Rare, tropical and subtropical fishes in Aotearoa New Zealand: monitoring occurrences and predicting impacts

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Abstract

Species redistribution due to climate change is occurring four times faster in the ocean than on land. As global temperatures rise, equatorial regions are becoming increasingly inhospitable, driving tropical and subtropical species to track favourable conditions poleward or at deeper depths, to keep within their thermal tolerances. The expectation is that tropical regions will become more inhospitable and temperate regions will become increasingly tropicalised as the ability for warmer water species to persist increases. Tracking range-shifts in the ocean is a difficult, time consuming and often expensive task, as many marine species are highly mobile, cryptic and wide ranging. As such, our understanding of climate induced distributional changes and the threats they pose is far from complete. Nevertheless, the increase of tropical and subtropical species in temperate regions has the potential to alter biodiversity, displace endemic species and cause significant shifts in ecosystem function. While Aotearoa New Zealand has remained relatively unimpacted by climate change to date, the frequency of tropical and subtropical arrivals will continue to increase as global climate change forces species to seek refuge in temperate regions. With a high level of endemism and a relatively depauperate ecosystem, the establishment of range-extending species in Aotearoa New Zealand has the potential to have negative impacts. This thesis contributes to the understanding of tropical, subtropical and rare marine fishes in Aotearoa New Zealand by highlighting the potential for citizen science as a means of monitoring occurrences, and through examining the morphology and ecological niches of arriving fishes to predict their potential impacts on Aotearoa New Zealand's native and resident species. First, through structured questionnaires, I demonstrate that citizen scientists can provide reliable (83.33% of questionnaires) observations of tropical and subtropical fishes without the need for photographic equipment or post-hoc validation, thus providing more equitable opportunities for citizens to contribute to marine science and monitoring initiatives. Second, through analysing the broadscale trophic niche, habitat preference and morphology of marine fishes I reveal there is considerable niche overlap between arriving marine fishes and native resident marine fishes (74.37%) suggesting there is high potential for competition should arriving species establish and increase in abundance in Aotearoa New Zealand. Overall, my results highlight the need for proactive monitoring of arriving fishes, to limit the potential impacts on native and resident species and our marine ecosystems.

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Forever present in everything I do, even though you are no longer by my side.

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Chapter One: General introduction

This thesis contributes to the understanding of tropical, subtropical and rare marine fishes in Aotearoa New Zealand (NZ). The aims of this thesis were to examine: how tropical, subtropical and rare species can be monitored through citizen-science activities, and how novel tropical, subtropical and rare marine fishes might assimilate into NZ's marine fish fauna. Chapter One presents a comprehensive literature review on climate-induced redistribution of marine species, the monitoring of species occurrences using citizen-science, how to predict potential impacts of novel species, and an overview of climate change and species distribution in NZ. A summary of subsequent chapters is outlined at the end of Chapter One.

1.1 Climate-induced redistribution of marine species

Climate change, associated with human-mediated anthropogenic activities is well documented across terrestrial (Parmesan & Yohe, 2003), marine (Poloczanska et al., 2016) and freshwater environments worldwide (Parmesan, 2006; Rosenzweig et al., 2008). On average, temperature has increased 0.6°C, globally in the last 100 years (NOAA, 2021) with 2021 temperatures averaging 1.11°C above pre-industrial (1850-1900) temperatures (WMO, 2021). The world's oceans have absorbed upward of 33% of CO2 emissions and 90% of excess heat from greenhouse gases and human activities, leading to a ~1°C increase in sea surface temperature (SST) globally (IPCC, 2013). Acting as the planets largest carbon sink and carrying much of the burden of climate change, the ocean and its inhabitants are one of the most vulnerable ecosystems on earth.

Owing to its heat capacity, the ocean is warming three times slower than terrestrial environments (Parmesan & Yohe, 2003), however the rate of change varies region to region. For example, the Baltic Sea is warming three times faster than the global average (at 0.99°C per decade), while the Indian Ocean is warming at 0.11°C per decade, 0.4°C – 0.6°C faster than the Atlantic and Pacific oceans, respectively (Hoegh-Guldburg, 2014). The varying rate and intensity of regional SST warming, particularly in high latitude regions, is often driven by climactic variability (e.g., El Niño-Southern Oscillation; Hoegh-Guldberg, 2014), localised weather patterns (e.g., storms and heatwaves; Wernberg et al., 2012) and large-scale current systems (e.g., Western boundary currents; Yang et al., 2016), which are altering in response to climate change (Hoegh-Guldberg, 2014; NOAA, 2021). For example, we have seen shifts in isotherm positions, such as the 217.5km shift per decade of the 10°C isotherm in the North Sea (Beaugrand et al., 2009) and the 187km shift of the 27°C isotherm in South Africa over 19 years (Lloyd et al., 2012). Similarly, changes to wind patterns forces the southern extension and intensification of large-scale ocean currents, which creates increased heat redistribution from lower latitudes to higher latitudes (Wu et al., 2012; Yang et al., 2016). For example, the strengthening and southern extension of the East Australian Current into Tasmania (Ridgway, 2007; Wu et al., 2012) and the Agulhas Current in South Africa (Lloyd et al., 2012). In general, continuous broad-scale warming is occurring in lower, tropical latitudes with variable warming in higher, temperate latitudes (NOAA, 2021).

The physical and chemical changes occurring in the ocean in response to climate change significantly impact species diversity and distributions (Pecl et al., 2017; Poloczanska et al., 2016). Many marine species are ectotherms with small thermal tolerances and are therefore sensitive to changes in their environment, especially an increase in temperature (Pinsky et al., 2019; Sunday et al., 2012). As an environment become unfavourable, species may respond in one of three ways: they can adapt in-situ; shift to more favourable conditions; or undergo localised extinctions (Bates et al., 2014; Maggini et al., 2011). With ongoing, broad-scale warming occurring in equatorial regions, the expectation is that species at the leading edge of their distribution will track favourable environmental conditions poleward or to increased depths (Parmesan et al., 1999; Parmesan & Yohe, 2003; Poloczanska et al., 2016) and those at the trailing edges of distributions will undergo range contraction, with possible localised extinctions (Bates et al., 2014; Pecl et al., 2017).

Climate induced range shifts are occurring four times faster in the marine environment than on land (Burrows et al., 2011; Poloczanska et al., 2016; Sorte et al., 2010). This is partially due to fewer dispersal barriers in the ocean, compared to terrestrial environments (Rapoport, 1994; Sunday et al., 2012) and also in part to species-specific traits, which may hinder or promote the rate and extent of a range shift into novel systems (Burrows et al., 2011; Poloczanska et al., 2016; Sunday et al., 2012). Many marine species are highly mobile, have long larval phases which are often planktonic and have high fecundity, increasing the potential for dispersal and establishment (Block et al., 2005; Pinsky et al., 2020; Pinsky et al., 2013). For these reasons, pelagic and mobile species such as phytoplankton, zooplankton and teleost fishes are known to have the fastest leading-edge range expansions (Poloczanska et al., 2016). Additionally, while many benthic marine fishes and invertebrates have relatively sessile lifestyles, they often have a dispersive planktonic phase as larvae, allowing distribution into novel habitats, during this phase (Leis et al., 2011; Shanks, 2009).

Large offshore currents are central to the distribution of marine species and penetrance of warmer waters into higher latitudes (Ridgway, 2007; Yang et al., 2016). Marine organisms, particularly in their larval life-stage, can be advected ~100-1000km in large-scale ocean currents, such as Western Boundary Currents (WBC; e.g., Booth et al., 2007; Feary et al., 2014; Figueira et al., 2009). WBC's are a series of unidirectional, subtropical gyres that move warm, tropical water into higher latitudes (Sunday et al., 2012; Yang et al., 2016). Regions with continuous tropical-temperate coastlines are strongly influenced by WBCs (e.g., north-eastern Australia, south-eastern Japan, northern Brazil, Chile, and south-east Africa) with record warming and novel species arrivals (Hobday & Pecl, 2013; Lloyd et al., 2012; Nakamura et al., 2013; Vergés et al., 2014). For example, the strengthening and poleward extension of the East Australian Current (EAC) has resulted in record temperature increases and range extensions of over 45 reef fishes (e.g., Porae *Nemadactylus douglasii* and Onespot demoiselle *Chromis hypsilepis*; Last et al., 2011) and 16 invertebrates (Pitt et al., 2010) including the barren forming Long-spined sea urchin *Centrostephanus rodgersii* (Ling et al., 2009) and the Gloomy octopus *tetricus* (Ramos et al., 2018).

Not all out-of-range individuals will have the ability to persist long term in a new community outside of their normal range (Feary et al., 2014; Poloczanska et al., 2016). Successful settlement, recruitment and persistence is constrained by the recipient ecosystems climate, species introduction effort, and species-specific traits (Cheung et al., 2013; Munday, 2008). Generalist species with broader fundamental niches are more successful in range-extension scenarios, due to their high tolerance to varied temperatures and habitats, broad-range diet and high phenotypic plasticity (Bates et al., 2014; Clavel et al., 2010; Gaston & Spicer, 2001; Weir & Salice, 2011). Conversely, specialist or endemic species often have small fundamental niches, are intolerant to environmental fluctuations and reliant on specialised habitat and diet sources (Clavel et al., 2010; Feary et al., 2014; Munday, 2008; Nakamura et al., 2013). For example, a lack of coral in temperate ecosystems is a limiting factor for many tropical fishes reliant on coral for settlement processes and diet (Feary et al., 2014; Holbrook & Schmitt, 2002; Pratchett, 2005). However, this is likely to change, as many subtropical and temperate systems continue to warm and 'tropicalise' under climate-change, affecting the persistence rates of many rare or specialist out-of-range species (Bates et al., 2014; Monaco et al., 2020).

Climate induced range redistributions has been extensively documented across numerous marine species including plants (Arrontes, 2002), invertebrates (Pitt et al., 2010) and fish (Last et al., 2011). For example, Mangrove forests in Louisiana, Texas and Florida have undergone range-expansion as a result of warmer winter temperatures (Cavanaugh et al., 2014; Osland et al., 2022) and in eastern Australia in association with La Niña and a marine heatwave event, habitat-forming seaweed *Scytothalia dorycarpa* lost ~100km of range, causing a significant shift in community structure (Wernberg et al., 2012). In Japan, increased temperatures have led to the poleward range shift of sea urchins *Heliocidaris crassispina* and *Hemicentrotus* (Feng et al., 2019; Agatsuma & Hoshikawa, 2007) and four coral species *Acropora hyacinthus*, *Acropora muricata*, *Acropora solitaryensis*, *Pavona decussata* (Yamano et al., 2011). Similarly, in eastern Australia, the barren forming urchin *Centrostephanus rodgersii* (Ling et al., 2009) and commercially important fish species have experienced range-shifts due to increased temperatures and the poleward extension of the East Australian Current (e.g., *Seriola lalandi* and *Coryphaena hippurus*; Champion et al., 2021; Champion et al., 2018). In Aotearoa New Zealand, five subtropical fish species *Acanthurus dussumieri, Amphichaetodon howensis, Abudefduf vaigiensis, Chrysiptera notialis* and *Coryphaena hippurus* have undergone varying levels of climate-induced range-extensions (Middleton et al., 2021) and in the Mediterranean

Sea, the range-expansion of tropical rabbitfish is owing to warmer temperatures and the opening of the Suez Canal (Vergés et al., 2014). Redistribution, including poleward range-extension will continue to increase in frequency as species respond to global climate change (Melbourne-Thomas et al., 2022; Poloczanska et al., 2016; Wernberg et al., 2012).

Climate change will result in continued species losses, forced redistributions and modifications to ecosystem structure and function (Parmesan & Yohe, 2003; Perry et al., 2005). The rate and intensity of climate-induced range-shifts, highlights the need for monitoring species undergoing range-extensions in an effort to mitigate the impact. Understanding how novel species might assimilate into the resident community is a crucial step to inform their likely impacts on biodiversity and ecosystem function (Albouy et al., 2011; Carscallen et al., 2012; Violle et al., 2011) which can be done through the monitoring out-of-range species and analysing their ecological niche in the novel habitat.

1.2 Monitoring novel marine species occurrences using citizen science

Early detection of out-of-range or novel species into a new environment plays an important role in assessing and minimising potential impacts (Bates et al., 2014; Weir & Salice, 2011). Early detection can prove tricky during the initial stages of arrival and establishment, as novel species can be considered similar to searching for a ‘needle in a haystack’, considering the rarity and patchy distribution of such species in a spatially large environment (Bates et al., 2014; Feary et al., 2014; McCarthy et al., 2013). Additionally, the marine environment itself, poses numerous challenges to scientists and observers. Surveying across such a large spatial and temporal scale in search of often cryptic, wide ranging and highly mobile species is time consuming, resource heavy, expensive and largely dependent on weather (Block et al., 2005; Delaney et al., 2007; Hubert et al., 2012). Large areas of the marine realm still remain severely under-surveyed due to these inherent challenges (Bates et al., 2014; Hortal et al., 2015) and therefore, scientists and environmental managers must often rely on diverse sources of information to bridge the knowledge gaps (Delaney et al., 2007; Robinson et al., 2015). This information may be in the form of online data repositories (e.g., FishBase [https://www.fishbase.se]; iNaturalist [https://www.inaturalist.org/]; Howarth et al., 2021), fisheries information (e.g., Robinson et al., 2015), museum collections (e.g., Chapter Three; Cheung et al., 2013; Perry et al., 2005) and records collected by citizens (e.g., Range Extension Database and Mapping Project [Redmap]; WhatsThatFishNZ; Middleton et al., 2021; Pecl et al., 2019)

Citizen science – the participation of the general public (i.e., non-scientists) contributing to the collection of data, planning, development and execution of scientific research (Eitzel et al., 2017) – has become a widely recognised way to support scientific research (Devictor et al., 2010; Lenanton et al., 2017; Soroye et al., 2018). While the concept is not new (i.e., the Christmas Bird Count is the most longstanding citizen science initiative starting in 1900; National Audubon Society, 2002) it has gained in popularity in recent years, with more scientists and stakeholders recognising its potential to contribute to environmental management and policy outcomes (Delaney et al., 2007; Madin et al., 2012; Soroye et al., 2018). The level of public participation and type of data collected is dependent on the project's goals. Most commonly, citizens involved in scientific research function as primary data collectors, by filling the labour focused goals of 'many hands make light work' (McKinley et al., 2017; Sandahl & Tøttrup, 2020). Collaborative or co-created projects are less common but involve citizens contributing beyond data collection, including involvement in the design and execution of the project (Sandahl & Tøttrup, 2020; Shirk et al., 2012). Often, collaborative projects produce greater long-term outcomes and conservation management (Bonney et al., 2009; Shirk et al., 2012).

Citizen science can be underutilised due to the variable quality and biases associated with it (Bird et al., 2014; Isaac et al., 2014). This is often unavoidable due to spatial and temporal biases (Boakes et al., 2010; Isaac & Pocock, 2015) including uneven sampling effort (Isaac et al., 2014) and variation among participants (Hochachka et al., 2012). For example, habitats that are easily accessible such as estuaries, intertidal habitats and shallow reefs tend to be over-represented in marine citizen science studies (Theobald et al., 2015; Thiel et al., 2014). In comparison, more demanding environments such as deep waters and offshore reefs are often under-represented, thus creating a spatially unequal sampling effort (Thiel et al., 2014). Additionally, personal interests of the participants generally drive participation rates (Martin et al., 2016; Shirk et al., 2012). For instance, species that are charismatic, commercially important or endangered are often the focus of many citizen science initiatives, as these species often generate the most interest from volunteers (Devictor et al., 2010; Isaac & Pocock, 2015; McKinley et al., 2017), for example ray-finned fishes and marine megafauna (Thiel et al., 2014). Furthermore, variables such as age, educational background and training can influence variation in detectability and data collection accuracy among participants, affecting data quality (Delaney et al., 2007; Thiel et al., 2014; Tiago et al., 2017).

Maximising the value of citizen science therefore requires striking a balance between data quality and data quantity (Hochachka et al., 2012). For example, some projects encourage non-targeted, unrestricted contributions, which allow for a high level of participation without the need for prior training (e.g., iNaturalist). While this type of data collection may be the most successful at gaining vast amounts of data, it can often lack quality control or methods to validate the contribution, which must be accounted for during analyses (Delaney et al., 2007; Pocock et al., 2017). Alternatively, volunteers may require training prior to participation in the project (e.g., Reef Life Survey). While this may reduce the number of participants involved, it will increase accuracy and allow for quality control (Edgar & Stuart-Smith, 2014). Furthermore, if a project sets a priori hypotheses and creates robust validation methods or post-hoc analyses, bias and variations in the data can be more easily be accounted for, increasing the quality of the data (e.g., Middleton et al., 2021; Robinson et al., 2015; Wotton & Hewitt, 2004)

One of the most common quality control measures in citizen science projects is to require an image to validate the species identity for a sighting. For example, global web-based applications such as iNaturalist (https://www.inaturalist.org/), BioDiversity4All (https://www.biodiversity4all.org/) and iSpot (https://www.ispotnature.org/) solicit images from users which are then validated using taxonomic voting systems (Roberts et al., 2022). Similarly, the Australian based Range Extension Database and Mapping Project (RedMap) and NZ based WhatsThatFishNZ (WTFNZ) both engage with citizens to collect images of rare or out-of-range fishes associated with climate mediated range-extension (Middleton et al., *in press*; Pecl et al., 2019). The images submitted by citizen scientists are cross validated by taxonomic experts to ensure correct species identification (Middleton et al., *in press*; Pecl et al., 2019). While these methods enable a high level of accuracy, it does limit participation to citizens who have access to photography or videography equipment.

Alternatively, projects may standardize variation by using surveys, questionnaires, or checklists, often paired with sampling protocols to increase confidence in the species identification (Sullivan et al., 2017). For instance, the long-standing marine survey project Reef Environmental Education Foundation (REEF) surveys species abundance and diversity using recreational snorkelers and divers (https://www.reef.org/). REEF firstly ranks a participant as 'expert' or 'novice', based on their prior experience and performance on fish identification tests before standardising variation by having all participants use the Roving Diver Technique (RDT) while conducting the survey (Pattengill-Semmens & Semmens, 2003; Schmitt, 1996). Similarly, online databases such as eBird (which provide data on bird distribution and abundance) use checklists that require a two-part verification system enabling quality control by flagging any unusual observations for expert review (https://ebird.org/home; Sullivan et al., 2009). Survey designs such as those used by REEF and eBird allow for participation without the need for photography or videography equipment and also have the advantage of providing presence-absence data, estimating sampling effort and the ability to collect contextual data such as sex, life-stage, behavioural and environmental data (Hermoso et al., 2015; McClintock, 2010; Sullivan et al., 2014).

Citizen science projects can be a good fit when monitoring novel species introductions and climate induced range-shifts (Delaney et al., 2007; Devictor et al., 2010; Roberts et al., 2022). Increasing the observational power of species that are inherently rare and unevenly distributed, is a proven and efficient monitoring option (e.g., Edgar & Stuart-Smith, 2014; Pattengill-Semmens & Semmens, 2003; Pecl et al., 2017). Their distinct morphological features and/or bright colouring, makes tropical and subtropical fishes highly observable and therefore ideal focal species. For example projects such as RedMap and WhatsThatFishNZ have demonstrated that having many eyes in the water can increase confirmed sightings of marine species shifting in response to warming oceans. RedMap was established 2012 and has collected over 2,300 confirmed sightings of marine species shifting poleward in response to climate change across Australia (Pecl et al., 2019) and similarly, WhatsThatFishNZ was founded in 2018 and now has an extensive database of over 2,000 sightings of rare, tropical, subtropical and range-shifting fishes in NZ’s waters (Middleton et al., *in press*). Additionally, by tracking occurrences of these species in new systems these projects, and projects with similar methods, have the potential to monitor environmental changes and ecological impacts due to these species redistributions (e.g., Edgar & Stuart-Smith, 2014; Pattengill-Semmens & Semmens, 2003; Sullivan et al., 2009).

Citizen based data acquisition provides real-time data that can fill existing information gaps and expedite the collection of large-scale, high-resolution data, which is often a challenge with traditional scientific techniques (Delaney et al., 2007; McKinley et al., 2017). The observational power of citizen science provides scientists with increased monitoring across large spatiotemporal scales in both terrestrial (Sullivan et al., 2009; Theobald et al., 2015) and marine settings (Malpica-Cruz et al., 2016; Pattengill-Semmens & Semmens, 2003; Pecl et al., 2019) and has contributed to detecting new species (Liggins et al., 2020), monitoring biodiversity (Theobald et al., 2015), tracking species distributions and range-extents (Middleton et al., 2021), and invasive species monitoring (Delaney et al., 2007; Malpica-Cruz et al., 2016). The happy flipside to this involvement, is the engagement with the public on scientific issues. Connecting local citizens and communities to scientific initiatives, often creates enhanced social licence, stewardship, and invested interest in scientific outcomes as well as creating opportunity for education on environmental issues (Sandahl & Tøttrup, 2020; Thiel et al., 2014).

