (Northland, Bay of Plenty, D'Urville Island, Pelorus Sound, Queen Charlotte Sound, Wellington, Kaikoura, Akaroa, Fiordland, Otago, Puysegur Point, Golden Bay); Stewart Island, Chatham Islands	Genetic population structure
Graham 1953	Review	Review

Henderson 2009	Marlborough Sounds	
Jiang 2002	Karitane, Cape Saunders, Foveaux Strait	Habitat
Jiang & Carbines 2002	Foveaux Strait	Habitat
Leach & Davidson 2001	Historical records	Historical records
Leach et al. 1999	Chatham Islands, Mana Island	Historical records
Mace & Johnston 1983	Marlborough Sounds	Home range
Mutch 1983	New Zealand	Distribution
Rapson 1956	Review	Review
Roberston 1980	Otago	Larval dispersal
Rodgers & Wing 2008	Fiordland	Habitat, movement
Smith 2012	North and South Island (Northland, Bay of Plenty, D'Urville Island, Pelorus Sound, Queen Charlotte Sound, Wellington, Kaikoura, Akaroa, Fiordland, Otago, Puysegur Point, Golden Bay); Stewart Island, Chatham Islands	Genetic population structure
Warren et al. 1997	Southland	Habitat
Willis et al. 2000	Leigh (CROP)	
Wing et al. 2012	Fiordland	Habitat
Snapper - *Pagrus/Chrysophrys auratus*		
Adcock et al. 2000		
Bernal-Ramirez et al. 2003	Hauraki Gulf, East Coast, Hawkes Bay, Tasman Bay, West Coast, Doubtless Bay	Genetic population structure
Cole et al. 1990	Goat Island	Effects of marine reserves
Compton et al. 2012	Hauraki Gulf	Habitat
Crossland 1976	Hauraki Gulf, Northland	Home range
Denny et al. 2004	Poor Knights	Home range
Egli & Babock 2004	Leigh (CROP)	Home range
Fowler et al. 2017	Australia	Movement
Francis 1995	Kawau Bay	Habitat, home range
Francis & Pankhurst 1988	Northeast NZ	Sex inversion
Harasti et al. 2015	Australia	Home range, movement
Hartill et al. 2003	Northern NZ	Home range
Hauser et al. 2002	Tasman Bay, Hauraki Gulf	Genetic diversity
Langlois et al. 2006	Leigh (CROP)	Effects of marine reserves
Leach & Davidson 2001	Historical records	Historical records
Le Port et al. 2017	Leigh (CROP)	Larval dispersal
Le Port et al. 2014	Leigh (CROP)	Larval dispersal
Pankhurst 1991	New Zealand	Larval information
Parsons & Egli 2005	Review	Home range, movement

Parsons et al. 2003	Leigh (CROP)	Home range
Parsons et al. 2014b	Whanapoua Harbour, Coromandel Peninsula	Habitat
Parsons et al. 2015	Whangerai Harbour	Habitat
Parsons et al. 2011	Hauraki Gulf	Habitat, movement
Parsons et al. 2010	Leigh (CROP)	Home range
Parsons et al. 2014a	Review	Habitat, home range, movement, connectivity
Paul 1967	New Zealand (review)	Home range
Paul & Tarring 1980	East Cape region	Habitat
Paulin 1990	New Zealand	
Radford et al. 2012	New Zealand (experiment)	
Ross et al. 2007	Leigh (CROP)	Habitat
Smith et al. 1978	Wellington Harbour, Hauraki Gulf, Tasman Bay, Marlborough Sounds, North Taranaki, Kaipara-Manakau, Ninety Mile Beach, Bay of Islands, Bream Bay, Bay of Plenty, East Cape, Hawke Bay	Genetic population structure
Smith 1979	Hauraki Gulf	Genetic population structure
Sumpton et al. 2003	Australia	Movement
Thrush et al. 2002	Kawau Bay	Habitat
Usmar 2012	Mahurangi Harbour	Feeding
Walsh et al. 2011	SNA8	Size, age
Walsh et al. 2006	West coast North Island	Size, age
Walsh et al. 2012	SNA2	Size, age
Willis & Millar 2005	Leigh (CROP)	Effects of marine reserves
Willis et al. 2000	Leigh (CROP)	
Willis et al. 2001	Leigh (CROP)	Home range, effects of marine reserves
Willis et al. 2003	Northern NZ (CROP, Hahei, Tawharanui)	Home range, movement
Bladder kelp – *Macrocystis pyrifera*		
Alberto et al. 2010	North America (California)	Genetic population structure (in relation to habitat)
Brown et al. 1997	Otago	Habitat
Edgar 1987	Tasmania	Dispersal
Fernandez et al. 2015	Otago	Climate effects
Filbee-Dexter 2018	Review	Review
Fyfe et al. 1999	Otago	
Geange et al. 2014	Wellington	Habitat, climate effects (sediment)
Gerard & Kirkman 1984	Stewart Island	Dispersal
Harrold & Lisin 1989	North America	Dispersal