In Aotearoa New Zealand, marine citizen science project WhatsThatFishNZ is the only programme actively monitoring the distribution and abundance of rare, tropical and subtropical fishes (https://www.facebook.com/WhatsThatFishNZ/). WhatsThatFishNZ solicits images from ocean-going citizens (e.g., scuba divers, spear fishers, fishers and boaters) which are then taxonomically verified by the WhatsThatFishNZ team. WhatsThatFishNZ has collected over 2000 records of tropical, subtropical and rare species in NZ since the programme was established, as well as recorded 17 new fish species to mainland NZ (Middleton et al., *in press*). Additionally, WhatsThatFishNZ has established the first baseline data for the spatiotemporal distribution of tropical, subtropical and rare fishes in NZ and identified several fish species that have potentially extended their range in NZ, effectively highlighting the utility of citizen science in biodiversity monitoring (Middleton et al., 2021; Middleton et al., *in press*). Understanding which of these species have the potential to impact resident species, or to change ecosystem functioning, is an important next step in predicting the impact of climate change on NZ's marine biodiversity.

1.3 Predicting potential impacts of novel species on recipient ecosystems

An ecological niche can be broadly defined as the way in which an organism fits into a community or environment (Chesson, 2000; Futuyma & Moreno, 1988). It encompasses both biotic and abiotic factors that influence a species survival and success in a given habitat, such as temperature, nutrient availability, competition and predation while also determining the interactions and impact the species has on the community (Futuyma & Moreno, 1988). Ecological niches allow for the coexistence of different species by limiting competition for resources such as space and food items (Chesson, 2000).

In general, species with smaller niches are considered specialist species and those with broader niches are considered generalist species (Clavel et al., 2010; Munday, 2008). Typically, endemic species have smaller niches and are often specialists, whereas wide-ranging generalists (such as successful range-extenders) typically have broader niches (Bates et al., 2014; Gaston & Spicer, 2001; Weir & Salice, 2011). If two species occupy the same niche space, forcing direct competition for habitat space and/or food items, one species will likely outperform the other species forcing the 'losing' species to adapt to a new niche space or, if its unable to adapt, become locally extinct (Clavel et al., 2010). By investigating a species ecological niche, scientists can explain fundamental ecological processes including species interactions, inter- and intra- specific competition, biodiversity and invasion success (Azzurro et al., 2014; Clavel et al., 2010; Dominguez Almela et al., 2021; Monaco et al., 2020; Smith et al., 2016).

Within a species ecological niche, we can further investigate spatial niche (i.e., the habitat it occupies), trophic niche (i.e., its position in the food web) and species morphology (as an indirect indication of how a species interacts with species and its environment; Azzurro et al., 2014). Trophic and spatial niche can be used to describe a species position in the food web (Carscallen et al., 2012) and competition for resources, space and diet items (Adamczuk, 2022; Albouy et al., 2011). Similarly, morphology indirectly dictates the position of a species in a given environment, therefore acting as a proxy for niche partitioning, species interactions and inter- and intra- specific competition (Azzurro et al., 2014; Smith et al., 2016). Overall, a species ecological niche and morphology provides scientists with quantifiable and ecologically meaningful features to predict likely environmental outcomes (Harvey et al., 2022).

Darwin's naturalisation hypothesis (1859) predicts that the colonisation of a new habitat is less likely, when the invading species are taxonomically similar to the resident species in the habitat (Van Kleunen et al., 2010; Violle et al., 2011). There are a number of reasons with this theory has held true for well over a century. For instance, species that are taxonomically similar, often exhibit niche overlap leading to increased intraspecific competition, thus reducing the opportunity for a species to increase in abundance (MacArthur & Levins, 1967). Likewise, novel species that differ taxonomically and/or functionally have greater opportunity for colonisation success if they can occupy an unexploited niche, thereby avoiding competition with resident taxa (Olden et al., 2006; Shea & Chesson, 2002). Ultimately, the expectation is that novel species will have a higher likelihood of persistence in a novel community if its traits are suited for the environmental conditions of the recipient habitat, but its traits are not similar to resident taxa within the community (Azzurro et al., 2014; Olden et al., 2006; Van Kleunen et al., 2010).

Ecosystems with high biodiversity are more resistant to novel species arrivals and climate induced changes than ecosystems with lower biodiversity, as greater species diversity and saturated niche spaces decreases the chance for a novel species to establish in a new ecosystem (Van Kleunen et al., 2010; Violle et al., 2011). As climate change drives species redistribution, novel species will be able to more easily colonise regions with niche space that is not already filled by resident species, and can consequently alter ecosystem functioning (Kingsbury et al., 2019). Whereas, when arriving species overlap in niche space with resident species, there is the potential for competition with resident species for niche space and altering ecosystem function (Adamczuk, 2022; Albouy et al., 2011).

The impacts of novel range-extending species on recipient ecosystems will vary depending on the species ecological role. Overall, generalist species (i.e., omnivores, habitat generalists, high tolerance to environmental fluctuations; (Daehler, 2001; Monaco et al., 2020) are more successful in the colonisation stage of range extension, giving them competitive dominance over specialist native or resident taxa (Clavel et al., 2010; Gilchrist, 1995). Therefore, if a newly established species occupies the same habitat and/or trophic niche as resident and native species, we will likely see novel species interactions, competition for resources and niche space, and in extreme cases, displacement or localised extinction of native taxa (Albins & Hixon, 2011; Azzurro et al., 2014; Smith et al., 2016). Alternatively, the newly established species may differentiate into a novel habitat and/or trophic niche space, creating little-to-no impact on resident taxa (Schoener, 1974; Kingsbury et al., 2019).

Regardless of competition with resident taxa, out-of-range species will likely impact ecosystem functioning through modifying species assemblages, food webs, and potentially causing whole ecosystem shifts (Holbrook, Schmitt, & Stephens, 1997; Ling et al., 2009; Madin et al., 2012). For example, the introduction of tropical generalist fishes is linked to a decline in native species through extreme predation and competition causing changes in biodiversity (Albins & Hixon, 2008; Albins & Hixon, 2011; Edelist et al., 2013). In extreme cases, increases in the abundance of tropical herbivores and omnivores has caused whole ecosystem shifts - from functional macroalgae ecosystems to barrens. For example, in the Mediterranean, the range-expansion of tropical herbivorous fishes lead to phase shifts from macroalgal forests to barrens (Vergés, Steinberg, et al., 2014; Vergés, Tomas, et al., 2014) and in Japan, the expansion of tropical corals and herbivorous fishes caused a novel community shift to coral dominated reefs (Kumagai et al., 2018; Yamano et al., 2011). Habitat forming species such as macroalgae, underpin ecosystem function in temperate systems and are particularly vulnerable to predation from generalist species and increasing temperatures (Ling & Johnson, 2009; Wernberg et al., 2012). As incidences of range-extension increase, determining the mechanisms by which range-extending species assimilate into a recipient ecosystem will help to inform likely outcomes on community and ecosystem function.

Loss of biodiversity is one of the main threats to marine ecosystems under climate change (Edelist et al., 2013; Munday, 2008; Poloczanska et al., 2016). The competitive dominance of range-extending species can cause biotic homogenisation through the increase of generalist range-extenders and displacement of specialist and native species (Dominguez Almela et al., 2021; Magurran et al., 2015). In biotic homogenisation, functional, genetic and taxonomic similarities increase in a community over time, leading to the loss of beta diversity, impacting ecosystem function (Olden et al., 2016; Magurran et al., 2015). While tropical systems often have high functional redundancy allowing community and ecosystem stability during species losses, temperate systems, which are relatively depauperate and susceptible to climate change impacts, often lack functional redundancy (Gilby et al., 2017; Micheli & Halpern, 2005). Biotic homogenisation and the decline in specialist and endemic species under climate change, has been widely documented for many temperate regions (Clavel et al., 2010; Olden et al., 2016; Richmond et al., 2005), and is likely to further impact regions as climate change continues.

1.4 Climate change and species distributions in Aotearoa New Zealand

Aotearoa New Zealand (NZ) consists of three main islands and over 700 coastal offshore islands (Gordon et al., 2010). Owing to its wide latitudinal range (34°S to 47°S) NZ's temperatures vary from north to south (Francis, 1993; Francis et al., 1987; Williams, 1988). This large variation in temperature drives the geographical distribution of NZ's marine fauna and flora, with greater diversity of marine life associated with the warmer subtropical waters in northern NZ, and lower diversity in the southern, subantarctic environments (Francis, 1993; Paulin & Roberts, 1993; Gordon et al., 2010; Brook, 2003). The higher diversity in the north can be partly attributed to the convergence of warm water currents, such as the East Auckland Current (EAUC; Francis, 1993; Roberts et al., 2015). The EAUC branches off the warm, slow-moving body of water known as the Tasman Front as it reaches Cape Reinga, moving southeast towards the East Cape (Laing et al., 1996; Stanton & Sutton, 2003). The EUAC is responsible for the sea surface temperature (SST) in the northeast being approximately 1°C – 2°C warmer than those on the western coastline at respective latitudes (Sutton & Roemmich, 2001). NZ's large latitudinal range and complex coastlines give way to a variety of different habitats, allowing a high level of species diversity, and endemism, in comparison to other isolated temperate countries (Roberts et al., 2015).

While research indicates long-term SST warming in certain parts of NZ's coastal waters (particularly in Wairarapa and Dunedin; Shears & Bowen, 2017; Sutton & Bowen, 2019), the rate and intensity of change is highly variable. This is, in part, to NZ's complex environment and oceanographic influences including tides, salinity and temperature fluctuations due to weather (i.e., El Niño, La Niña, and localised weather events including storms; Bowen et al., 2017; Sutton et al., 2005). Most substantial SST variations are attributed to the cooler annual temperatures during El Niño years, which see cooler south-westerly winds, and warmer annual temperatures during La Niña years, which correlate with warmer north-easterly winds (Bradford-Grieve et al., 2005; Shears & Bowen, 2017). Both weather systems impact the EAUC by driving it further away (causing cooler inshore waters) or driving it closer to the coast (causing warmer inshore waters; Bradford-Grieve et al., 2005; Shears & Bowen, 2017).

NZ's marine realm remains relatively unimpacted by climate change in contrast to regions at similar latitudes (e.g., Johnson et al., 2011; Ridgway & Hill, 2012). Nevertheless, there are a few documented records associated with long term climate change and heatwave impacts, including: the shift in abundance and distribution of Snapper *Chrysophrys auratus* and Kingfish *Seriola lalandi*, two commercially important species (StatsNZ, 2019); localised extinction of in Bull kelp *Durvillea poha* which resulted in high recruitment of the invasive kelp *Undaria pinnatifida* (Thomsen et al., 2019) and biomass loss of Giant kelp, *Macrocystis pyifera* (Tait et al., 2021).

Tropical and subtropical fishes have been recorded in NZ mainland waters for the last century (Roberts et al., 2015). Tropical and subtropical fishes are commonly transported as larvae via large-scale ocean currents (e.g. Tasman Front, East Auckland Current) from places such as eastern Australia, Norfolk Island and Lord Howe Island, as well as from the Rangitāhua Kermadec archipelago (Francis & Evans, 1993). During warm summer periods and/or in association with La Niña years, we see an influx of tropical and subtropical fishes, generally recorded as in juveniles (Francis & Evans, 1993). While some tropical and subtropical fishes may grow and spawn, it is unlikely for many to survive through winter, with temperatures dropping below their thermal thresholds of ~18°C (Francis & Evans, 1993; Booth et al., 2018). This may not always be the case, with NZ's oceans warming at 3.5°C per century, NZ is on trajectory to reach many tropical and subtropical fishes' thermal thresholds within the next 50 years (Shears & Bowen, 2017).

NZ is home to a diverse array of fish fauna with approximately 22% being endemic (i.e. only found in NZ waters; Roberts et al., 2015). Additionally, there are several regions of high endemism across NZ (i.e., Rangitāhua, Manawatawhi Three Kings Islands and Motu Ihupuku Campbell Island; Roberts et al., 2015). This signifies that many of our endemic species are highly adapted to specific habitats, are likely vulnerable to environmental and temperature changes, and may be susceptible to new arrivals in their habitats (Clavel et al., 2010). Novel interactions between arriving species and native species has the potential to impact specialist species in favour of generalist species (i.e., those species more capable of exploiting a habitat and dealing with environmental changes), leading to losses of native species and ecosystem functions (Monaco et al., 2020; Munday, 2008). Through competition for food sources, space and habitat, as well as being better equipped to deal with predators, generalist tropical and subtropical species pose a significant threat to our native fauna (Bates et al., 2014; Sunday et al., 2012).

1.5 Overview of thesis

This thesis comprises two empirical data chapters (Chapters Two and Three), and a general discussion chapter (Chapter Four). Chapters Two and Three are written in manuscript format as I expect to submit these for peer-review as co-authored manuscripts shortly after receiving the examiner's comments, so I use "we" (first-person plural) to acknowledge this. Nonetheless, this thesis is my own work, completed under the guidance of my supervisors. Given that these chapters are intended as independent publishable units, there is also some repetition of background information and methodologies throughout the thesis.

Chapter Two investigates the utility of citizen-science data collection solicited via questionnaires for monitoring subtropical and tropical fishes in Aotearoa New Zealand. Using structured questionnaires for popular dive sites around Tawhiti Rahi Poor Knights Islands, I assessed how observable subtropical and tropical fishes were from the perspective of recreational divers and snorkelers and whether this varied according to a species conspicuousness (body size, behaviours, and ability to camouflage) and lifestyle (habitat and position in the water column). The questionnaires presented eight fish species specific to each dive site, including; four tropical or subtropical 'species-of-interest', two negative control species and two positive control species, which were used to verify the quality of the participants observations. I also included contextual questions including; life-stage, behaviours, and co-occurring species, to assess whether citizen scientists could reliably collect additional information that is important for understanding the potential impact of these species. I predicted that a high proportion of respondents would accurately identify the positive and negative control species within the questionnaire, providing us with reliable occurrence and contextual data for the species we are interested in. I also predicted that a species conspicuousness and mobility would influence the likelihood of the species being observed, and the likelihood that the respondent provided additional contextual information in three optional questions. Finally, I expected that the abundance data collected on the species-of-interest via the questionnaires, would be comparable to previously collected citizen-science data requiring photographic equipment and post-hoc taxonomic validation, thus evidencing the reliability and robustness of our method.

Chapter Three examines the morphology, trophic level and broadscale habitat preferences of 244 marine ray-finned fishes from 79 taxonomic families to predict likely outcomes of tropical, subtropical and rare fishes arriving and establishing in Aotearoa New Zealand, on the resident fish fauna. I collected discrete trophic sores and 10 morphological measures for all 244 species using images provided by the comprehensive literature of Roberts et al., 2015 and FishBase, a global biodiversity information system holding an extensive record of fish species. Additionally, I established broadscale habitat preferences for each species, including; true benthic, benthopelagic, coastal pelagic and oceanic pelagic as well as dietary grouping including; herbivore, omnivore, invertivore, mixed carnivore and carnivore. I assessed which species may overlap based on morphology, trophic and habitat data and how that may impact resident species and ecosystem functioning. Specifically, I predicted that arriving species would overlap in their morphology and occupy the same niche space (i.e. same trophic, dietary and habitat preferences) as some of the resident species, but that the majority of arriving species would differ in their morphology and niche space they may occupy novel niche spaces in the NZ fish fauna, therefore altering ecosystem functioning.

Chapter Four considers the significant results, drawing conclusions from Chapter Two and Chapter Three, including how their findings cross inform each other. I also discuss limitations and caveats of this research and propose future directions and applications of this research.

Chapter Two: Questionnaires solicit species observations and important contextual information from marine citizen scientists

2.1 Abstract

The occurrence of tropical and subtropical fishes in temperate waters is a known indicator of climate-mediated biodiversity change. These species can negatively impact recipient ecosystems, making early detection and monitoring crucial. Because monitoring these rare species is challenging using traditional scientific surveys, citizen-science observations of species have been used to expand monitoring efforts. However, validating these observations requires citizens to provide quality images of the observed species in-situ, which limits the involvement of citizens who do not have photographic equipment. Here, we used questionnaires to gather written records of species sightings from citizens and validate the integrity of their species identifications through the inclusion of positive controls (species that should always be sighted), and negative controls (species that should never be sighted). We gathered 102 questionnaires, each presenting eight species (four species-of-interest, two positive controls and two negative controls) at four sites frequently snorkelled and dived at Tawhiti Rahi (Poor Knights Islands). We found that 83.33% (N=83) of the questionnaires could be used based on correct responses for our control species, recovering validated sightings for ten tropical and subtropical fishes. The relative frequency and abundance of these species-of-interest sighted over eight months of the study, matched ranks gained through image-validated citizen sightings for the same sites between 2018 and 2020. Furthermore, we found that the ‘conspicuousness’ (i.e., how detectable the species is based on visual and behavioural traits) and ‘mobility’ (i.e., whether the species was benthic and home-ranging versus benthopelagic and mobile) of these species did not affect the likelihood of a participant observing it, or the ability of participants to provide additional contextual information about the sighting, including observed behaviours. Nonetheless, participants were more likely to report co-occurring species when the species-of-interest was considered more pelagic and mobile. Our study provides proof-of-concept that citizens can provide reliable observations without requiring images for post-hoc expert validation, thus increasing the breadth of citizen sightings that can be used in the monitoring of rare species and creating a more equitable opportunity for citizens to contribute to science and monitoring initiatives.

2.2 Introduction

"Citizen-science" - the participation of the general public (i.e., non-scientists) in data collection contributing to scientific enquiry (Eitzel et al., 2017) - has become a widely recognised way to engage the general public in science, facilitate scientific data collection supporting scientific research (Devictor et al., 2010; Eitzel et al., 2017; Lenanton et al., 2017; Soroye et al., 2018) and contribute to environmental management and policy outcomes (Delaney et al., 2007; Madin et al., 2012). Engaging the general public in the collection of biodiversity data has contributed to detecting new species (Liggins et al., 2020) and monitoring biodiversity (Middleton et al., 2021) in both terrestrial (Sullivan et al., 2009; Theobald et al., 2015; Tiago et al., 2017; E.g., The Great British Birdcount, MonarchWatch.org) and marine settings (Malpica-Cruz et al., 2016; Pattengill-Semmens & Semmens, 2003; Pecl et al., 2019; e.g., Range Extension Database and Mapping Project [Redmap]; Reef Environmental Education Foundation [REEF]). Citizen-based data acquisition provides real-time data that can fill existing information gaps and expedite the collection of large amounts of data – a challenging ask with traditional scientific techniques (Delaney et al., 2007; McKinley et al., 2017; Pecl et al., 2019). As a result, citizen-science provides scientists with the opportunity to monitor a broad range of species across large spatial and temporal scales and has increased our understanding of species distributions and range extents (Pimm et al., 2014; Middleton et al., *in press*).

There can be hesitancy from the scientific community to engage citizens in scientific data collection due to the variable quality and biases associated with citizen-science data (Bird et al., 2014; Isaac et al., 2014). These biases are often unavoidable due to variation among participants including uneven temporal and spatial detectability (Boakes et al., 2010; Isaac & Pocock, 2015), uneven sampling effort (Isaac et al., 2014) and imperfect detection of focal species (Bird et al., 2014; McClintock, 2010). Therefore, maximising the value of citizen-science data often requires striking a balance between data quality and data quantity (Hochachka et al., 2012). By incorporating robust validation methods or post-hoc analyses, scientists can ensure quality control and increase data quality. For example, the use of decision trees that draw on existing knowledge can help contextualise data contributed by citizen scientists (Robinson et al., 2015; Wotton & Hewitt, 2004), and definitive identification by taxonomists

(Middleton et al., 2021; Pecl et al., 2019; e.g., WhatsThatFishNZ [WTFNZ]; Range Extension Database and Mapping Project [Redmap]) or the use of taxonomic voting systems (E.g., iNaturalist; BioDiversity4All; iSpot) have been widely used to provide confidence in the sighting representing a real species occurrence.

One of the most common quality control measures in citizen-science projects is to require an image to validate a sighting (e.g., iNaturalist, RedMap, WhatsThatFishNZ). However, this can limit participation to citizens who have access to photography or videography equipment. As an alternative to images, some citizen-science projects use surveys, questionnaires or checklists, often paired with sampling protocols to increase confidence in the species identification (Sullivan et al., 2017). For example, eBird (https://ebird.org/home) uses a two-part verification system of automated filters and regional editors, which enables quality control by flagging any unusual observations for expert review (Sullivan et al., 2009). Similarly, REEF (https://www.reef.org/) firstly ranks a participant as ‘expert’ or ‘novice’ based on prior experience and their performance on fish identification tests, before standardising variation by having all participants use the Roving Diver Technique during survey (Pattengill-Semmens & Semmens, 2003; Schmitt, 1996). Structured survey designs like those employed by REEF, allow for participation in citizen-science without the need for specialist photography or videography equipment. Furthermore, these structured survey designs have the advantage of providing presence-absence data (as opposed to presence-only data; Hermoso et al., 2015; McClintock, 2010), an estimation of sampling effort, as well as motivating the collection of ancillary data such as sex, life-stage, behaviours and environmental context (Sullivan et al., 2014).

The occurrence of tropical and subtropical fishes in temperate regions is recognised as an early indicator of climate-mediated biodiversity change (Fogarty et al., 2017). As the ocean climate has changed, fishes have undergone range shifts into high-latitude regions (Feary et al., 2014), impacting resident temperate species and recipient ecosystems (Holbrook, 1997; Madin et al., 2012). Range-extending of tropical and subtropical fishes are often rare (Bates et al., 2014; Feary et al., 2014), patchily distributed (McCarthy et al., 2013) and can be cryptic or highly mobile (Block et al., 2005; Hubert et al., 2012) making them difficult to survey systematically (Bates et al., 2014). Nevertheless, because of their often-distinct morphological features and bright colouring, tropical and subtropical fishes are highly observable and are therefore ideal focal species for collecting occurrence data through citizen-science observations. Gaining occurrence information across broad spatiotemporal scales, such as through citizen science, is crucial for understanding the range dynamics of tropical and subtropical fishes in their early stages of arrival and population establishment in a novel region (Middleton et al., *in press*). Furthermore, using citizen observations without requiring images can increase the volume of data received, and the use of quality controls with the citizen science data used can help overcome limitations and biases in the data (Fink, 2010; Hochachka et al., 2012; Kelling et al., 2015; Sullivan et al., 2014), supplying scientists and policymakers with a source of reliable, relevant and timely data.

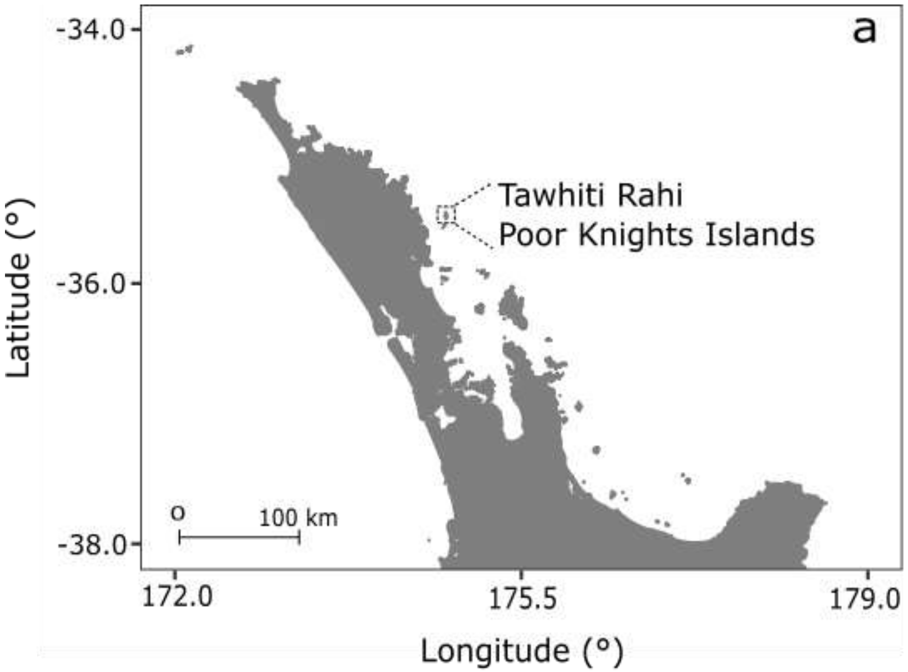
As an island nation with many ocean-going citizens, establishing a public monitoring programme has immense potential to contribute to scientific research. Recent research (Middleton et al., 2021) has highlighted the potential value of opportunistic citizen sightings, by collecting over 2,000 observations of tropical and subtropical fishes and through mining passive citizen-science observations. Analyses of citizen-science based photos or videos was used by Middleton et al (2021) to describe new arrivals and range-extensions of marine fishes, identify “range extension hot-spots” (i.e., where high frequency of range extensions occur, Middleton et al., *in press*), as well as document several new-to-New-Zealand species (Middleton et al., 2021). While the work of Middleton et al. (2021) demonstrates the value of validated images or videos of target species sourced from citizen scientists, many untrained citizens without access to camera equipment may have adequate observational skills to correctly identify a species, without the need for posthoc sighting validation by experts.

Here we determine whether ocean-going citizen-scientists (i.e., scuba divers and snorkelers who have not been trained by scientists and are typical members of the general public) may provide reliable sightings of marine fishes for use in scientific research without the need for images to undergo posthoc expert validation. Using species-specific questionnaires for dive sites around Tawhiti Rahi (Poor Knights Islands) – a hot-spot for range-extension and citizen records (Middleton et al., *in press*) – we assessed how observable tropical and subtropical fishes were from the perspective of recreational divers/snorkelers, and whether this varied according to the conspicuousness (body size, behaviours and ability to camouflage) and mobility (their position in the water column and whether they are home-ranging) of a species. We also assessed whether citizen scientists could reliably collect information that is important for understanding the potential impact of these species on recipient ecosystems, such as their life-stage, behaviours, and co-occurring species, using our questionnaires. Overall, we evaluate the value of structured questionnaires in collecting reliable observations of potential range-shifting sub/tropical fishes, making citizen-science in the marine realm more accessible.

2.3 Methods

2.3.1 Site selection

Tawhiti Rahi (Poor Knights Islands) is a group of islands situated on the east coast of Northland, Aotearoa New Zealand, 23km off the coast of Tutukaka (Figure 1). The islands are considered a “hot-spot” for the occurrence and range extension of tropical and subtropical fishes (Middleton et al., *in press*) and are a popular scuba dive/snorkel location. From over 50 well-known dive sites on Tawhiti Rahi, we selected 12 sites, that we subsequently grouped to form our four study sites. These locations were Northern Arch, Middle Arch, Maroro Bay (which included the sites: Brady’s Corner, Trevor’s Rock, El Torito Cave, The Gardens, Meditation Wall, and Great Wall) and South Harbour (which included the sites: Blue Maomao Arch, Magic Wall, Labrid Channel and Pinakitanga Point; Figure 1). The selection of study sites and study species (described below) was informed by discussions with local businesses and individuals who frequently dive/snorkel in Tawhiti Rahi.



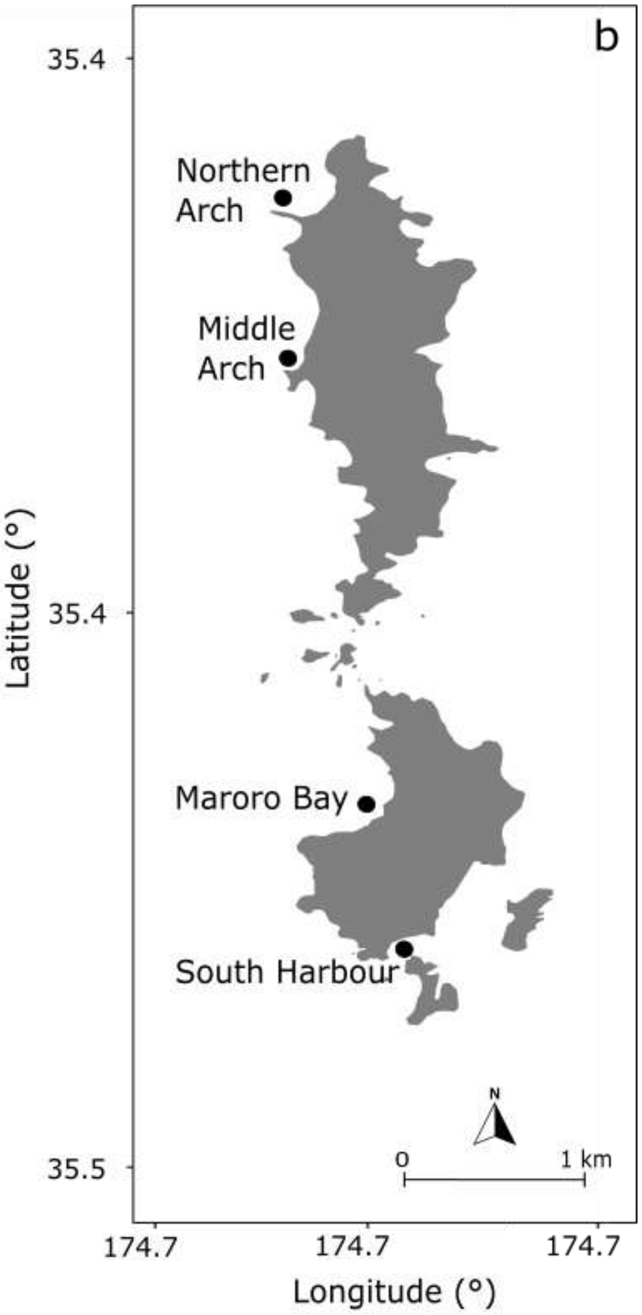


Figure 1: (a) The location of Tawhiti Rahi (Poor Knights Islands) relative to northern Aotearoa New Zealand, indicated by the dashed rectangle. (b) Map of Tawhiti Rahi, including the four study sites included in this study (Maroro Bay, Middle Arch, Northern Arch and South Harbour).

2.3.2 Questionnaire administration and procedure

The questionnaires were advertised and made available to the public via Facebook pages (e.g.WhatsThatFishNZ, OCD-Obsessive Compulsive Divers, Massey University Underwater Club, Biology – Massey University Albany, Auckland Scuba Dive, Yukon Dive, Dive! Tutukaka) and local dive shops and charter boats (e.g., Dive! Tutukaka, Auckland Scuba Dive, Kiwi Scuba Divers, Yukon Dive, and Epic Scuba) from 1st March 2021 to 30th October 2021. The questionnaires were made accessible as online forms via QR codes and as hard copies (circulated to dive/snorkel charter boats and clubs). When circulating the hard copies, we included an information sheet for staff that outlined our research, participation requirements, and contact details (Supplement 3). As part of our requirements, we asked that the questionnaires be filled out anonymously, and voluntarily and participation was not invited to those under 16 years of age. At the bottom of the questionnaire participants were also provided with our contact information, information regarding where they can go to share any ethical concerns or to find out more about the research programme that the questionnaire is contributing to (including the results they have contributed to, once completed).

2.3.3 Questionnaire design

The questionnaires were designed to be filled in by citizens following their dive/snorkel at our study sites. The questionnaires were specific to each study site and presented eight fish species. The questionnaires asked the participant whether they had observed each species and whether they could recall further information about any observed species using six multi-choice questions and two open text questions (Supplement 1).

The questionnaires were structured by first showing the participant a photo(s) of the species (including life-stages and sex, if relevant) and then asked the participant if they observed the species, to which, the participants answered by selecting either Yes/No/Unsure (Question 1). If a participant did observe a species, the questionnaire then had an additional five multi-choice questions and two open text questions (per species) which were: Question 2 – How many did you see? (Participants answered by selecting one of either 1/2/3-5/6+); Question

3 – Life-stage(s)? (Participants answered by selecting all that apply: Juvenile/Adult/Unsure); Question 4 – Sex of individual(s) observed? (Participants answered by selecting all that apply: Female/Male/Unsure; (note: this question was asked only in species that show sexual dimorphism); Question 5 – at what depths did you observe the individual(s)? (Participants answered by selecting all that apply: 0-5m/5-10m/10-15m/15-20m/20+/Unsure); Question 6 – Did you observe any of the following behaviours? (Participants answered by selecting all that apply: Feeding/Aggression/Territorial/Nest-Guarding/Courtship/Schooling/Hiding); Question 7 – Was it associated with any other species? (Participants answered in an open text field); Question 8 – Anything else of note? (Participants answered in an open text field).

The questionnaire design, including the species within each category (i.e., positive control, species-of-interest, and negative control, see below) was single-blind, whereby no participant was aware of which category a species was in, and the species presented in each questionnaire were shown in randomised order.

2.3.4 Selection of species

Two species were included in the questionnaire for each study site to function as “positive controls”. These were species that we anticipated should be observed by participants on every snorkel or dive at the study site and therefore could be used to verify the quality of the participants' observations. Our two positive control species for each site were taken from a pool of species informed by Reef Life Survey data (https://reeflifesurvey.com/survey-data/). Reef Life Survey is a citizen-science programme that engages scuba divers and snorkelers to conduct visual surveys of reef biodiversity on rocky and coral reefs around the globe (Edgar & Stuart-Smith, 2014). We filtered all available Reef Life Survey data for Tawhiti Rahi (including 2008, 2009, and 2012) and cross-referenced the geographic coordinates of the surveys with our four study sites to identify 35 species observed in Tawhiti Rahi.

Four species included in the questionnaire for each study site were our “species-of-interest”. These were tropical and subtropical species that could be indicators of climate change impacts, and we were interested in verified observations of these species, any related information, and whether any characteristics of the species particularly influenced whether they were observed. The species-of-interest were selected from the database created by Middleton et al. (2021) and WhatsThatFishNZ (https://www.facebook.com/WhatsThatFishNZ). WhatsThatFishNZ is a database of records, including from citizen sightings, of species-of-interest used in understanding the local biodiversity impacts of climate change in Aotearoa New Zealand. To inform our selection of species, the database was queried for all species records across our study sites. In total, the database provided us with 55 species-of-interest across our four study sites.

Two species were included in the questionnaire for each study site to function as "negative controls". These were species that we anticipated should not be observed by participants and so could be used to verify the quality of the participants' observations. The two species selected to be the negative controls for each site were selected from species recorded within the WhatsThatFishNZ database but filtered to exclude any species sighted within Tawhiti Rahi.

Within these three categories (i.e., positive control, species-of-interest, and negative control), species were selected for inclusion in the questionnaire based on characteristics that may influence their probability of being detected, including conspicuousness and mobility.

For positive control species, we refined the list to species that had relatively high abundance and conspicuousness scores (as described below), to ensure a high probability of detection by snorkelers/divers. We then selected species for inclusion, ensuring we had equal coverage across both mobility scores (i.e., one species that was "home-ranging" and one that was "mobile").

For the species-of-interest, we aimed for equal coverage across conspicuousness scores (two species that were "inconspicuous" and two species that were "conspicuous") and mobility scores (two species that were "home-ranging" and two species that were "mobile").

For negative control species, we queried the list of species from the WhatsThatFishNZ database that did not occur at Tawhiti Rahi for species that had high conspicuousness scores, and equal coverage across both mobility scores (i.e., one species that was “home-ranging” and one that was “mobile”).

Figure 2: Species used in the study including: species-of-interest (a – j), positive controls (k – p) and negative controls (q – v). Italicised letter on each image corresponds with the species scientific name in Table 1 and Table 2. Where morphology or colouration varies between life-stages (juvenile and adult) or sexes, representative images are provided. Images: I. Middleton, K. Littlewood.

2.3.5 Species abundance scoring

To ensure the species-of-interest and positive control species selected for inclusion in each of the questionnaires were relatively abundant at a given dive site we measured the local abundances of each species at each study site. This was done by calculating the number (i.e., the median number of individuals recorded in a single observation/survey) and the frequency (i.e., the number of observations/surveys it occurred) of each species. For example, Toadstool grouper *Trachypoma macracanthus* was recorded on four separate occasions at the South Harbour study site (frequency = 4). Across all 4 of these records, the median number of *Trachypoma macracanthus* observed during a single observation was 1 individual (number = 1). For the species-of-interest, we used the species occurrence database of Middleton et al. (*in press*) to inform abundance scoring (Supplement 2). For positive controls, abundance scoring was based on data gathered from Reef Life Survey data (https://reeflifesurvey.com/survey-data/; Supplement 2). To do this, we queried the Reef Life Survey data portal to recover all surveys with geographical coordinates corresponding to our study sites. For a given species at a specific study site, we calculated the frequency based on the number of “surveyIDs” it occurred in, and the number was the median of total abundance estimated per surveyID (i.e., summing blocks 1 and 2; see https://reeflifesurvey.com/survey-data/ for full methods. Abundance scoring was not relevant to negative controls, as these species should not be observed at these sites). Both number and frequency were qualitatively used to infer relative abundance, and in some instances, was additionally informed by local expert knowledge of species abundance at our study sites. When comparing recorded abundance to previous monitoring efforts by Middleton et al. (2021), we chose to use frequency only (as opposed to both frequency and number) as this provided a more realistic baseline for abundance, as number can also be dependent on lifestyle.

2.3.6 Species conspicuousness scoring

A species' morphological and behavioural traits can make them more observable (i.e., bright or unique colouration, large in size and overt behaviours) or not (i.e., cryptic colouration or countershading, small in size or evasive behaviours; Bayley, 2001; Bozec et al., 2011). We scored all species for conspicuousness using the method of Robinson et al. (2015) and used by Middleton et al. (2021). Specifically, overall conspicuousness was scored based on: camouflage (scored 0 if the species camouflages and 1 if the species does not); body size (scored 0 if the maximum standard length is under 30cm and 1 if it is over 30cm); and cryptic behaviours (scored 0 if the species generally hides away and 1 if it does not). The scores from each category were then combined and those species that had an overall score of 2 or above were considered “conspicuous” and those that had an overall score of 1 or below, were considered “inconspicuous” (Table 1).

2.3.7 Species mobility scoring

Aspects of species habitat and mobility, such as its position in the water column (pelagic or demersal) and tendency to move over distance, could influence whether the species is observed. We categorised species as either ‘home-ranging’ or ‘mobile’, according to our own understanding of the species habits. A species was considered ‘home-ranging’ if it stayed within a given territory and was associated with the substrate (i.e., it generally occupied the same area within a reef (e.g., Mosaic moray *Enchelycore ramosa*). A species was considered ‘mobile’ if it did not occupy a specific home territory and was generally a more pelagic or benthopelagic species (E.g., Mado *Atypichthys latus*; Table 1).

Table 1: Table 1: Summary of study design including 4 study sites (Maroro Bay, Middle Arch, Northern Arch and South Harbour), 10 species-of-interest, 6 positive control species and 6 negative control species, abundance scores (obtained from WhatsThatFishNZ and ReefLifeSurvey), conspicuousness scores (C = conspicuous, I = Inconspicuous) and categories of mobility (H = Home-ranging, M = Mobile). Conspicuousness was scored from 0 to 3 where a species was considered "inconspicuous" if the total score was less than 2 or "conspicuous" if the total score was equal to, or greater than 2, based on: Camouflage (0 = background matching, disruptive colouration, mimicry or disguise, 1 = does not show any of the previous mentioned; Body Size (0 = mature life-stage is <30cm length, 1 = mature life-stage is ≥30cm length and; Hiding (0 = may conceal itself within an object or substrate, 1 = does not display hiding behaviours). A species was considered "home-ranging" if it was primarily associated with the benthos and occupied the same area of reef or "home" territory. A species was considered "mobile" if it spent more time in the water column, and/or did not have a "home" territory. Habitat and lifestyle informing conspicuousness and mobility scores were obtained through peer-reviewed literature, online databases and/or expert knowledge.