Hay 1990	New Zealand	Habitat, distribution
Hepburn et al. 2012	Otago	Relationship to epifauna
Hepburn et al. 2007	Stewart Island	Habitat
Hepburn & Hurd 2005	Otago	Relationship to epifauna
Hepburn et al. 2006	Otago	Relationship to epifauna
Hernández-Carmona et al. 2006	North America	Dispersal
Hobday 2000	North America	Dispersal
Hurd & Pilditch 2011	Otago	Habitat
Kain Jones 1982	Otago	Growth
Krumhansl et al. 2016	Review	Review
Leal et al. 2015	Otago	Climate effects (heavy metals)
Macaya &, Zuccarello 2010b	Kau Bay, Fiordland, Stewart Island, Antipodes Island, Campbell Island, Enderby Island	Genetic population structure, phylogenetics
Macaya &, Zuccarello 2010a	19 locations worldwide (Southern Ocean, North America, Chile)	Dispersal, genetic population structure, phylogenetics
Macaya Horta 2010	Picton, Wellington, Kaikoura, Timaru, Fiordland, Bluff, Nugget Point	Dispersal, genetic population structure, phylogenetics
Norton 1992	Review	Dispersal
Nyman et al. 1993	Otago (and North America – California)	Habitat
Nyman et al. 1990	Otago	Growth
Perez-Matus & Shima 2010	Wellington	Grazer-predator-algae relationship
Perissinotto & McQuaid 2010	Prince Edward Island	Habitat
Pirker 2002	Banks Peninsula, Marlborough Sounds (Tory Channel)	Habitat
Reed et al. 2009	North America (Southern California)	Productivity
Reed 1987	North America (Southern California)	Productivity
Schiel 1988	Review	Habitat, distribution
Schiel et al. 1995	Chatham Islands	Habitat
Schiel & Hickford 2001	Kaikoura, Banks Peninsula, Fiordland, Chatham Islands	Habitat
Stephens & Hepburn 2014	Otago, Stewart Island	Habitat
Vasquez et al. 1998	Chile	General ecology
Villegas et al. 2008	Chile	General ecology
New Zealand sea lion – *Phocarctos hookeri*		
Auge et al. 2011b	Auckland Islands	Habitat
Auge et al. 2011a	Otago	Home range
Auge et al. 2009	Auckland Islands	Home range
Baker et al. 2019	Report	Threats

Beentjes 2006	Otago	
Bradshaw et al. 1998	Otago	Feeding
Campbell et al. 2006	Review	Home range
Childerhouse & Gales 2000	Enderby Island	
Childerhouse & Gales 1998	New Zealand	Distribution
Childerhouse et al. 2015a	Campbell Island	Report
Childerhouse et al. 2015b	Auckland Islands	Report
Childerhouse et al. 2005	Auckland Islands	Distribution, abundance, growth
Chilvers 2012	Auckland Islands	Report
Chilvers 2009	Auckland Islands	Habitat, home range
Chilvers 2008	Enderby Island	Home range
Chilvers et al. 2011a	Auckland Islands	Habitat, home range
Chilvers & Wilkinson 2008	Auckland Islands	Home range
Chilvers et al. 2007	Auckland Islands	Demography
Chilvers et al. 2005a	Enderby Island	Home range
Chilvers et al. 2011b	Auckland Islands	Habitat, home range
Chilvers et al. 2005b	Enderby Island	Habitat
Collins et al. 2017	Otago, Stewart Island, Campbell Island, Auckland Islands	Genetic population structure
Collins et al. 2015	Historical records	Genetic assessment of population size overtime
Costa & Gales 2000	Enderby Island	Habitat
Crawley & Cameron 1972	Snares Island	Distribution
Crocker et al. 2011	Southern New Zealand	Feeding
DOC and MPI 2017	New Zealand	Threats
Gales & Fletcher 1999	Auckland Islands, Campbell Island	Abundance, distribution
Gales & Matting 1997	Enderby Island	Habitat
Geschke & Chilvers 2009	Enderby Island	
Lalas & Bradshaw 2003	Otago	Demography
Large et al. 2019	Auckland Islands	Threats
Lento et al. 2003	New Zealand	
Leung et al. 2012	Enderby Island	Home range
MacMillan et al. 2016	Otago, Catlins	Habitat
Maloney et al. 2009	Campbell Island	Home range
Middleton 2019	Auckland Islands	Threats
McConkey 1997	Otago	Demography
McConkey et al. 2002	Otago	Home range
McNally et al. 2001	Campbell Island	Home range
McNally 2001	Campbell Island, Snares Island, Catlins	Demography, movement
Meyer et al. 2015a	Auckland Islands	Demography
Meyer et al. 2015b	Auckland Islands	Demography, threats
Meyer et al. 2017	Auckland Islands	Threats