				Abundance Score		**Conspicuousness Score**				**Mobility**
Species	**Common Name**	**Study Site/s**	**Inclusion in study**	**Number**	**Frequency**	**Camouflage**	**Body size**	**Hiding**	**SCORE**	**Home-ranging (H) or Mobile (M)**
Bo	Lord Howe butterflyfish	Northern Arch	Species-of-interest	Individual	23	1	1	0	**C**	H
Anampses elegans[b]	Elegant wrasse	South Harbour	Species-of-interest	Individual	6	1	0	1	**C**	H
Atypichthys latus[c]	Mado	Maroro Bay, South Harbour	Species-of-interest	Individual	15	1	0	1	**C**	M
Canthigaster callisterna[d]	Clown toado	Middle Arch	Species-of-interest	Individual	2	1	0	1	**C**	M
Enchelycore ramosa[e]	Mosaic moray	Middle Arch, South Harbour	Species-of-interest	Individual	1	0	1	0	**I**	H
Girella cyanea[f]	Bluefish	Northern Arch	Species-of-interest	Individual	3	1	1	1	**C**	M
Labracoglossa nitida[g]	Blue knifefish	Maroro Bay, Middle Arch, Northern Arch, South Harbour	Species-of-interest	Few (2-5)	1	0	0	1	**I**	M
Suezichthys aylingi[h]	Crimson cleanerfish	Middle Arch	Species-of-interest	Individual	6	1	0	1	**C**	H
Thalassoma lunare[i]	Moon wrasse	Maroro Bay	Species-of-interest	Individual	5	1	0	1	**C**	H
Trachypoma macracanthus[j]	Toadstool grouper	Maroro Bay, Northern Arch	Species-of-interest	Individual	7	1	0	0	**I**	H
Bodianus unimaculatus[k]	Red pigfish	Middle Arch	Positive Control	School (6+)	2	1	1	1	**C**	H
Chromis dispilus[l]	Two-spot demoiselle	Middle Arch, South Harbour	Positive Control	School (6+)	5	1	0	1	**C**	M
Chrysophrys auratus[m]	Australasian snapper	Maroro Bay	Positive Control	Few (2-5)	4	1	1	1	**C**	M
Coris sandeyeri[n]	Sandager's wrasse	South Harbour	Positive Control	School (6+)	4	1	1	1	**C**	H
Parma alboscapularis[o]	Black angelfish	Maroro Bay, Northern Arch	Positive Control	Few (2-5)	4	1	0	1	**C**	H
Scorpis violacea[p]	Blue maomao	Northern Arch	Positive Control	School (6+)	2	0	1	1	**C**	M
Abudefduf vaigiensis[q]	Sergeant major	Middle Arch	Negative Control	0	0	1	0	1	**C**	H
Chaetodon guentheri[r]	Gunther's butterflyfish	Maroro Bay	Negative Control	0	0	1	0	1	**C**	H
Forcipiger flavissimus[s]	Long-nose butterflyfish	Northern Arch	Negative Control	0	0	1	0	1	**C**	H
Naso unicornis[t]	Bluespine unicornfish	Middle Arch, Northern Arch	Negative Control	0	0	1	1	1	**C**	M
Ostracion cubicus[u]	Yellow boxfish	Maroro Bay, South Harbour	Negative Control	0	0	1	0	1	**C**	M
Platax teira[v]	Batfish	South Harbour	Negative Control	0	0	0	1	1	**C**	H

2.3.8 Statistical analysis

First, we analysed the questionnaires for completeness and quality. Specifically, we examined: the overall completion rate of the questionnaire as well as completion rates for multichoice questions and open text questions; the proportion of questionnaires that could be used based on a correct record of positive and negative control species; and observations and contextual information provided for the 10 species-of-interest.

To determine whether species conspicuousness and/or mobility influenced the probability of a citizen-science observation by a diver/snorkeler we used generalised linear mixed models (GLMMs). The response variable was binary where 0 indicated the species was not observed and 1 indicated the species was observed. For these models, we assumed a binomial error distribution and used a logit link. The fixed effects included in the model were ‘conspicuousness’ with two levels: conspicuous and inconspicuous, and ‘mobility’ with two levels: home-ranging and mobile. Random effects included in the model were ‘species’ with ten levels (one for each species-of-interest), ‘study site’ with four levels (Maroro Bay, Middle Arch, Northern Arch and South Harbour) and ‘questionnaire’ with 85 levels (total number of questionnaires that passed quality control). Due to the uncertainty in the participants’ ability to identify Blue knifefish *Labracoglossa nitida*, we chose to repeat all our analyses excluding *Labracoglossa nitida*. In models focused on the dataset where *Labracoglossa nitida* were removed, it was not possible to test the interaction of conspicuousness and mobility and so we only examine their main effects.

We then examined whether a diver/snorkeler was more likely to provide additional information accompanying their observation if the species was conspicuous and mobile. Here, we considered three different types of additional information; behaviours observed (Question 6), co-occurring species observed (Question 7) and additional notes provided (in response to Question 8) and analysed each of these as a GLMM. The response variable in each model was binary where 0 indicated the participant did not respond to the optional question and 1 indicated the participant did respond to the optional question. The error distribution, link function, fixed and random effects used in the GLMMs investigating questionnaire completeness were the same as those described above for the model examining the probability of observation.

For all GLMMs, we used the lme4 package (Bates et al., 2018) in R Studio version 1.4.1106 (R Core Team, 2020; RStudio Team, 2020). Backward model selection by single term deletion using the *drop1* function in the lmerTest package (Kuznetsova et al., 2015) was used to examine the significance of the fixed effects in our models.

To compare the frequency that each species-of-interest was recorded in our questionnaires to the frequency recorded within the WhatsThatFishNZ database, we ranked each species according to their relative frequency at each study site (Table 2). Species-of-interest were ranked from 1 to 4 (where 1 indicates the species with the highest relative frequency at the study site and 4 indicates the species with the lowest relative frequency at the study site). We compared the species-of-interest ranks between the two datasets using a Friedman Test implemented in the R base package (R Core Team, 2020), where 'species' with 10 levels (one for each species-of-interest) and 'site' with 4 levels (Maroro Bay, Middle Arch, Northern Arch and South Harbour) were categorical predictors.

2.4 Results

2.4.1 Species selection

Across the four sites, using our methods of species selection, we had a total of 22 unique fish species, including six positive controls, six negative controls, and ten species-of-interest. Across the 22 species included, eight species were represented across multiple study sites (including two positive control species: Twospot demoiselle *Chromis dispilus* and Black angelfish *Parma alboscapularis*, two negative control species: Yellow boxfish *Ostracion cubicus* and Bluespine unicornfish *Naso unicornis*, and four species-of-interest: Mado *Atypichthys latus,* Mosaic moray *Enchelycore ramosa,* Blue knifefish *Labracoglossa nitida* and Toadstool grouper *Trachypoma macracanthus* providing spatial replication for some species across study sites (Table 1).

2.4.2 Questionnaire completion and quality

We recovered 102 questionnaires from the four study sites, (21 from Maroro Bay, 22 from Middle Arch, 35 from Northern Arch and 24 from South Harbour). Of these, 77 were from individuals using our online version (21 from Maroro Bay, 17 from Middle Arch, 27 from Northern Arch and 12 from South Harbour) and 25 of these were from individuals using our printed versions left onboard Auckland Scuba, Kiwi Scuba Divers, Dive! Tutukaka and Yukon Dive charter boats (5 from Middle Arch, 8 from Northern Arch and 12 from South Harbour). The questionnaires were filled 95.1% by scuba divers and 4.9% by snorkelers between 1st March 2021 to 30th October 2021 on 41 separate dates.

Of the 102 questionnaires, individuals responded to 90-100% of the questions asked within the questionnaire, with a mean of 93.38% of questions answered. Of the 6.62% of unanswered questions, Question 8 was left unanswered 25.25% of the time, Question 7 was left unanswered 20.34% of the time, Question 6 was left unanswered 6.86% of the time and Questions 3 and 5 were left unanswered 0.25% of the time.

Based on the positive control species (i.e., questionnaires where both positive control species were observed), 92.16% (n=94) of questionnaires could be used for inferences regarding the species-of-interest. Based on the negative control species (i.e., questionnaires where both negative control species were not observed), 91.18% (n=93) of questionnaires could be used for inferences regarding the species-of-interest. Based on both forms of quality control (both considering appropriate responses for the positive and negative control species), 83.33% (n=85) of questionnaires could be used for inferences about the species-of-interest.

Negative control species that were putatively observed (i.e. participant responded Yes or Unsure to the question: Did you observe this fish?) included: Sergeant major *Abudefduf* *vaigiensis* - on two occasions at Middle Arch; Batfish *Platax tiera* – on three occasions at South Harbour; Bluespine unicornfish *Naso unicornis* – on three occasions at Northern Arch; Longnose butterflyfish *Forcipiger flavissimus* – on one occasion at Northern Arch; and Gunther's butterflyfish *Chaetodon guentheri* – on two occasions at Maroro Bay.

Positive control species that were overlooked (i.e., the participant responded No or Unsure to the question: Did you observe this fish?) included: Black angelfish *Parma alboscapularis* - on two occasions at Northern Arch; Red pigfish *Bodianus unimaculatus* - on two occasions at Middle Arch; Twospot demoiselle *Chromis dispilus* – on one occasion at Middle Arch and one occasion at South Harbour; Sandagers wrasse *Coris sandeyeri* – on one occasion at South Harbour.

All questionnaires that falsely recorded a positive or negative control, were removed prior to subsequent analysis.

2.4.3 Observations of species-of-interest

Toadstool grouper *Trachypoma macracanthus* was included in two study site questionnaires (Maroro Bay and Northern Arch) and was observed (i.e., Question 1 – Did you observe this species?, participants answered “Yes”) in 14.89% (n=7) of all questionnaires at these sites with an additional 4.26% (n=2) of participants being “Unsure” if they observed this species. Of the participants who did observe this species, 85.71% (n=6) observed 1 individual and 14.29% (n=1) observed 2 individuals (Question 2 – How many did you see?). 71.43% (n=5) of participants observed “Adults”, while 28.57% (n=2) of participants were “Unsure” on the species life-stage (Question 3 – Life-stage(s)?). Question 4 – Sex of individual(s) observed? was not included for this species. 100% (n=7) of participants observed this species over a depth range of 10-15m and 14.29% (n=1) additionally observed this species at a depth range of 15-20m (Question 5 – at what depths did you observe the individual(s)?). 100% of participants observed “Hiding” behaviours, and 14.29% (n=1) additionally observed “Feeding” behaviours (Question 6 – Did you observe any of the following behaviours?). 14.29% (n=1) of participants recorded observing “Scorpionfish” and “Blennies” (Question 7 – Was it associated with any other species?). There were no responses for Question 8 – Anything else of note.

Mosaic moray *Enchelycore ramosa* was included in two study site questionnaires (Middle Arch and South Harbour) and was observed (i.e., Question 1 – Did you observe this species?, participants answered "Yes") in 18.92% (n=7) of all questionnaires at these sites with an additional 5.41% (n=2) of participants being "Unsure" if they observed this species. Of the participants who observed this species, 85.71% (n=6) observed 1 individual and 14.29% (n=1) observed 2 individuals (Question 2). 42.86% (n=3) of participants observed "Adults", while 57.14% (n=4) of participants were "Unsure" (Question 3). Question 4 was not included for this species. 42.86% (n=3) of participants observed this species over a depth range of 15-20m, 28.57% (n=2) observed this species over a depth range of 0-15m and 28.57% (n=2) observed this species at 20m+ (Question 5). 57.14% (n=4) observed "Hiding" behaviours and 25.57% observed "Territorial" behaviours (Question 6). 14.29% (n=1) noted they observed a "Scorpionfish" co-occurring with this species (Question 7) and 14.29% (n=1) noted, "Hiding in its rock so hard to know its size/age" (Question 8).

Moon wrasse *Thalassoma lunare* was included in one study site questionnaire (Maroro Bay) and was observed (i.e., Question 1 – Did you observe this species?, participants answered "Yes") in 10% (n=2) of questionnaires at these sites with an additional 5% (n=1) of participants being "Unsure" if they observed this species. 100% (n=2) of the participants who did observe this species, observed two individuals (Question 2). 50% (n=1) of participants observed "Adults", while 50% (n=1) of participants were "Unsure" (Question 3). Question 4 was not included for this species. 50% (n=1) of participants observed this species over a depth range of 0-5m and 50% (n=1) observed this species over a depth range of 10-15m (Question 5). 100% (n=2) of participants noted observing "Feeding" behaviours (Question 6). There were no responses to Question 7 or Question 8.

Mado *Atypichthys latus* was included in two study site questionnaires (Maroro Bay and South Harbour) and was observed (i.e., Question 1 – Did you observe this species?, participants answered "Yes") in 48.72% (n=19) of questionnaires at these sites with an additional 12.82% (n=5) of participants being "Unsure" if they observed this species). Of the participants who did observe this species, 36.84% (n=7) observed two individuals, 52.63% (n=10) observed 3-5 individuals and 10.53% (n=2) observed 6+ individuals (Question 2). 94.74% (n=18) of participants observed "Adults" while 5.26% (n=1) of participants were "Unsure" (Question 3).

Question 4 was not included for this species. 10.53% (n=2) observed this species over a depth range of 0-5m, 47.37% (n= 9) observed this species over a depth range of 5-15m, 31.78% (n=6) observed this species over a depth range of 15-20m and 10.53% (n=2) observed this species at 20m+ (Question 5). 47.67% (n=9) of participants noted observing “Schooling” behaviours, 21.10% (n=4) noted “Feeding” behaviours, 10.53% (n=2) noted “Territorial” behaviours and 10.53% (n=2) noted “Hiding” behaviours (Question 6). 42.11% (n=8) of participants noted co-occurring species, with 26.32% (n=5) noting “Blue Maomao”, 15.79% (n=3) noting “Two Spot Demoiselle”, 10.53% (n=2) noting “Black Angelfish” and “Sandagers Wrasse” and 5.26% (n=1) noting “Snapper” and “Koheru” (Question 7). There were no responses to Question 8.

Lord Howe butterflyfish *Amphichaetodon howensis* was included in one study site questionnaire (Northern Arch) and was observed (i.e., Question 1 – Did you observe this species?, participants answered “Yes”) in 78.57% (n=22) of questionnaires at this site, there were no responses to “Unsure”. Of the participants who did observe this species, 27.27% (n=6) observed one individual, 45.45% (n=10) observed 2 individuals, 18.18% (n=4) observed 3-5 individuals and 9.09% (n=2) observed 6+ (Question 2). 86.36% (n=19) observed “Adults” while 13.64% (n=3) were “Unsure” (Question 3). Question 4 was not included for this species. 45.45% (n=10) observed this species at a depth range of 5-15m, 36.36% (n=8) observed this species at a depth range of 15-20m and 18.18 (n=9) observed this species at 20m+ (Question 5). 31.82% (n=7) of participants noted “Hiding” behaviours, 9.09% (n=2) noted “Territorial” behaviours, 4.55% (n=1) noted “Courtship” behaviours and 4.55% (n=1) noted “Schooling” behaviours (Question 6). 4.55% (n=1) of participants noted the species co-occurring with “Blue Maomao” (Question 7). There were no responses to Question 8.

Elegant wrasse *Anampses elegans* was included in one study site questionnaire (South Harbour) and was observed (i.e., Question 1 – Did you observe this species?, participants answered “Yes”) in 31.58% (n=6) of questionnaires at this site, with an additional 5.26% (n=1) of participants being “Unsure” if they observed this species (Question 1). Of the participants who did observe the species, 33.33% (n=2) observed 1 individual, 33.33% (n=2) observed 2 individuals and 33.33% (n=2) observed 3-5 individuals (Question 2). 83.33% (n=5) observed

“Adults” while 16.67% (n=1) was “Unsure” (Question 3). 50% (n=3) of participants observed both “Male” and “Female” in the same observation while 16.67% (n=1) observed “Male”, 16.67% (n=1) observed “Female” and 16.67% (n=1) was “Unsure” (Question 4). 50% (n=3) observed this species at a depth range of 5-15m and 33.33% (n=2) observed this species at a depth range of 0-5m (Question 5). 100% (n=6) of participants noted “Feeding” behaviours, with 33.33% (n=2) additionally noting “Courtship” or “Hiding” behaviours (Question 6). There were no responses to Question 7 and one participant noted “one had a big yellow spot, and both had bright blue flecks all over” (Question 8).

Crimson cleanerfish *Suezichthys aylingi* was included in one study site questionnaire (Middle Arch) and was observed (i.e., Question 1 – Did you observe this species?, participants answered “Yes”) in 11.11% (n=2) of questionnaires at this site, with an additional 27.78% (n=5) of participants being “Unsure” if they observed this species. Of the participants who did observe this species, 100% (n=2) observed 1 individual (Question 2) and 100% (n=2) observed “Adults” (Question 3). Question 4 was not included for this species. 100% (n=2) of participants observed this species at a depth range of 5-15m (Question 5) and 100% (n=2) noted “Hiding” behaviours (Question 6). There were no co-occurring species noted (Question 7) and 100% (n=2) noted “Kept hiding from me in the Kelp but I have a photo if you want it” and “looked similar to a juvenile Sandagers wrasse” (Question 8).

Clown Toado *Canthigaster callisterna* was included in one study site (Middle Arch) and was observed (i.e., Question 1 – Did you observe this species?, participants answered “Yes”) in 38.89% (n=7) of questionnaires at this site with an additional 5.56% (n=1) of participants being “Unsure” if they observed this species. Of the participants who did observe this species, 85.71% observed 1 individual and 14.29% observed 2 individuals (Question 2). 57.14% (n=4) observed “Adults”, 28.57% (n=3) were “Unsure” and 14.29% (n=1) observed both “Adults” and “Juvenile” in one observation (Question 3). Question 4 was not included for this species. 57.14% (n=4) observed this species at a depth range of 5-10m, 28.57% (n=2) observed this species at a depth range of 15-20m and 14.29% (n=1) observed this species at 20m+ (Question 5). 57.14% (n=5) noted “Hiding” behaviours, 28.57 (n=2) noted “Territorial” behaviours and 14.29% (n=1) noted

“Aggression” (Question 6). There were no responses to Question 7 and 33.33% (n=2) noted “Juvenile and adult sighted in the same area, near kelp” and “Pretty sure it was a male because the blue lines were really vivid, and it kept following me and being aggressive - I learnt that from a post you guys did on Facebook” (Question 8).

Bluefish *Girella cyanea* was included in one study site (Northern Arch) and was not observed in any of the questionnaires (n=37) at this study site.

Blue knifefish *Labracoglossa nitida* was included in all four study sites (Maroro Bay, Middle Arch, Northern Arch and South Harbour) and was observed (i.e., Question 1 – Did you observe this species?, participants answered “Yes”) in 44.71% (n=38) of questionnaires at these sites with an additional 15.29% (n=13) of participants being “Unsure” if they observed this species. Of the participants who did observe this species, 89.47% (n=34) observed 6+ individuals, and 10.53% (n=4) observed 3-5 individuals (Question 2). 55.26% (n=21) observed “Adults”, 34.21% (n=13) were “Unsure” and 10.53% (n=4) observed both “Adults” and “Juveniles” (Question 3). Question 4 was not included for this species. 63.16% (n=24) of participants observed this species at a depth range of 5-15m, 18.42% (n=7) observed this species at a depth range of 5-10m and 18.42% (n=7) observed this species at a depth range of 15-20m (Question 5). 81.58% (n=31) observed “Schooling” behaviours and 7.89% (n=3) observed “Feeding” behaviours (Question 6). 28.95% (n=11) of participants noted the species co-occurring with Two Spot Demoiselles (18.42%; n=7), Blue Maomao (13.16%; n=5), Koheru (10.53%; n=5) and Pink Maomao (7.89%; n=3) (Question 7). 13.16% (n=5) of participants noted “not sure if it was Koheru or blue knife fish, can provide video if needed”, “might have been Koheru”, “potentially were Koheru really hard to tell”, “Very hard to distinguish with Koheru so only about 80% sure they were knife fish” and “with the Koheru school but these ones were a lot more blue than the Koheru” (Question 8).

Overall, *Amphichaetodon howensis*, *Atypichthys latus* and *Labracoglossa nitida* were observed more often than not with *Amphichaetodon howensis* having the highest number of observations. Observation uncertainty (i.e., participants being "unsure" of species ID) was highest for *Suezichthys aylingi* and *Labracoglossa nitida* and lowest for *Amphichaetodon howensis. Girella cyanea* had the lowest number of observations across all species-of-interest followed by *Thalassoma lunare*.

2.4.4 The influence of conspicuousness and mobility on participant observations of species-of-interest

We found no evidence for an interaction between species conspicuousness and mobility on the likelihood that participants observed the species-of-interest at our study sites (i.e., Question 1 – Did you observe this species?; χ_1^2 = 2.158, *P* = 0.142). Examining the main effects of conspicuousness and mobility, we found no evidence that conspicuousness nor mobility affected the likelihood that participants observed the species-of-interest at our study sites (χ_1^2= 0.00, *P* = 0.995 and χ_1^2= 1.509, *P* = 0.219 for conspicuousness or mobility respectively). Consistent with this result, when excluding *Labracoglossa nitida* from the model (due to the uncertainty in the participants' ability to identify *Labracoglossa nitida*), we found no evidence that conspicuousness and mobility affected the likelihood that participants observed the species-of-interest at our study sites (χ_1^2= 0.888, *P* = 0.346 and χ_1^2 = 0.160, *P* = 0.899 for conspicuousness or mobility respectively).