Meyer et al. 2018	Auckland Islands	Threats
Meyneir et al. 2009	Auckland Islands	Habitat
Meyneir et al. 2008	Auckland Islands	Habitat
Osborne 2011	Auckland Islands	Genetic population structure
Osborne et al. 2016	Auckland Islands	Genetic population structure
Osborne et al. 2013	Auckland Islands	
Rawlence et al. 2016	Chatham Islands	Distribution (historic records)
Roberts et al. 2018b	Auckland Islands, Snares Shelf	Prey distribution
Roberts et al. 2018a	Auckland Islands	Threats
Roberts 2019	Auckland Islands	Demography, threats
Robertson & Chilvers 2011	Review	Demography, threats
Thompson & Abraham 2009	Auckland Islands	Threats
Hector's & Māui dolphins - *Cephalorhynchus hectori hectori* and *C. hectori māui*		
Baker et al. 2019	Report	Threats
Baker et al. 2016	North Island	Abundance
Bejder 1997	Porpoise Bay	Habitat, home range
Bejder & Dawson 2001	Porpoise Bay	Habitat, home range
Brager et al. 2002	Banks Peninsula	Home range
Brager et al. 2003	EC, WC of South Island	Habitat
Brager & Schneider 1998	WC of South Island	Distribution, abundance
Brager 1998	EC, WC South Island	Home range
Burkhart & Slooten 2003	EC, WC, SC of South Island; WC of North Island	Demography
Cameron et al. 1999	Banks Peninsula	Demography
Cooke et al. 2019	North Island	Demography, threats
Dawson et al. 2006	Review	Review
Dawson 1991	New Zealand	
Dawson et al. 2013	EC of South Island	Habitat
Dawson & Slooten 1993	Banks Peninsula	Marine mammal protection
DOC Fisheries 2019	Report	Threats
Du Fresne 2010	North Island	Distribution
Gormley et al. 2005	Banks Peninsula	Abundance
Hamner 2014	EC, WC, SC of South Island; WC of North Island	Home range,
Hamner et al. 2017	Cloudy Bay	Abundance
Hamner et al. 2013	North Island (Clark's Beach, Opunake, Peka Peka Beach, Wellington Harbour)	Home range, movement
Hamner et al. 2012	EC, WC, SC of South Island; WC of North Island	Genetic population structure
MacKenzie & Clement 2016	WC of South Island	Abundance, distribution
Martien et al. 1999	New Zealand	Threats

Miller et al. 2012	WC, SC of South Island	Feeding
Nelson & Radford 2019	WC of North Island	Home range
Oremus et al. 2012	WC of North Island	Home range
Pichler 2002	Cloudy Bay, Kaikoura, Pegasus, Akaroa, Timaru, Jackson Bay, Greymouth, Westport, Te Waewae, North Island	Genetic population structure
Pichler 2001	Cloudy Bay, Kaikoura, Pegasus, Akaroa, Timaru, Jackson Bay, Greymouth, Westport, Te Waewae, North Island	Genetic population structure
Pichler & Baker 2000	Historical records, North Island, EC of South Island	Genetic diversity
Pichler et al. 1998	EC, WC of South Island, EC of North Island	Genetic population structure
Rayment et al. 2010	Banks Peninsula	Habitat, home range
Rayment et al. 2009	Bank Peninsula	Home range
Rayment 2008	Banks Peninsula, WC of South Island	Habitat, home range
Roberts et al. 2019	Report	Threats
Russell 1999	North Island	Home range
Slooten 1991	New Zealand	Growth, reproduction
Slooten 1990	Banks Peninsula	Demography, behaviour
Slooten 2013	Banks Peninsula	Effects of protection, habitat
Slooten et al. 2006a	WC of North Island	Abundance
Slooten & Dawson 2020	Review	Threats, demography
Slooten et al. 1992	Banks Peninsula	Demography
Slooten et al. 2006b	WC of South Island (Farewell Spit to Milford Sound)	Abundance
Slooten et al. 2005	North Island	Home range
Slooten et al. 1993	Banks Peninsula	Behaviour
Slooten & Lad 1991	New Zealand	Threats
Slooten et al. 2010	Banks Peninsula	Home range, effects of protection
Thorpe & Bates 1991	New Zealand	Echolocation
Little blue penguin – *Eudyptula minor* and *E. Novaehollandiae*		
Agnew et al. 2014	Oamaru	Reproduction
Allen et al. 2011	Banks Peninsula	White-flippered penguin
Banks et al. 2002	Northern New Zealand, Cook Strait, Chatham Island, Banks Peninsula, Otago, Australia	Genetic population structure, phylogenetics
Blyth et al. 2006	South Westland	Reproduction
Braidwood 2009	South Westland, Wanganui River Harihari, Buller	Reproduction
Braidwood et al. 2011	South Westland, Buller	Habitat

Bull 2000a	Matiu/Somes Island	Reproduction
Bull 2000b	Matiu/Somes Island	Habitat
Challies & Burleigh 2004	Banks Peninsula	White-flippered penguin, habitat
Chiaradia et al. 2007	Oamaru, Motuara Island	Habitat
Chilvers 2019	Motuara Island, Marlborough Sounds (compared to 3 other sites from previous papers - Stewart Island, Abel Tasman, Tauranga)	Home range
Chilvers 2017	Pearl Island, Abel Tasman (compared to Somes Island, Motuara Island, Banks Peninsula, Oamaru, Ackers Point, Leisure Island)	Home range
Clark et al. 2013	Otago, Banks Peninsula	Phylogenetics
Daniel et al. 2007	Australia	Behaviour
Dann 1994	Otago	Habitat
Flemming et al. 2013	Banks Peninsula, Oamaru, Stewart Island	Feeding
Fraser & Lalas 2004	Oamaru	Feeding
Grosser et al. 2015	North and South Islands (Northland, Bay of Plenty, Hawke's Bay, Wellington, Kaikoura, Banks Peninsula, Oamaru, Otago Peninsula, Katiki Point, Porpoise Bay, West Coast South Island, Golden Bay); Stewart Island, Chatham Islands (plus Australia)	Genetic population structure, phylogenetics
Grosser et al. 2016	North and South Islands (Northland, Bay of Plenty, Hawke's Bay, Wellington, Kaikoura, Banks Peninsula, Oamaru, Otago Peninsula, Katiki Point, Porpoise Bay, West Coast South Island, Golden Bay); Stewart Island, Chatham Islands (plus Australia)	Genetic population structure, phylogenetics
Hawke & Clark 2010	Motunau Island	
Heber et al. 2008	South Westland (between Westport and Punakaiki)	Habitat
Hocken 2000	Oamaru, Otago	Demography
Johannesen et al. 2002	Otago	Demography
Kinsky 1958	Matiu/Somes Island	Home range
Kinsky & Falla 1976	New Zealand	Morphological differentiation
Mattern 2001	Motuara Island, Oamaru	Home range
Mattern & Wilson 2018	Review	Review