There was no evidence of an interaction between species conspicuousness and mobility on response rates to Question 6 – Did you observe any of the following behaviours? (χ_1^2 = 2.246, *P* = 0.134) or Question 7 – Was it associated with any other species? (χ_1^2= 0.042, *P* = 0.838). For Question 6 and 7 the main effects of conspicuousness and mobility showed no evidence that conspicuousness had an effect on response rates (χ_1^2= 0.054, *P* = 0.817, χ_1^2= 0.513, *P* = 0.474, for Question 6 and Question 7 respectively), however, mobility did appear to affect the likelihood that participants would provide additional information (χ_1^2 = 3.482, *P* = 0.062, χ_1^2 = 6.031, *P* = 0.014 for Question 6 and Question 7 respectively). For Question 8 – Anything else of note? we found no evidence that the interaction of conspicuousness and mobility (χ_1^2 = 2.127, *P* = 0.145) or their main effects influenced the likelihood that participants provided additional information (χ^2_1= 0.628, *P* = 0.428 and χ^2_1 = 2.457, *P* = 0.117 for conspicuousness or mobility respectively). After removing *Labracoglossa nitida* from the model, we found no evidence that conspicuousness or mobility affected on the likelihood that participants answered Question 6 (χ^2_1= 0.889*, P* = 0.346 and χ^2_1 = 0.163*, P* = 0.687 for conspicuousness or mobility respectively), Question 7 (χ^2_1= -22.125*, P* = 1.000 and χ^2_1 = 3.075, *P* = 0.079 for conspicuousness or mobility respectively) or Question 8 (χ^2_1= 0.710*, P* = 0.399 and χ^2_1 = 0.000, *P* = 0.999 for conspicuousness or mobility respectively).

2.4.5 Comparison of relative abundances across citizen-science datasets

We found no difference in the rank frequency scores for our species-of-interest between our data and previously collected citizen-science data from Middleton et al., (*in press*) across the four study sites at Tawhiti Rahi including (χ^2_1= 0.400, *P* = 0.527) and excluding *Labracoglossa nitida* (χ^2_1= 0.333, *P* = 0.563; Table 2).

Table 2: Species-of-interest comparison of abundance and associated ranks from both the WhatsThatFishNZ database (WTFNZ Abundance) and this study (Study Abundance), including ranks following the exclusion of Blue knifefish *Labracoglossa nitida* (see reasoning in main text). Species-of-interest were ranked from 1 to 4 (where 1 indicates the species with the highest relative abundance at the study site and 4 indicates the species with the lowest relative abundance at the study site).

			WTFNZ Abundance		**Study Abundance**		**Ranks**		**Ranks ex. Blue knifefish**	
Study Site	**Species**	**Common Name**	**Number**	**Frequency**	**Number**	**Frequency**	**WTFNZ**	**STUDY**	**WTFNZ**	**STUDY**
Maroro Bay	*Atypichthys latus*[c]	Mado	Individual	23	Few (2-5)	12	1	1	1	1
Maroro Bay	*Thalassoma lunare*[i]	Moon wrasse	Individual	5	Few (2-5)	1	3	4	3	3
Maroro Bay	*Trachypoma macracanthus*[j]	Toadstool grouper	Individual	10	Individual	2	2	3	2	2
Maroro Bay	*Labracoglossa nitida*[g]	Blue knifefish	0	0	School (6+)	8	4	2	-	-
Middle Arch	*Canthigaster callisterna*[d]	Clown toado	Individual	2	Individual	7	2	2	2	1
Middle Arch	*Enchelycore ramosa*[e]	Mosaic moray	Individual	1	Individual	5	4	3	3	2
Middle Arch	*Labracoglossa nitida*[g]	Blue knifefish	School (6+)	1	School (6+)	10	3	1	-	-
Middle Arch	*Suezichthys aylingi*[h]	Crimson cleanerfish	Individual	6	Individual	2	1	4	1	3
Northern Arch	*Amphichaetodon howensis*[a]	Lord Howe butterflyfish	Individual	23	Few (2-5)	22	1	1	1	1
Northern Arch	*Girella cyanea*[f]	Bluefish	Individual	3	0	0	4	4	3	3
Northern Arch	*Labracoglossa nitida*[g]	Blue knifefish	Few (2-5)	6	School (6+)	7	2	2	-	-
Northern Arch	*Trachypoma macracanthus*[j]	Toadstool grouper	Individual	5	Individual	5	4	4	3	3
South Harbour	*Anampses elegans*[b]	Elegant wrasse	Individual	6	Few (2-5)	6	2	3	2	2
South Harbour	*Atypichthys latus*[c]	Mado	Individual	7	Few (2-5)	7	1	2	1	1
South Harbour	*Enchelycore ramosa*[e]	Mosaic moray	Individual	2	Individual	2	3	4	3	3
South Harbour	*Labracoglossa nitida*[g]	Blue knifefish	School (6+)	1	School (6+)	13	4	1	-	-

2.5 Discussion

Species records collected by citizens for use in scientific enquiry generally require citizens to provide images or videos and post-hoc validation by taxonomic experts, thus rendering many written and verbal observations unusable. Here we used structured questionnaires designed with in-built quality controls, enabling written records to be used to fill information gaps. Importantly, our approach allows equitable participation, allowing citizens who do not have access to camera equipment the opportunity to participate in citizen-science data collection. Through this method, we have recovered 109 validated sightings of ten tropical and subtropical species whose occurrence and abundance changes are indicators of climate change impacts (Middleton et al., 2021). Alongside these observational records, using our questionnaires we have also captured contextual information about these species (such as their life-stage, sex, behaviours and species interactions) that is relevant to understanding their potential impact on Aotearoa New Zealand's temperate ecosystem.

A species' morphology and behavioural traits can influence its detectability by humans, including citizen scientists (Bayley, 2001; Bozec et al., 2011). In this study, we considered whether a species' conspicuousness (body size, behaviours, and ability to camouflage; as defined in Robinson et al., 2015) and lifestyle (mobility and position in the water column) influenced the detectability of our species-of-interest. We found that the conspicuousness and mobility of our species-of-interest did not influence the likelihood a participant would observe them. This is likely because all species-of-interest, irrespective of conspicuousness and mobility scores, are noticeable in comparison to our resident and native species. In general, their morphology – such as bright colouration and distinct body shapes (e.g., *Amphichaetodon howensis*) – and rarity make them highly noticeable in contrast to our native or resident species of temperate Aotearoa New Zealand. Nonetheless, we did observe that participants were more likely to be 'unsure' of the taxonomic identity for species that were 'inconspicuous' (either by noting 'unsure' to Question 1 – Did you observe this species or commenting on the open text field in Question 8 – Anything else of note?). In particular, *Labracoglossa nitida* were often confused with Koheru *Decapterus koheru*, and *Suezichthys aylingi* were likely sometimes confused with juvenile Sandagers wrasse *Coris sandeyeri*. Taxonomic confusion (misidentification of morphologically similar species) was not assessed here, however, this should be considered in future studies to avoid using species that may be easily misidentified.

Understanding a person's rationale for participating in data collection is important in any citizen-science initiative (Martin et al., 2016; Shirk et al., 2012). While accessibility (Isaac & Pocock, 2015; Tiago et al., 2017) and ease of data collection (Pocock et al., 2017; Roberts et al., 2022) are important, a citizen-science programme's success is often dependant on piquing the interest of volunteers by including 'weird' and 'wonderful' creatures (Devictor et al., 2010; Isaac & Pocock, 2015; McKinley et al., 2017). Our results show a 99.87% completion rate for multichoice questions (Questions 1,2,3,4, 5 and 6) and 77.10% completion rate for open text questions (Questions 7 and 8). However, when analysing species conspicuousness and mobility on questionnaire completeness for the three optional questions (Questions 6, 7 and 8) we found that conspicuousness and mobility did not influence questionnaire completeness for Questions 6 (i.e., Did you observe any of the following behaviours?) and Question 8 (i.e., Anything else of note?). This strengthens the hypothesis that (in the case of tropical and subtropical fishes) a species does not have to be particularly 'interesting' or 'attractive' to look at, for a participant to be more or less interested in filling out a questionnaire. This supports, Sandahl & Tøttrup (2020) who observed that (in the case of engaging marine citizen-science volunteers) the emblematic appeal (i.e. the attractiveness) of the study organism may not play as critical role as previously thought. Nonetheless, participants were more likely to answer Question 7 (i.e., Was it associated with any other species?) if the species-of-interest was mobile. This result may be due to species interactions being more common in species with more mobile lifestyles (e.g., schooling species such as *Labracoglossa nitida*) compared to benthic species that may be more sedentary and therefore more solitary (e.g., *Enchelycore ramosa*).

While occurrence data is important for monitoring climate-induced species redistribution, through asking contextual questions such as the number of individuals observed, their life-stage and sex (Questions 2, 3 and 4) our questionnaire design may also help to gauge a species' potential for reproduction and track their stage of establishment. For example, *Amphichaetodon howensis* were most often observed as a pair (10 out of 22 questionnaires) of adults (19 out of 22 questionnaires). *Atypichthys latus* was most often observed as a group of 3 to 5 (10 out of 19 questionnaires) adults (18 out of 19 questionnaires) and *Labracoglossa nitida* was most often observed in groups of 6 or more (34 out of 38 questionnaires) as adults (21 out of 38 questionnaires). Observing adults, or pairs/groups of adults indicates there is the potential for reproduction, or that the species may now be established. Furthermore, *Canthigaster callisterna* and *Labracoglossa nitida* were observed as both adults (4 out of 7 questionnaires and 21 out of 38 questionnaires, respectively) and juveniles (1 out of 7 questionnaires and 4 out of 38 questionnaires, respectively), which can indicate continuing recruitment and, that the populations may have established a self-sustaining population at Tawhiti Rahi.

Our questionnaire design and results have the potential to increase ecological understanding of these species, and their potential impacts at Tawhiti Rahi. For instance, in response to Question 6 (Did you observe any of the following behaviours?), *Anampses elegans* was noted in 2 out of 6 questionnaires as displaying ‘courtship’ behaviours and *Canthigaster callisterna* was observed being ‘aggressive’ and ‘territorial’ in 3 out of 7 questionnaires and additionally noted by one participant that the individual observed was a male with very vivid blue lines that kept following and being aggressive (in Question 8 - Anything else of note?). These responses indicate that the *Canthigaster callisterna* was exhibiting breeding behaviours, as male *Canthigaster callisterna* are known to showcase their colourings and display more aggressive behaviours prior to, and during periods of breeding. Additionally, participants noted feeding behaviours in *Atypichthys latus* (4 out of 19 questionnaires), *Anampses elegans* (6 out of 6 questionnaires), *Trachypoma macracanthus* (1 out of 7 questionnaires), *Thalassoma lunare* (2 out of 2 questionnaires), and *Labracoglossa nitida* (3 out of 38 questionnaires). Observation of feeding behaviours can provide information on resource use and help predict competitive interactions among species.

Furthermore, contextual information, such as depth range, and what other species the species-of-interest co-occur with (i.e. Questions 5, and 7) could assist in predicting the impacts these novel species may have on resident taxa and biodiversity. For instance, *Labracoglossa nitida* were most commonly recorded at 5-10m depth (27 out of 38 questionnaires) displaying schooling behaviours (31 out of 38 questionnaires) and often observed co-occurring with a resident or native species (11 out of 38 questionnaires), including Blue Maomao *Scorpis violacea*, Twospot demoiselles *Chromis dispilus* and *Decapterus koheru*. Similarly, *Atypichthys latus* was most commonly recorded at 5-15m depth (9 out of 19 questionnaires) often co-occurring with a resident or native species (8 out of 19 questionnaires), including *Scorpis violacea*, *Chromis dispilus*, *Coris sandeyeri* and *Parma alboscapularis*. Co-occurrence of species-of-interest with native and resident taxa, in schools, or within the same depth zones, also helps to predict the potential for competition for resources (such as food and niche space) and assess which tropical and subtropical species may displace native and resident species or suppress their populations.

In the face of global environmental change, ensuring conservation action and management are informed by the best available science is crucial and information must be salient, timely and credible (Cook et al., 2013; Sullivan et al., 2017). With species redistribution occurring at an alarming rate, establishing monitoring programmes to track these changes is more important than ever. Citizen-science projects help close the gap between data collection and conservation action by allowing large volumes of real-time data to be collected. By gaining contextual data alongside occurrence data, we can build a better overall picture of what these novel species are doing in our waters and their potential impacts on native and resident species. Our approach yields similar frequency data for the species-of-interest as previous citizen-science efforts requiring images and post-hoc validation, thus showcasing the potential utility of this data source and the built-in quality control measures within the questionnaires without the need for photographic evidence, therefore allowing a more equitable approach to citizen-science.

2.6 Supplementary Data:

2.6.1 Supplement 1

Questionnaires the four study sites at Tawhiti Rahi (Maroro Bay, Middle Arch, Northern Arch and South Harbour) including the online versions (which can be viewed by scanning the QR codes).

https://1drv.ms/u/s!AoI1vxSjocLhhIY7D2Aaiy4y4KaraA?e=Yf2tb3

2.6.2 Supplement 2

Raw data from the WhatsThatFishNZ database and ReefLifeSurvey Portal used for informing species-of-interest, negative control species (WhatsThatFishNZ) and positive control species (ReefLifeSurvey). The "Tab Overview" provides a list of all subsequent tabs within the workbook. The "Terms_Raw_Data WTFNZ_Records" tab provides an explanation of the column headers, descriptions and vocabulary used in "Raw_Data WTFNZ records" which subsequently provides the occurrence records from the WhatsThatFishNZ database and their relevant metadata. The "Terms_Raw_Data_RLS records" provides an explanation of the column headers, descriptions and vocabulary used in the "Raw_Data_RLS records" which subsequently provides the survey records from the Reef Life Survey database.

https://1drv.ms/x/s!AoI1vxSjocLhhIY-vOFXHkFgBiNIjA?e=a93mrx

2.6.3 Supplement 3

Results from the 102 completed questionnaires during this study. The "Terms_PKI_Data" tab provides an explanation of the column headers, descriptions and vocabulary used in the "PKI Data" tab. The "PKI Data" tab contains the raw data from the 102 completed questionnaires filled out by citizen scientists during this research.

https://1drv.ms/x/s!AoI1vxSjocLhhIY_fYaypYAt5ko1yA?e=eYe57Y

Chapter 3: Predicting the impact of arriving tropical and subtropical fishes on the fauna of Aotearoa New Zealand

3.1 Abstract

The increased arrival of tropical and subtropical fishes in temperate regions is a clear indicator of climate mediated biodiversity change. As tropical and subtropical species increase in abundance and establish in temperate systems, understanding how these species will assimilate is important in predicting how they may impact resident species and ecosystem function. Range-extending species have the potential to compete with resident species for diet items and habitat space, increasing pressure on specialist and endemic species and on ecosystem functioning. Globally, range extending species have caused the displacement of endemic and specialist taxa, biotic homogenisation and ecosystem destruction. In Aotearoa New Zealand, occurrences of tropical and subtropical species have been recorded for over a century however our understanding of these species and their potential impacts are still relatively unknown. Here, we compared the broadscale trophic niche, habitat preference, and morphology of 139 tropical, subtropical and rare fishes (termed 'focal species') that are arriving in Aotearoa New Zealand, with 105 New Zealand native and resident fishes (termed 'NZ native species') to examine which focal species may compete with NZ native species and/or alter NZ's fish morphospace by filling an empty niche. Overall, 74.36% of focal and NZ native species, overlapped in morphology and trophic group and 76.10% of focal and NZ native species overlapped in morphology and habitat group. Across both habitat groups and trophic groups, only 48 focal species (27.34%) had differing morphology to NZ natives. The high levels of morphological and ecological niche overlap suggest there is high potential for interspecific competition and highlights the vulnerability of NZ native species, should focal species continue to arrive and establish in NZ.

3.2 Introduction

Species redistribution associated with climate change is well documented in terrestrial (Parmesan & Yohe, 2003), freshwater (Parmesan, 2006) and marine (Poloczanska et al., 2016) environments. In the marine realm, the rate of redistribution is occurring four times faster than in terrestrial environments (Burrows et al., 2011; Poloczanska et al., 2016; Sorte et al., 2010), with frequencies projected to increase as ocean temperatures continue to rise (Parmesan & Yohe, 2003; Perry et al., 2005). As the arrival, recruitment and establishment of range-extending species in higher latitudes increases, understanding how they might assimilate into the resident community is crucial to informing their likely impacts on the resident biodiversity and ecosystem.

There are a number of environmental factors and species-specific traits that determine a species ability to persist in a novel system (Feary et al., 2014). For species with the potential to disperse to new locations, their successful colonisation can be constrained by the climate of the recipient location (Holbrook & Schmitt, 2002), the availability of suitable trophic resources (i.e., habitat, diet items and niche space; Booth & Hixon, 1999) and the composition of the resident community (Beukers-Stewart et al., 2011; Sweatman, 1988). Typically, generalist species (i.e., species with broad fundamental niches, broad diet, high phenotypic plasticity, tolerant to environmental changes) are more successful at colonising novel habitats than specialist species (i.e., species with small fundamental niches, specific diet and habitat requirements, sensitive to environmental changes; Azzurro et al., 2014; Monaco et al., 2020).

Nonetheless, locations with high levels of biodiversity wherein the available niches are already saturated may be more difficult for a range-extending species to colonise (Van Kleunen et al., 2010; Violle et al., 2011), particularly when the novel species is not distinct from species within the recipient community (Darwin, 1859; MacArthur & Levins, 1967). If a particular niche is already filled by a resident species, the introduction of a novel species into that niche may create competition, forcing the 'losing' species to adapt to a new niche space, or to become locally extinct (Clavel et al., 2010). Unfortunately, evidence suggest that these losing species are quite often specialist and native species (Albins & Hixon, 2008; Edelist et al., 2013; Vergés et al., 2014).

Endemic species are often specialists having adapted to smaller, distinct niches overtime in order to take advantage of available resources, to enhance coexistence and reduce competition among species (Futuyma & Moreno, 1988; Kneitel, 2018). Therefore, the competitive dominance of generalist range-extenders is likely to most severely impact resident endemic species through increased competition for limited resources and habitat space (Clavel et al., 2010; Gilchrist, 1995). However in systems that are relatively depauperate with vacant niches, novel species have the potential to fill these unoccupied niches, thereby avoiding competition with resident taxa (Kingsbury et al., 2019; Schoener, 1974). Higher latitude and temperate systems are typically less speciose than low latitude tropical regions (Gilby et al., 2017; Micheli & Halpern, 2005). Consequently, range-extending species may impact ecosystem function through filling available niche space (Kingsbury et al., 2019).

A species ecological niche can be used to predict how it will fit into a community and environment (Chesson, 2000; Futuyma & Moreno, 1988). Through analysing the ecological niche of arriving species, we can predict the potential impact they may have on the resident community and ecosystem. For example, trophic and habitat niches have often been used to describe a species position in the food web and predict competition for diet items, resources and the habitat use (Adamczuk, 2022; Albouy et al., 2011; Carscallen et al., 2012). Similarly, morphology indirectly dictates the position of a species in a given environment and can be used to infer species interactions and interspecific competition (Azzurro et al., 2014; Harvey et al., 2022; Smith et al., 2016). By comparing the ecological niche and morphology of novel species to that of the resident taxa, we can predict which species are likely to co-occur and compete with resident taxa for habitat and/or diet items, which novel species may fill vacant niches and ultimately, how the resident taxa and ecosystem may be impacted.

Aotearoa New Zealand (NZ) is an isolated nation in the Southwest Pacific with a relatively depauperate fish fauna (~1260 species), but high endemism of fish species (~22%; Roberts et al., 2015). The majority of NZ's fish species are temperate, but due to the large latitudinal span of the nation (34°S to 47°S), subtropical and subantarctic fishes are also found in the fauna (Brook, 2003; Gordon et al., 2010; Paulin & Roberts, 1993). Tropical and subtropical marine fishes have been recorded arriving for over 100 years (Francis, 1993; Roberts et al., 2015), particularly into the north of NZ (Francis & Evans, 1993). These species are presumably transported to NZ as larvae via ocean currents including the Tasman Front and East Auckland Current (EAUC), from Southeast Australia, Lord Howe Island, Norfolk Island, and from the Rangitāhua Kermadec archipelago in the Northeast (Francis & Evans, 1993). In the northeast of mainland NZ, these rare and arriving subtropical and tropical species often co-occur with resident temperate and subtropical fishes (Middleton et al., 2021; Chapter Two). For example, in Tawhiti Rahi, NZ resident species such as Blue maomao *Scorpis violacea*, Two-spot demoiselle *Chromis dispilus* and Koheru *Decapterus Koheru* are often seen co-occurring with rare subtropical species, such as Mado *Atypichthys latus* and Blue knifefish *Labracoglossa nitida* (Chapter Two).

Typically, tropical and subtropical species are present in higher numbers in NZ's north-eastern waters during summer and autumn months when sea surface temperatures (SST) are highest, and in association with La Niña (Francis & Evans, 1993; Middleton et al., 2021). However, NZ's ocean temperatures are rising at a rate of 3.5°C per century, and mean winter temperatures have increased (Shears & Bowen, 2017). Consequently, several rare and newly arriving tropical and subtropical fish species are occurring in greater numbers, and persisting through winter to reach maturity (Middleton et al. *In press*). As these novel species continue to arrive in numbers and start to persist, they have the potential to compete with resident fish species, threatening the local survival of temperate and particularly endemic species, and altering community and ecosystem function.

Here we examine the morphology, trophic niche, and broadscale habitat preferences of 244 marine ray-finned fishes from 79 taxonomic families to predict likely outcomes of tropical, subtropical and rare fishes arriving and establishing in Aotearoa New Zealand, on the resident fish fauna. Based on 105 NZ native species (i.e. species that are resident in NZ) and 139 focal species (i.e., tropical and subtropical species that occur in NZ, but are not resident, or are rare) we compare ten standard morphological measurements as well as the trophic level and habitat preferences of species to assess: (1) which species may overlap morphologically and occupy the same niche space (based on tropic level and habitat preference), and therefore have the potential to co-occur and compete with each other for dietary items and/or for space; and (2) which tropical and subtropical fishes may occupy novel niche spaces in the NZ fish fauna and alter ecosystem functioning.

3.3 Methods

3.3.1 Species selection

We compiled a list of "NZ native species" (i.e. species that are resident in NZ) and "focal species" (i.e. tropical and subtropical species that occur in NZ, but are not resident, or are rare) focussed on marine ray-finned fishes (Class Actinopterygii).

Our list of NZ native species was based on the most complete record of NZ fishes compiled by (Roberts et al., 2015), and subsequent updates (Roberts et al., 2017; Roberts et al., 2020), but excluded species resident in the subtropical Rangitāhua-Kermadec Islands and not temperate NZ (according to Francis, 2012; Roberts et al., 2020; Roberts et al., 2015) to maintain our study focus on the temperate mainland region of NZ. Our list of focal species was based on that compiled by Middleton et al. (*in press*) who examined the NZ fish fauna, using Roberts et al. (2015, 2017, 2020, Francis (2012), and other published and unpublished sources, for all species described with any one of the following keywords: vagrant, rare, infrequent, occasional, tropical, subtropical, immigrant, and uncommon (*see* Middleton et al., *in press*). Following methods from Middleton et al. (*in press*) we excluded migratory species that appear annually in mainland NZ albeit seasonally (e.g., Striped marlin, *Kajikia audax*), but we retained migratory species that vary in their year-to-year appearance (e.g., Wahoo, *Acanthocybium solandri*). Manually, we removed any species that were classified as 'freshwater' as well as any species whose morphology did not have all ten morphological features required for our subsequent analysis (i.e. Anguilliformes, see 2.2 below).

We further refined both species lists to fishes that could be observed or caught shallower than 50m depth according to FishBase (www.fishbase.org; FishBase, 2019), OBIS (https://obis.org/,2020) or published literature (e.g. Francis, 2012; Roberts et al., 2020; Roberts et al., 2017; Roberts et al., 2015). This step retained some species that are most abundant at deeper depths, if the species had been recorded within the first 0-50m at any stage of their life.

To verify the species names used in both lists, and to align them with the taxonomic names used by FishBase, we used the validate_names function within the *rfishbase* package (Boettiger et al., 2012) in R Studio version 1.4.1106 (R Core Team, 2020; RStudio Team, 2020). Any species that were not validated (i.e. spelling errors, updated genus, or species with no records in FishBase) were manually cross referenced and either updated to match the taxonomic name used in the FishBase record or removed from the dataset and added to a secondary list of "query species" (see 2.5 Query Species).

3.3.2 Morphological measures

To examine morphological overlap between NZ native species and focal species, we obtained morphological data for each species from FishBase. The morphological measures provided by FishBase are generated by an algorithm that uses landmarks (i.e., precise morphological points that can be defined across all species) from specimen images submitted by citizens around the globe to provide relative (i.e. not absolute) measures (www.fishbase.org; Froese & Pauly, 2019).

Measurements were extracted using the morphometrics function in the rfishbase package (Boettiger et al., 2012) in R. Any species for which the measures were based on hand-drawn images rather than photographs were removed. We also removed any species that was missing data for any of our 10 chosen morphological measures: total length (TL), standard length (SL), fork length, head length (HL), pre-anal length (PAL), pre-dorsal length (PDL), pre-pectoral fin length (PPEL), eye diameter (ED), pre-orbital length (POL) and body depth (BD; Figure 1). For those species that do not have a forked tail (i.e. the measurement for FL was zero) we opted to place the measurement for TL in its place and retained the species in our dataset (e.g. Sandagers wrasse, *Coris sandeyeri*). When morphological data was available for more than one specimen per species, we used the largest specimen photographed, to increase the likelihood of capturing adult morphology.

Rather than examining morphological variation among groups based on pixels in a submitted image (i.e. the default morphological image from FishBase) we transformed these data to proportions (to enable shape comparison among species) and absolute linear measurements (to enable shape and size comparison among species). For the proportions data we scaled each measurement based on pixels, relative to the SL measurement based on pixels. To generate absolute linear measurements from these proportions data, we gathered the maximum size for each species and used this to generate measurements for all morphological features in millimetres (mm). We used maximum size as median and mean sizes for fishes were not available for most species whereas maximum size was regularly reported. When possible, these maximum sizes were gathered from Roberts et al. 2015 to provide a regionally relevant size for the species; where maximum size was not reported by Roberts et al. (2015), maximum size data was taken from FishBase (www.fishbase.org; Froese & Pauly, 2019). Maximum size was recorded as either total length (TL), standard length (SL) or fork length. Any species of interest that did not have morphological data available on FishBase were retained and added to the secondary list of “query species” (see 2.5 Query species).

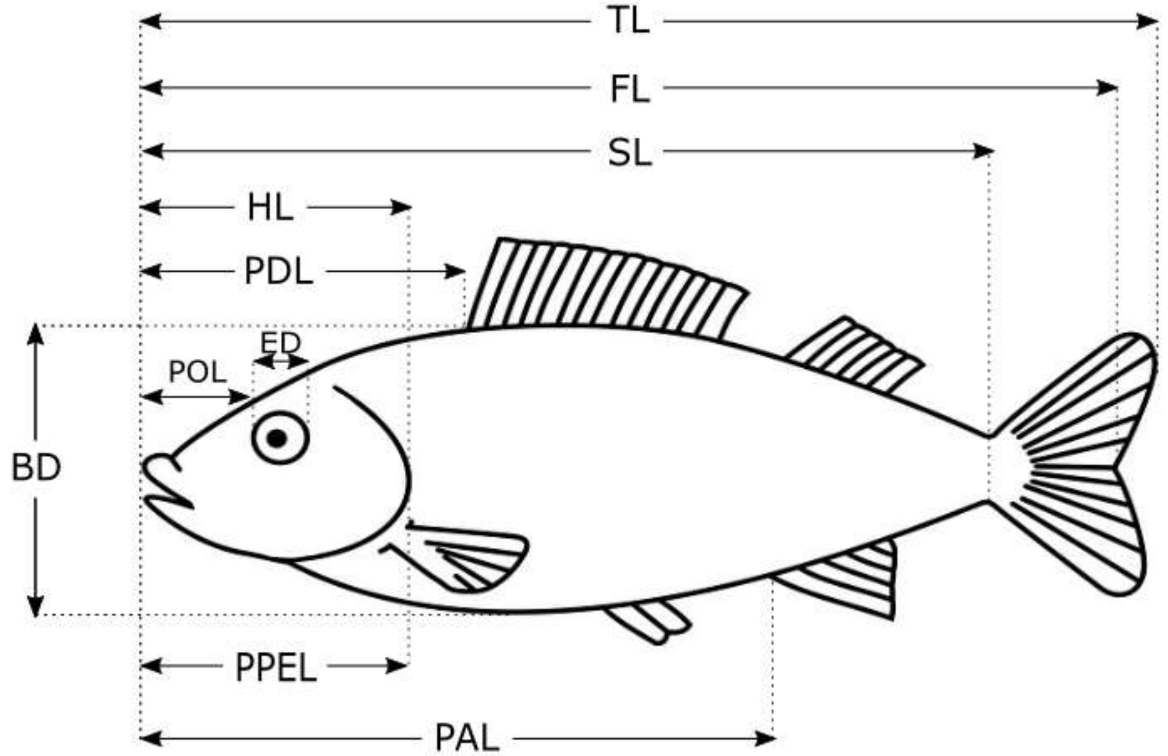


Figure 1: Lateral view of a generic fish illustrating the morphological measures used in this study, including: total length (TL), measured from the upper lip to the end of the caudal fin; fork length , measured from the upper lip to the fork in the caudal fin; standard length (SL), measured from the upper lip to the base of the caudal fin; head length (HL), measured from the upper lip to the opercula flap; pre-dorsal length (PDL), measured from the upper lip to the base of the first dorsal spine; pre-anal length (PAL), measured from the upper lip to the base of the first anal spine; pre-pelvic fin length (PPL), measured from the upper lip to the base of the pelvic spine; pre-pectoral length (PPEL), measured from the upper lip to the base of the pectoral fin; eye diameter (ED), measured from the diameter of the eye; pre-orbit length (POL), measured from the upper lip to the rim of the eye; body depth (BD), measured from the base of the dorsal fin to the base of the pelvic fin.

3.3.3 Trophic grouping

To examine potential overlap in diet between NZ native and focal species, we queried FishBase for trophic scores. In FishBase, trophic scores are based on diet information and/or food items, which are listed in many of the species' records. Items that are recorded in diet information and/or food items include: organisms that have been analysed from stomach contents or are known to be consumed by a given species. Dietary information held in FishBase is supported by over 800 citations and over 16,000 records (Carscallen et al., 2012; Froese & Pauly, 2019). For species that do not have diet information or food item records, FishBase calculates the trophic score based on the maximum size of the species and the trophic score of its closest relative (Freose & Pauly, 2019).

FishBase assigns discrete trophic scores to all species in the database, specifically: trophic score 1 is designated to primary producers and detritus (including associated bacteria); trophic scores between 2 and 2.19 are designated to primary consumers (i.e., herbivores and detritivores), which consume mainly plants or detritus; trophic scores between 2.2 and 2.79 are designated to omnivores, which consume mainly plants, detritus as well as animals; trophic scores greater than 2.8 are designated to secondary consumers, which consume a variety of invertebrates and vertebrates; and trophic scores greater than 4.0 are designated to tertiary consumers (carnivores), which consume mainly vertebrates (see www.fishbase.org).

Within our study, the secondary consumers group was very large (*see* Supplement 1). Accordingly, we chose to split the secondary consumers group (trophic scores between 2.8 – 3.99) into two groups. Specifically, species with a trophic score between 2.80 and 3.59 that consumed mainly invertebrates (including crustaceans, echinoderms and molluscs) were assigned to an invertivore group; and species with a trophic score between 3.60 and 3.99 that consumed both invertebrates and vertebrates were assigned to a mixed carnivore group (Table 1). There was a clear cut-off between the upper trophic levels of "invertivores" and the lower trophic level of "mixed carnivores", which fell approximately between 3.50 (where invertebrates were still the main diet items, with few vertebrates) and 3.60 (where the main diet items were vertebrates with fewer invertebrates; see appendix 1).

Our species list retained very small numbers of both herbivores and omnivores. To enable us to make robust statistical comparisons among dietary groups, we opted to combine the herbivores and omnivores into a combined 'lower trophic' group.

Table 1: Assigned trophic groups including the minimum and maximum trophic score of each group and the dietary items. Trophic scores and dietary items were sourced from www.fishbase.org.

Dietary Group	Trophic score	Main dietary items	Example of food items
Herbivore	2.00 – 2.19	plant items	benthic weeds, benthic algae, phytoplankton, detritus
Omnivore	2.20 – 2.79	plant items and invertebrates	benthic and/or planktonic crustaceans, worms, molluscs, echinoderms, cnidarians, fish eggs/larvae, sponges/tunicates, jellyfish/hydroids + some herbivore items
Invertivore	2.80 – 3.59	Invertebrates	benthic and/or planktonic crustaceans, worms, molluscs, echinoderms, cnidarians, fish eggs/larvae, sponges/tunicates, jellyfish/hydroids
Mixed Carnivore	3.60 – 3.99	Fishes and invertebrates	Benthic and planktonic crustaceans, worms, molluscs, echinoderms, cnidarians + some carnivore items
Carnivore	4.00 – 4.50	Cephalopods fishes and other vertebrates	bony fish, scales, mucus, skin, carcasses, cuttlefish, squid, turtles

3.3.4 Habitat Grouping

We also classified species into four broad habitat groups, specifically: true benthic, benthopelagic, coastal pelagic and oceanic pelagic based on their adult habitat preferences and lifestyle. True benthic species were considered to spend the majority of their time within or in contact with, the sea floor or substrates. Examples of species in this group include flatfishes, lizardfishes and goatfishes. Benthopelagic species swim freely in the water column but are closely associated to reefs or seafloor, spending some of their time interacting with the substrate. Examples of species in this group are butterflyfishes, wrasses, damselfishes and perches, who all forage or find shelter on substrate, but spend most of their time above the seafloor. Coastal pelagic species are considered to spend most of their time in the epipelagic to mesopelagic zones within the limits of the continental shelves, spending very little time on or near substrates. Examples of species in this group include mackerel, mullet, jacks and anchovy. Oceanic pelagic species are those that spend most of their time in the epipelagic to mesopelagic zones outside the limits of continental shelves. They may be considered migratory species and rarely associate with shallower coastal waters or the benthos. Examples of species in this group include sunfish, tuna, and marlin (*see* Supplement 1 for full list).

3.3.5 Query Species

For all species that did not have a record within FishBase, were lacking morphological measures on FishBase, or species with measures based on hand-drawn images in FishBase, we held in a secondary 'query' list. We cross referenced this list and retained 77 species that were from taxonomic families already included in our current dataset, so as to maximise sampling within these families. For these species, where possible, photographic images were provided by the authors of The Fishes of New Zealand book (Roberts, Stewart, & Struthers, 2015) or from the National Fish Collection of Te Papa Tongarewa Museum of New Zealand. The 10 standard measurements (as described in 2.2 morphological measures) were measured for each species from the provided photographic images using ImageJ (Schneider et al., 2012) using a landmark based approach to attain linear measurements.

Our final dataset comprised 244 species including 105 NZ Native and 139 Focal species across 79 taxonomic families (Supplement 1).

3.3.6 Statistical analysis

To examine morphological differences between NZ native species and focal species belonging to the same trophic group and habitat group we used a univariate linear model assuming a gaussian error using the lm function in the *base* R package (R Core Team, 2020). A linear model was fit to each response variable in turn, where the response variables were the ten morphological measurements, specifically; total length (TL), standard length (SL), fork length (FL), head length (HL), pre-anal length (PAL), pre-dorsal length (PDL), pre-pectoral fin length (PPEL), eye diameter (ED), pre-orbital length (POL) and body depth (BD). For the comparison of trophic groups, we used four planned independent comparisons comparing differences in morphological measurements between NZ native and focal mixed omnivores, NZ native and focal invertivores, NZ native and focal mixed carnivores and NZ native and focal carnivores. For the comparison of habitat groups, we used four planned independent comparisons comparing differences in morphological measurements between NZ native and focal true benthic species, NZ native and focal benthopelagic species, NZ native and focal coastal pelagic species and NZ native and focal oceanic pelagic species. Using planned independent comparison allowed us to directly assess the hypothesis of interest using one-degree of freedom t-tests without wasting degrees of freedom on uninformative comparisons, for example the differences between focal carnivores and NZ native species in lower trophic groups. The results were then plotted using the *ggplot2* R package (Wickham, 2016).

To examine morphological overlap in NZ native and focal species, we used a linear discriminant analysis (LDA) using the lda function of the *MASS* R package (Venables & Ripley, 2002). LDA calculates the axes of morphological variation that result in the maximum separation between the group centroids. The response variable in the LDA analyses were either trophic group or habitat group and the ten morphological measurements for the NZ native species, were the predictor variables. Focusing on the NZ native species allowed us to depict the morphospecies of the resident fish fauna that focal species would be invading. For trophic group, we examined morphological differences among lower tropic (herbivores and omnivores; n=24), invertivore (n=113), mixed carnivore (n=52) and carnivore (n=55). For habitat group we examined morphological differences among true benthic (n=58), benthopelagic (n=118), coastal pelagic (n=41) and oceanic pelagic (n=27). Overall, there were four LDA models examining absolute inter-landmark distances and proportional inter-landmark distances for both habitat groups and trophic groups.

For each LDA model we projected the scores for the focal species into the NZ native species morphospace to determine their overlap with the existing fish fauna of NZ. For each focal species we then determined the identity of the NZ native species with the most similar morphology (i.e., the NZ native species with the minimum Euclidean distance from the focal species). Furthermore, to determine which NZ native species are at greatest risk of increased competition from focal species, we identified the NZ native species with the most similar morphology that also fell within the same habitat and trophic group as the focal species.

3.4 Results

3.4.1 Morphological differences between Focal species and NZ Native species within the same trophic group

The univariate results based on absolute inter-landmark distances revealed no significant differences between NZ native and focal species within the invertivore, mixed carnivore and carnivore groups. For the lower trophic group (including herbivores and omnivores), pre-anal length (PAL) was marginally larger in NZ native species compared with the focal species (P = 0.088; Figure 2; Supplement 2; Table S2.1).

The univariate results based on inter-landmark distances scaled by standard length (SL) revealed that the focal species and NZ native species were most distinct from each other within the lower trophic group (including herbivores and omnivores) where, relative to standard length, NZ natives had smaller total lengths (TL; P = 0.02), smaller eye diameters (ED; P = 0.065) and body depths (BD; P = 0.001) than focal species. NZ native invertivores had smaller pre-anal lengths than focal invertivores (PAL; P = 0.05) and the pre-orbital length (POL) of focal mixed carnivores was marginally larger than for NZ native mixed carnivores relative to standard length (P = 0.091). There were no significant differences in focal and NZ native carnivores shape (Figure 3; Supplement 2; Table S2.2)

The LDA based on absolute inter-landmark distances (Figure 4) revealed that NZ native carnivores had the highest classification success (92%). NZ native invertivores also had high classification success (75%), followed by lower trophic group (73%) and mixed carnivores (63%; Supplement 2; Table S2.3). Nearly all of the species within the focal lower trophic group occupied a similar morphospace to the NZ native lower trophic group (97.74%, n=18), with only one species (*Naso Unicornis*) occupying a different morphospace. The majority of focal invertivores (73.33%; n=44) occupied a similar morphospace to NZ native invertivores. Many of the focal mixed carnivores occupied the same morphospace as NZ native mixed carnivores

(62.5%; n = 15) and similarly, most NZ native and focal carnivores occupied the same morphospace (63.89%; n=23; Figure 4). In total, 63 NZ native species were a close morphological match to at least one of the 139 focal species with several NZ native species being the closest match for multiple focal species. For example, the NZ native wrasse, *Notolabrus fucicola* was the closest morphological match for four focal species (*Bodianus flavifrons, Parma polylepis, Abudefduf vaigiensis and Monocentris japonica*). Overall, 35 of the NZ native species had similar morphology and were in the same trophic group as 55 focal species (Supplement 2; Table S2.4).

The LDA based on inter-landmark distances scaled by standard length (SL) revealed that the NZ native lower trophic group had the highest classification success (98%), followed by carnivores (72%), invertivores (68%) and mixed carnivores (62%; Supplement 2; Table S2.5). Overall, 57.89% (n=11) of focal lower trophic group had a similar shape as NZ native species in the lower trophic group. The majority of focal invertivores (73.33%; n=44) occupied a similar shape morphospace to NZ native invertivores. Many of the focal mixed carnivores occupied the same shape morphospace as NZ native mixed carnivores (58.33%; n = 14). Nearly all NZ native and focal carnivores occupied the same shape morphospace (83.33%; n=30; Figure 5). Sixty NZ native species had similar shape to at least one of the 139 focal species with several NZ native species being a close morphological match for multiple focal species. Overall, 33 NZ native species had similar shape and were in the same trophic group as 59 focal species (Supplement 2; Table S2.6).