Meredith & Sin 1988	Onaw Peninsula, Motunau Island, Maud Island, Poor Knights	Genetic population structure
Miyazaki & Waas 2002	Tiritiri Matangi Island, Hauraki Gulf	Reproduction
Numata et al. 2004	Motuara Island, Oamaru	Demography
Numata et al. 2000	Motuara Island, Oamaru	Home range
Perriman et al. 2000	Otago, Oamaru	Climate effects
Perriman & McKinlay 1995	Otago, Oamaru	Habitat
Peucker et al. 2009	North and South Island (Northland, Auckland, Wellington, Cook Strait, Kaikoura, Motunau Island, Pegasus Bay, Banks Peninsula, Oamaru, Otago, Catlins, Haast, West Coast, Marlborough Sounds, Golden Bay); Stewart Island, Codfish Island, Chatham Islands	Genetic population structure, phylogenetics
Poupart et al. 2017	Wellington, Motuara Island, Marlborough Sounds, Buller region	Habitat, home range
Richdale 2016	Review	Review
Van Heezik 1990	Codfish Island	Habitat
Van Rensburg 2010	Tiritiri Matangi Island, Hauraki Gulf	Reproduction, demography
Waas 1990	New Zealand	Habitat
Zhang et al. 2015	Matiu/Somes Island	Habitat
Yellow-eyed penguin - *Megadyptes antipodes*		
Boessenkool et al. 2008	South Island, Campbell Island, Auckland Island	Historic distribution, movement
Boessenkool et al. 2010	South Island, Campbell Island, Auckland Island	Genetic population structure
Boessenkool et al. 2009	South Island, Campbell Island, Auckland Island	Genetic population structure
Browne et al. 2011	Stewart Island, Codfish Island	Habitat
Chilvers et al. 2014	Stewart Island	Habitat, home range
Collins et al. 2014	New Zealand (historic records)	Historical records
Darby & Seddon 1990	Otago	Habitat
Ellenberg & Mattern 2012	Review	Habitat, home range, connectivity
Ellenberg et al. 2009	Otago	
Ellenberg et al. 2007	New Zealand	
French et al. 2019	Enderby Island	
Gill & Darby 1993	Otago	Demography
Hocken 2004	Otago	
King et al. 2012	Stewart Island	Reproduction

Lopes & Boessenkool 2010	South Island, Campbell Island, Auckland Island	Genetic population structure (immigration rate)
Massaro & Blair 2003	Stewart Island, Codfish Island	Abundance
Mattern 2007	Stewart Island, Codfish Island	Habitat
Mattern et al. 2007	Oamaru	Habitat, home range
Mattern et al. 2013	Otago	Habitat
Mattern et al. 2018	Review	Review
Moore 2001	South Island, Stewart Island	Habitat
Moore 1999	Otago, Catlins	Habitat, home range
Moore et al. 1995	Otago, Catlins	Habitat, home range
Muller et al. 2020	Auckland Islands	Abundance
Peacock et al. 2000	Otago	Climate effects
Richdale 1957	Review	Habitat, home range
Seddon & van Heezik 1990	Southern NZ	Habitat, home range
Setiawan et al. 2004	Otago	
Setiawan et al. 2005	Otago	Home range
Stein et al. 2017	Otago	
Triggs & Darby 1989	Otago Peninsula, Catlins, Enderby Island (Auckland Island), Campbell Island	Genetic population structure
Van Heezik 1990	Codfish Island	Habitat
Van Heezik 1989	Otago	Habitat
Young 2009	Enderby Island	
Fiordland crested penguin - *Eudyptes pachyrhynchus*		
Cole et al. 2019	New Zealand (current versus historic records)	Distribution
Ellenberg et al. 2015	South Westland and Fiordland	
Long 2017	South Westland (Cascade River to Martins Bay)	Habitat
Long et al. 2010	South Westland	Surveys
Long et al. 2011	Hokitika	Surveys
Mattern 2017	Milford Sound, Piopiotahi	Habitat
Mattern et al. 2018	Gore River, South Westland	Home range
Mattern & Wilson 2018	Review	Review
McLean et al. 2000	Taumaka, Open Bay Islands	
McLean & Russ 1991	Fiordland	Habitat
Otley et al. 2018	South Westland and Fiordland	Demography
Otley et al. 2016	South Westland (Jackson Head and Monro Beach)	Home range
Phillipson 1991	Taumaka Island	Reproduction
Russ et al. 1992	Fiordland	Habitat
St. Clair 1992	Taumaka Island	Reproduction
St. Clair et al. 1999	Open Bay Island	Home range
Studholme 1994	Taumaka Island	
Van Heezik 1990	Codfish Island	Habitat

Warham 1974	South Westland	Habitat, home range
Young et al. 2015	Otago	Dispersal, movement