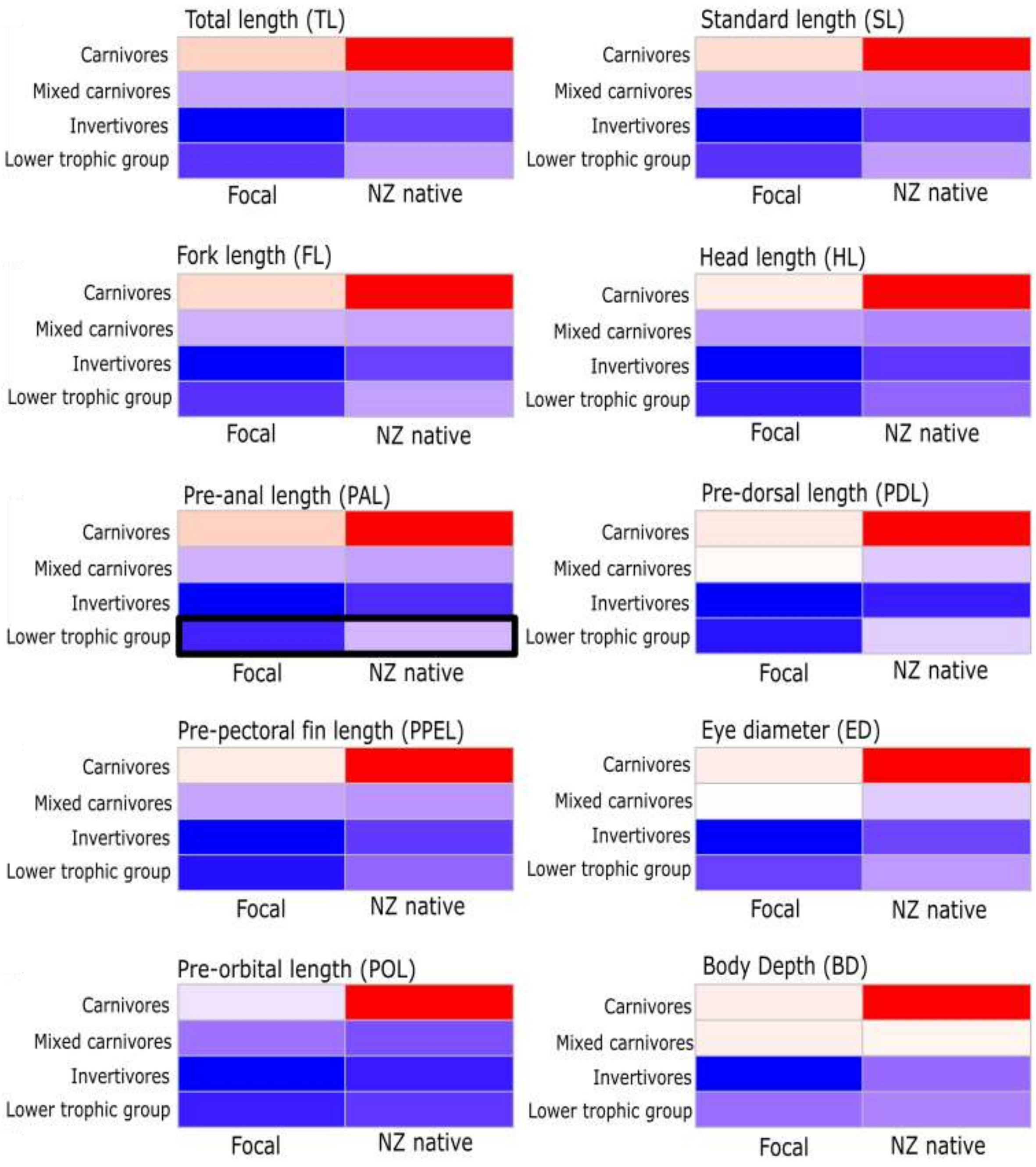


Figure 2: Pairwise comparisons of absolute measures for ten morphological features of NZ native and focal species within four trophic groups: lower trophic (herbivore and omnivore), invertivore, mixed carnivore and carnivore. The intensity of red or blue indicates the relative absolute length of the morphological measure for that group. Darkest red denotes the largest morphological measurement for a given trophic group and darkest blue is the smallest morphological measure for a given trophic group. For example, in the comparison of total length (TL), NZ native carnivores are darkest red, indicating they have the largest TL, whereas focal invertivores have the smallest TL (darkest blue). Significant morphological differences between focal species and NZ native species within each trophic group are indicated by the heavy black outline.

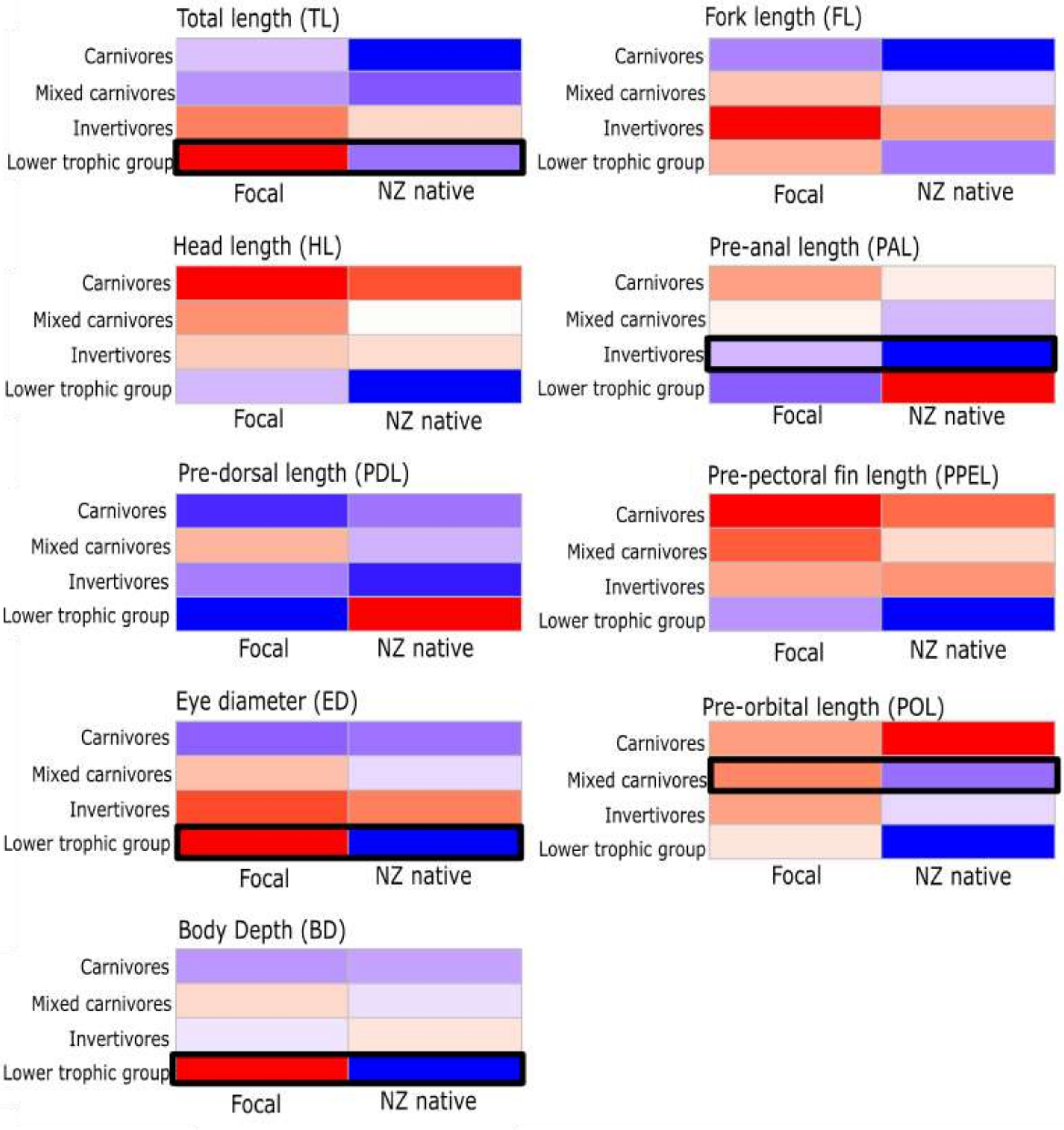


Figure 3: Pairwise comparisons of inter-landmark distances relative to standard length for nine morphological features (providing a comparison on shape) of NZ native and focal species within four trophic groups: lower trophic (herbivore and omnivore), invertivore, mixed carnivore and carnivore. The intensity of red or blue indicates the relative proportions of the morphological feature for that group of the morphological measure for that group. Darkest red denotes the proportionally largest morphological feature for a given trophic group and darkest blue is the proportionally smallest morphological feature for a given trophic group. For example, in the comparison of total length (TL), the focal lower trophic group is darkest red, indicating they have the proportionally largest TL, whereas NZ natives in the carnivore trophic group have the smallest TL in proportion to their Standard Length (SL; darkest blue). Significant morphological differences between focal species and NZ native species within each trophic group are indicated by the heavy black outline

Figure 4: Linear discriminant analysis (LDA) of variation in fish morphology (absolute inter-landmark distances) among trophic groups. Ellipses are the 95% confidence ellipses for the NZ native fish fauna from the LDA. The closed symbols are focal species that fell within the confidence ellipse of NZ native species of the same trophic group. Focal species that fell outside of the 95% confidence ellipse of NZ native species of the same trophic group are indicated in text.

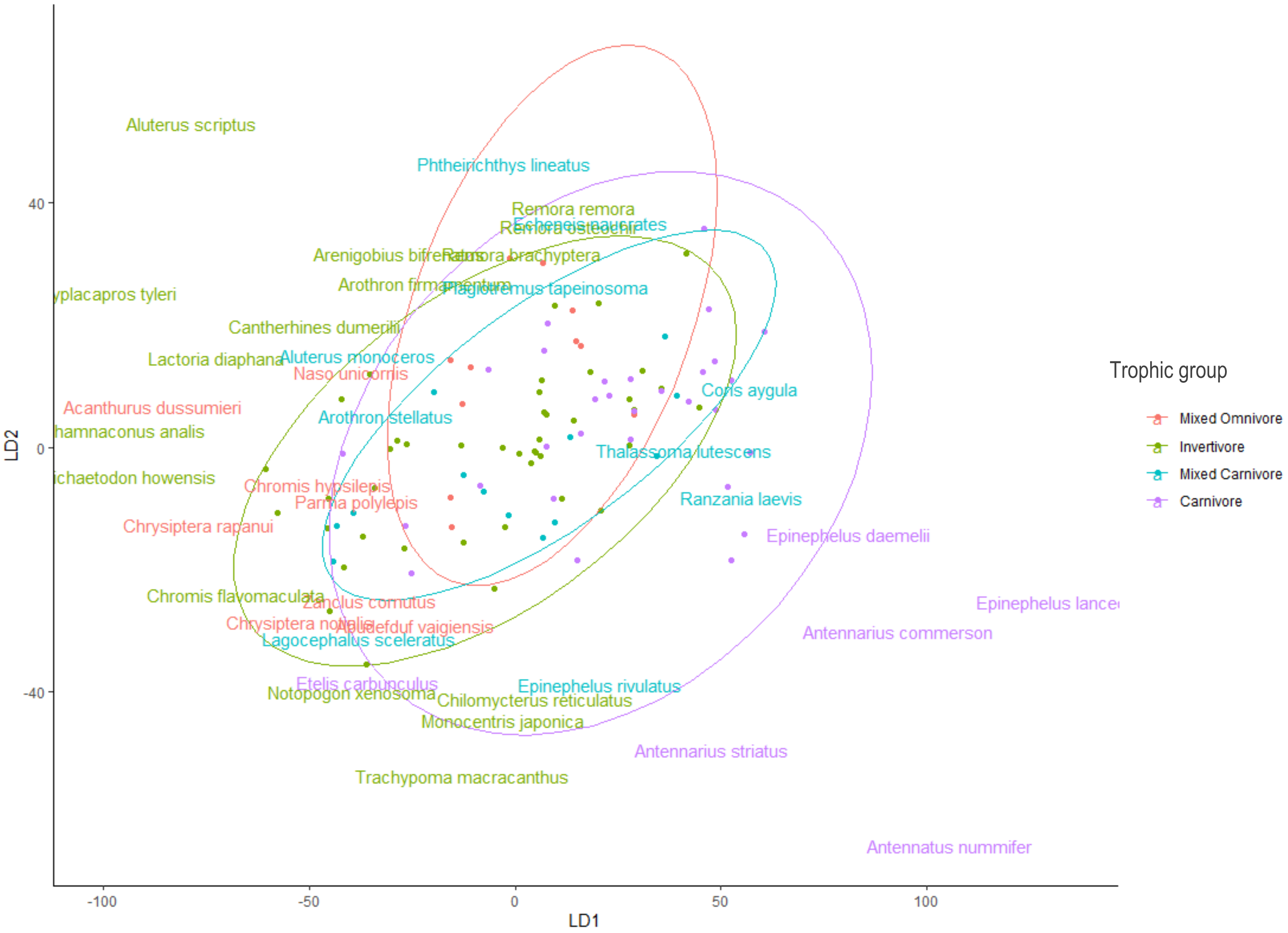


Figure 5: Linear discriminant analysis (LDA) of variation in fish morphology (scaled by standard length; SL) among trophic groups. Ellipses are the 95% confidence ellipses for the NZ native fish fauna from the LDA. The closed symbols are focal species that fell within the confidence ellipse of NZ native species of the same trophic group. Focal species that fell outside of the 95% confidence ellipse of NZ native species of the same trophic group are indicated in text.

3.4.2 Morphological differences between Focal species and NZ Native species within the same habitat group

The univariate results based on absolute inter-landmark distances revealed that focal and NZ native species were most distinct from each other within the oceanic pelagic group where NZ natives were larger in body depth (BD; *P* = 0.016), pre-orbital length (POL; *P* = 0.005), head length (HL; *P* = 0.006), pre-pectoral fin length (PPEL; *P* = 0.007), eye diameter (ED; *P* = 0.044) and marginally larger in pre-anal length (PAL; *P* = 0.063), pre-dorsal length (PDL; *P* = 0.063) and total length (TL; *P* = 0.085). There were no significant differences between NZ native and focal species within coastal pelagic, benthopelagic or true benthic groups (Figure 6; Supplement 3; Table S3.1).

The univariate results based on inter-landmark distances scaled by standard length (SL) revealed that focal and NZ native species differed from each other within the oceanic pelagic group where, relative to standard length, focal species had smaller pre-pectoral fin length (PPEL; *P* = 0.037), as well as proportionally smaller head lengths (HL; *P* = 0.007) and body depths (BD; *P* = 0.01) than NZ native species. Conversely, focal coastal pelagic species had larger total length (TL; *P* value = 0.041), body depth (BD; *P* = 0.035) for fork length (FL; *P* = 0.094) than NZ native coastal pelagic species. Focal benthopelagic species had larger pre-orbital lengths (POL; *P* = 0.021) than NZ native benthopelagic species, and focal true benthic species had larger head length (HL; *P* = 0.018) and pre-pectoral fin length (PPEL; *P* = 0.075; Figure 7; Supplement 3; Table S3.2) than NZ native true benthic species.

The LDA based on absolute inter-landmark distances (Figure 8) revealed that oceanic pelagic had the highest classification success (87%), followed by true benthic (82%), benthopelagic (75%) and coastal pelagic (74%; Supplement 3; Table S3.3). Nearly all oceanic pelagic species occupied a similar morphospace (87.50%; n=14) with two focal oceanic pelagic species occupying a different morphospace (*Istiophorus platypterus, Masturus lanceolatus*). Majority of NZ native and focal species that were coastal pelagic occupied a similar morphospace (70.59%; n=12) and similarly, most focal benthopelagic species and NZ native benthopelagic species occupied the same morphospace (75.95%; n=60). Most focal and NZ native true benthic species occupied a similar morphospace (70.37%; n=19; Figure 8). In total, 67 NZ native species were a close morphological match to at least one of the 139 focal species, with several NZ native species being a closest match for multiple focal species. Overall, 35 of the NZ native species had similar morphology and were in the same habitat group as 58 focal species (Supplement 3; Table S3.4).

The LDA based on inter-landmark distances scaled by standard length (SL) revealed the coastal pelagic group had the highest classification success (82%), closely followed by true benthic (81%), Benthopelagic (79%) and oceanic pelagic (76%; Supplement 3; Table S3.5). Half of focal true benthic species occupied the same shape morphospace as NZ native true benthic species (51.85%, n=14). Majority of focal and NZ native benthopelagic species occupied the same shape morphospace (78.48%, n=62) and similarly, focal coastal pelagic species often occupied similar shape morphospace to NZ native coastal pelagic species (76.47%, n=13). All focal and NZ native oceanic pelagic species occupied the same shape morphospace (100%, n=16; Figure 9). In total, 62 NZ native species had similar shapes to at least one of the 139 focal species, with several NZ native species being a close morphological match for multiple focal species. Overall, 36 NZ native species had similar shapes and were in the same habitat group as 55 focal species (Supplement 3; Table S3.6).

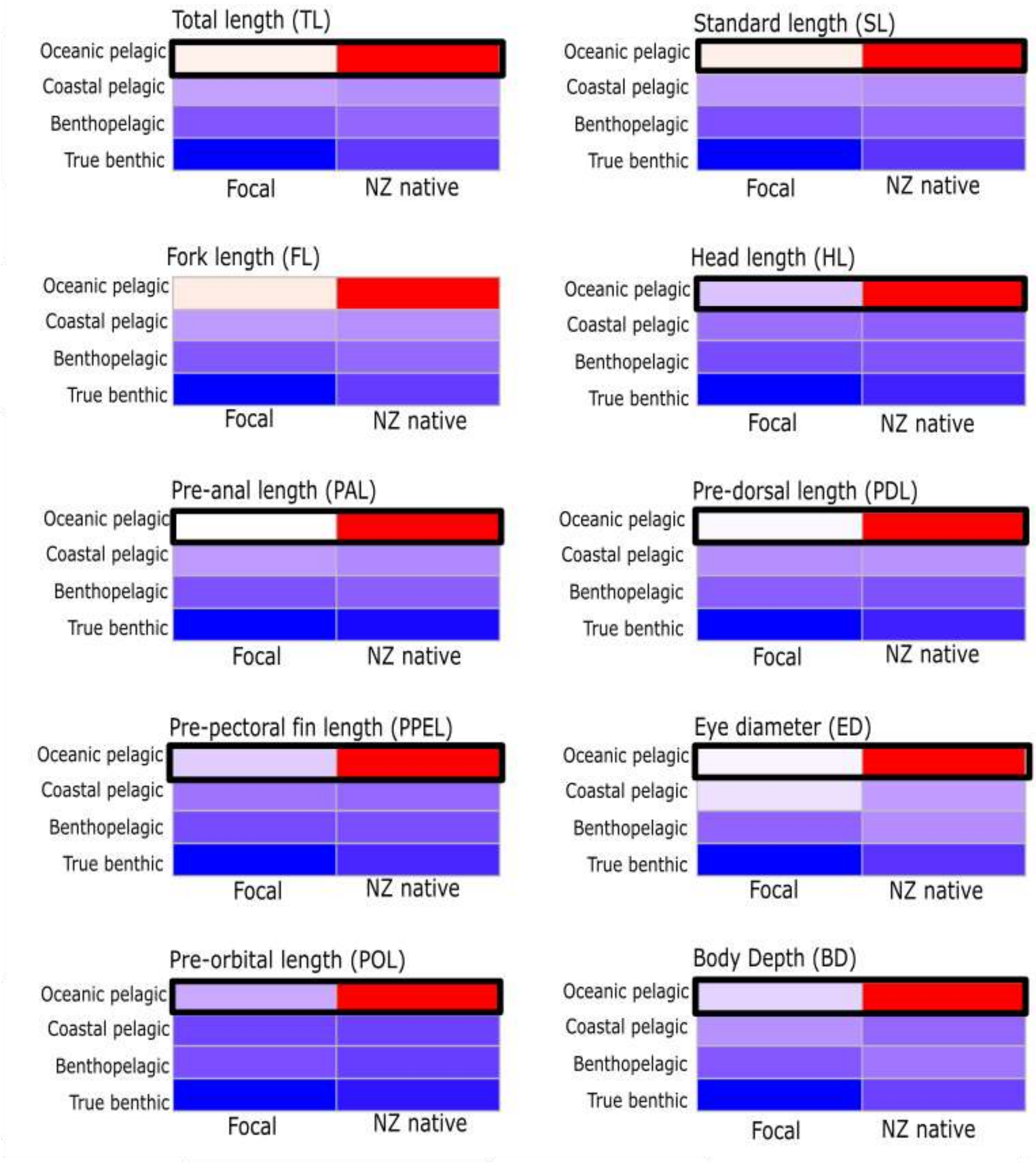
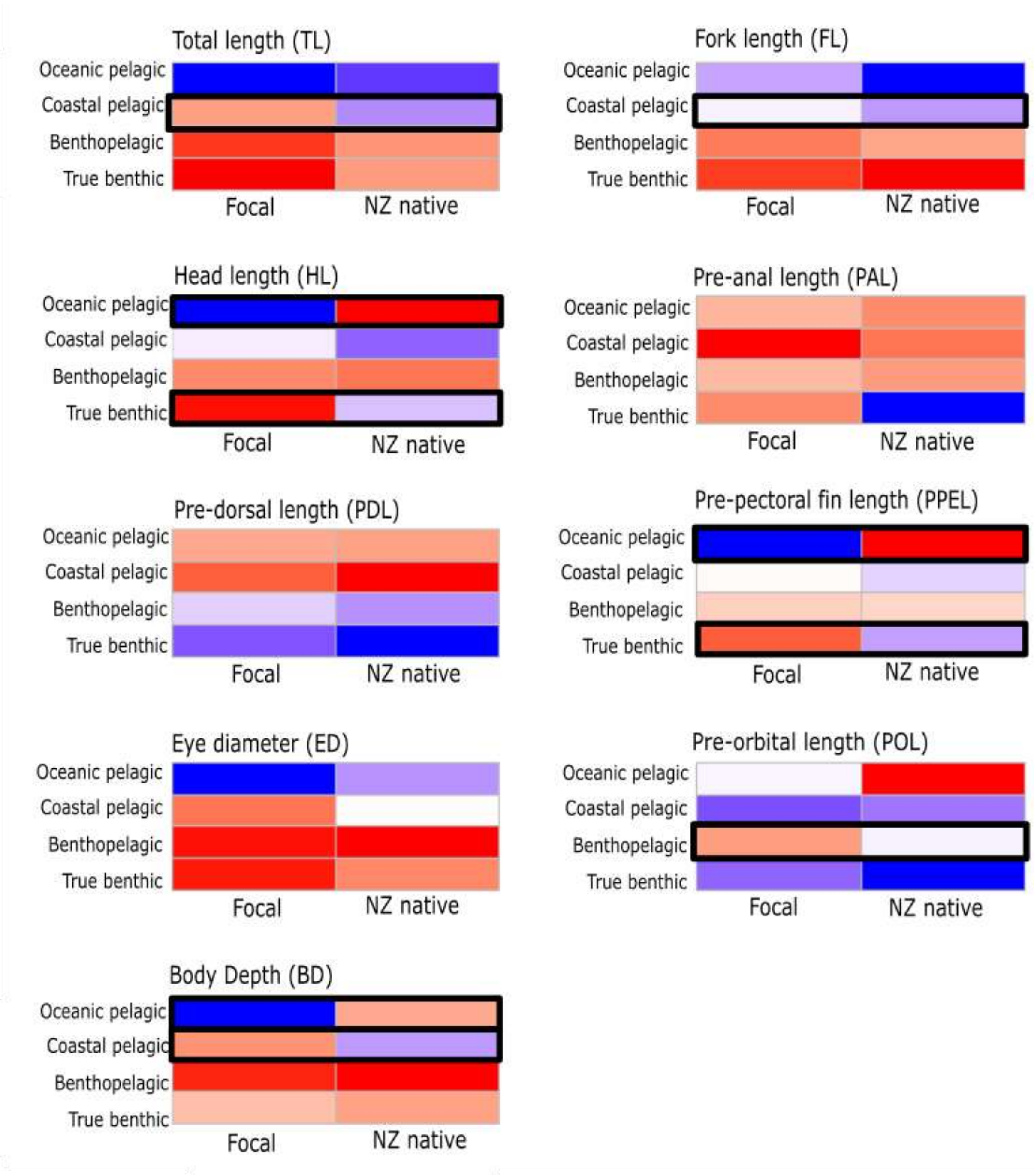


Figure 6: Pairwise comparisons of absolute measures for ten morphological features of NZ native and focal species within four habitat groups: true benthic, benthopelagic, coastal pelagic and oceanic pelagic. The intensity of red or blue indicates the relative absolute length of the morphological measure for that group. Darkest red denotes the largest morphological measurement for a given habitat group and darkest blue is the smallest morphological measure for a given habitat group. For example, in the comparison of Total length (TL), NZ native oceanic pelagic species are darkest red, indicating they have the largest TL, whereas focal true benthic species have the smallest TL (darkest blue). Significant morphological differences between Focal species and NZ Native species within each habitat group are indicated by the heavy black outline.



Total length (TL)

Fork length (FL)

Head length (HL)

Pre-anal length (PAL)

Pre-dorsal length (PDL)

Pre-pectoral fin length (PPEL)

Eye diameter (ED)

Pre-orbital length (POL)

Body Depth (BD)

Figure 7: Pairwise comparisons of inter-landmark distances relative to standard length for nine morphological features (providing a comparison on shape) of NZ native and focal species within four habitat groups: true benthic, benthopelagic, coastal pelagic and oceanic pelagic. The intensity of red or blue indicates the relative proportions of the morphological feature for that group of the morphological measure for that group. Darkest red denotes the proportionally largest morphological feature for a given habitat group and darkest blue is the proportionally smallest morphological feature for a given habitat group. For example, in the comparison of total length (TL), the focal true benthic group is darkest red, indicating they have the proportionally largest TL, whereas NZ natives in the oceanic pelagic group have the smallest TL in proportion to their Standard Length (SL; darkest blue). Significant morphological differences between focal species and NZ native species within each habitat group are indicated by the heavy black outline.

Figure 8: Linear discriminant analysis (LDA) of variation in fish morphology (absolute inter-landmark distances) among habitat groups. Ellipses are the 95% confidence ellipses for the NZ native fish fauna from the LDA. The closed symbols are focal species that fell within the confidence ellipse of native species of the same habitat group. Focal species that fell outside of the 95% confidence ellipse of NZ native species of the same habitat group are indicated in text.

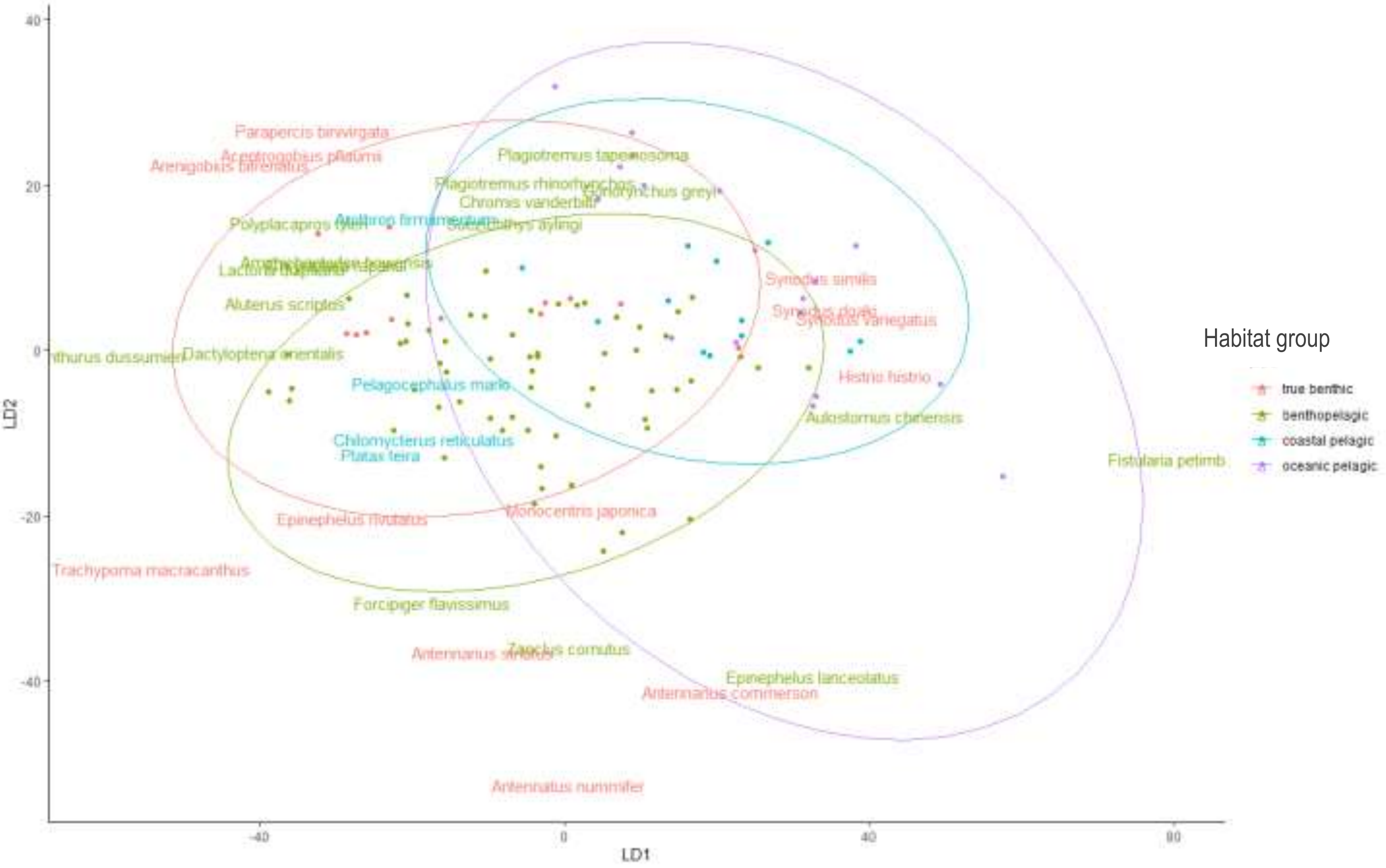


Figure 9: Linear discriminant analysis (LDA) of variation in fish morphology (scaled by standard length; SL) among habitat groups. Ellipses are the 95% confidence ellipses for the NZ native fish fauna from the LDA. The closed symbols are focal species that fell within the confidence ellipse of NZ native species of the same habitat group. Focal species that fell outside of the 95% confidence ellipse of NZ native species of the same habitat group are indicated in text.

3.4.3 Morphologically similar focal species and NZ native species within the same trophic group and habitat group

Overall, nine focal species were most morphologically similar to a NZ native species (based on Euclidean distance between species for the LDA of inter-landmark distances) of the same trophic group and habitat group (Table 2).

Table 2: Focal species that were most morphologically similar (based on absolute measures) to a NZ Native species of the same trophic group and habitat group.

Focal species				**NZ native match**	
Common name	**Scientific name**	**Trophic group**	**Habitat group**	**Common name**	**Scientific name**
Clown toado	*Canthigaster callisterna*	invertivore	benthopelagic	Snipefish	*Macroramphosus scolopax*
Silverspot	*Chironemus maculosus*	invertivore	true benthic	Southern bastard cod	*Pseudophycis barbata*
Sargassum fish	*Histrio*	mixed carnivore	true benthic	NZ halfbanded perch	*Hypoplectrodes dimidius*
Sailfish	*Istiophorus platypterus*	carnivore	oceanic pelagic	Swordfish	*Xiphias gladius*
Sharptail sunfish	*Masturus lanceolatus*	mixed carnivore	oceanic pelagic	Sunfish	*Mola alexandrini*
Latchet	*Pterygotrigla polyommata*	mixed carnivore	true benthic	Jock stewart	*Helicolenus percoides*
Kermadec barracuda	*Sphyraena waitii*	carnivore	oceanic pelagic	Balloonfish	*Sphoeroides pachygaster*
Rainbowfish	*Suezichthys arquatus*	invertivore	benthopelagic	Slender roughy	*Optivus elongatus*
Darkvent leatherjacket	*Thamnaconus analis*	invertivore	benthopelagic	Leatherjacket	*Meuschenia scaber*

3.5 Discussion

As range-extending species increase their establishment and abundance in temperate systems, understanding how these species will assimilate is important in predicting how they might impact resident species and ecosystem function (Clavel et al., 2010; Edelist et al., 2013; Figueira et al., 2009). Here, we compared the diet and habitat preferences as well as the morphology of 139 rare, tropical and subtropical fishes that are arriving in NZ, with 105 NZ native and resident fishes to predict which species may compete with NZ resident taxa and/or alter NZ's fish morphospace by filling a vacant niche. The focal species had high levels of morphological overlap with NZ native species across the four trophic groups (74.37%; n = 100) and four habitat groups (76.10%; n = 105). Across the four trophic groups, we identified 39 focal species with morphology that differed from NZ native species, and 34 focal species differed in morphology from NZ native species across the four habitat groups. Nine focal species overlapped with NZ native species in morphology, trophic group and habitat group; of these, two of the NZ native species are endemic to Aotearoa New Zealand.

Morphology may limit a range-extending species ability to persist long-term in a novel environment, determining its ability to compete, avoid predation, and adapt to environmental changes (Adamczuk, 2022; Albouy et al., 2011; Carscallen et al., 2012). Our results show that carnivorous fishes were larger than all other trophic groups of fishes, with NZ native carnivores being largest (Howarth et al. 2021). Fishes that were invertivores were smaller than all other trophic groups, with focal invertivores being the smallest. When comparing species within habitat groupings, oceanic pelagic species were larger than fishes found in other habitat groups, with NZ native oceanic pelagic species being the largest. Fishes that were true benthic were smaller than all other habitat groups, with focal true benthic species being smallest. These results are supported by our general understanding that that carnivores and oceanic pelagic species are often predators and/or migratory, which has been found to confer larger body sizes. Additionally, our finding that NZ native species tended to be larger in size, follows ecogeographical rules that suggest species at higher latitudes will be larger than those found in lower latitudes (e.g., Bergmann, 1847). This advantage of NZ native species afforded by their large size at temperate latitudes however, may not persist in a changed ocean climate. Here, the absolute linear and proportions measurements were generated using the maximum size of each species, opposed to the mean or median size, as these were often unavailable. Using the mean or median size should be considered for future analyses to provide results on the average size.

The external morphology of fishes is often used as a proxy for niche differentiation among co-occurring species as well as for understanding diet requirements (Arrontes, 2002; Smith et al., 2016). In our analysis we found a high level of morphological overlap between focal species and NZ native species within trophic groups (74.37%), suggesting that focal species will likely compete with NZ native species for dietary items if focal species continue to increase in numbers and/or become resident in NZ. Because of this competition, NZ native species may be displaced by the range-extending species. Such displacement of native fishes has been recorded in several regions globally, for instance, in the Mediterranean where newly established taxa out-competing native species causing a decline in endemic species and a shift in biodiversity (Edelist et al., 2013). In extreme cases, increases in the abundance of lower trophic taxa (i.e., herbivores and omnivores) has led to a decrease in biomass of keystone kelp species (Vergés, Steinberg, et al., 2014), causing phase shifts from macroalgae to barrens (Ling & Johnson, 2009), ultimately reducing biodiversity (Bates et al., 2014; D. Booth et al., 2018; Delaney et al., 2007). To better anticipate whether we will see similar patterns of species displacement in Aotearoa New Zealand, requires an understanding of which range-extending species pose an imminent threat based on their stage of establishment in NZ, as well as what specific NZ Native species they overlap with in habitat and geographical distribution.

Recent research (Middleton et al. 2021, *in press*) has described the current range extent of several tropical and subtropical species in NZ, as well as classifying whether they have undergone a recent range-extension in NZ, or are increasing in arrival frequency but do not yet persist (Middleton et al., *in press*). Species confirmed to have extended their ranges include Indo Pacific sergeant *Abudefduf vaigiensis*, Eyestripe surgeonfish *Acanthurus dussumieri*, Lord Howe coralfish *Amphichaetodon howensis* and Southern damselfish *Chrysiptera notialis*. According to our analysis, all of these species overlapped in morphology with NZ native species within their trophic groups. Furthermore, Clown toado *Canthigaster callisterna* and Painted moki *Morwong ephippium* - both Australasian subtropical species - have high morphological and trophic overlap with the NZ native species Snipefish *Macroramphosus scolopax* and Trumpeter *Latris lineata*, respectively. While the current range extents of *Canthigaster callisterna* and *Morwong ephippium* are exclusively on the northeastern coastline of NZ and are stable (Middleton et al., *in press*), if these species continue to increase in abundance and warmer temperatures allow them to extend into novel locations, they may compete with NZ native species such as *Macroramphosus scolopax* or *Latris lineata* for dietary items. Of particular concern are tropical and subtropical species already known to co-occur with resident NZ native species in their habitat. For instance, Blue knifefish *Labracoglossa nitida* has morphological overlap with NZ native species of the same trophic groups, including Blue maomao *Scorpis violacea*, with which it is known to often co-occur (based on the results from Chapter Two).

Morphologically similar species occupying the same habitat can increase competition among species for space and diet items as well as increase pressure on prey items and ecosystem function (Azzurro et al., 2014; Smith et al., 2016). Our analysis revealed a high level of morphological overlap between focal and NZ native species within habitat groups (76.10%), indicating that focal species will likely occupy similar habitat spaces as NZ residents, potentially causing novel species interactions and increased competition. Similar to the trophic group results, this analysis revealed that four confirmed range-extending species *Abudefduf vaigiensis*, *Acanthurus dussumieri*, *Amphichaetodon howensis* and *Chrysiptera notialis* overlapped in morphology with the NZ natives within their habitat groups. Specifically, *Acanthurus dussumieri* showed significant morphological overlap with NZ native species Scarlet wrasse *Pseudolabrus miles*, indicating that novel species interactions may occur if *Acanthurus dussumieri* continues to range-extend and increase in abundance. Focal species *Labracoglossa nitida* and *Atypichthys latus* also had morphological overlap with NZ native species of the same habitat groups, highlighting their potential for competition with NZ native species, should their NZ populations extend or increase in abundance. Additionally, Bluefish *Girella cyanea* (a species-of-interest in Chapter Two) also showed morphological overlap within its habitat group, particularly with NZ native Blue moki *Latridopsis ciliaris* which is endemic to NZ. While the range extent of *Girella cyanea* is currently stable in NZ waters (Middleton et al., *in press*), monitoring the distribution and abundance of this species may be important, given its morphological and habitat overlap with endemic, recreationally and commercially important NZ species such as Tarakihi *Nemadactylus macropterus* and Porae *Nemadactylus douglasii*. Furthermore, confirmed range-extender Mahimahi *Coruphaena hippurus* (Middleton et al., *in press*) showed morphological overlap with NZ native species in its habitat group, particularly with Sunfish *Mola alexandrini*. However, given that *Coruphaena hippurus* and *Mola alexandrini* are both oceanic pelagic species, highly migratory and don’t share trophic groups (*Coruphaena hippurus* is a carnivore and *Mola alexandrini* is a mixed carnivore) it is unlikely for these species to compete for food items.

As the arrival of tropical and subtropical species increases in frequency and many begin to colonise temperate systems, it is crucial to understand which resident species are at greatest risk of being outcompeted. In many other range-extension scenarios, it is often the endemic and native species at particular risk of being out-competed due to their unique niche and habitat requirements (e.g., Adamczuk, 2022; Albins & Hixon, 2011; Edelist et al., 2013). Our analysis highlighted nine focal species that overlapped with NZ native species across all three categories of morphology, trophic group and habitat group. Except for one species (*Canthigaster callisterna*), the range extent and range dynamics of these species in Aotearoa New Zealand are unknown (Middleton et al., *in press*), signalling that closer monitoring of these species via citizen science (Chapter Two, Middleton et al., *in press*), or alternative methods such as using environmental DNA (e.g. Balasingham et al., 2018; Nester et al., 2020) is warranted. By prioritizing the monitoring of focal species most likely to threaten NZ native species we can gain a better understanding of their range extents and abundance changes, and limit the potential impacts on NZ native species and their habitats.

Our analysis also suggests that there are particular NZ Native species that are most at risk of being impacted by tropical and subtropical species colonising NZ. For instance, Rock cod *Lotella rhacina* was the NZ native species that was most morphologically similar to 16 different focal species, that it also shared habitat and/or trophic group with. Additionally, Trevally *Pseudocaranx dentex* - an important species in the NZ recreational fishery - was most morphologically similar to eight different focal species that is also shared a habitat and/or trophic group with, while another important recreational fish, Red gurnard *Chelidonichthys kumu* was morphologically similar to seven different focal species within its habitat and/or trophic group. Furthermore, two endemic species Slender roughy *Optivus elongatus* and Olive rockfish *Acanthoclinus fuscus* both overlapped with 6 different focal species (Supplementary Tables 5 and 11). These results emphasise the need for monitoring NZ Native species (as well as tropical and subtropical species). By extending monitoring programmes to include NZ native species most at risk, there is the potential to mitigate the impacts before it’s too late.

Arriving species that are morphologically different to the resident taxa in the novel environment may have more opportunity to exploit an unoccupied niche space, reducing competition and overall impact on resident taxa (Kingsbury et al., 2019; Schoener, 1974). The analyses revealed 48 species occupied a morphospace distinct from NZ native fishes according to their trophic group (39 species) and habitat group (34 species). Interestingly, our analysis confirmed that the sub-tropical species Spotted black groper *Epinephelus daemelii*; Middleton et al., *in press*) is morphologically different to species within its trophic group and habitat group, indicating it may possibly occupy a novel niche if it continues to repatriate in NZ waters. Similarly, Toadstool groper *Trachypoma macracanthus* differed in morphology to all other NZ natives within its trophic group and habitat group. While the range-extent of *Trachypoma macracanthus* is unknown, we are aware of potential increases in abundance through anecdotal records such as those from Middleton et al., (*in press*) and from the observations of this species in Chapter Two. An increase in abundance of these novel predatory fishes may negatively impact native prey species. For instance, the introduction of Lionfish *Pterois volitans* in Florida and the Caribbean has caused an extreme decline in native species due to Pterois volitans habitat generality, competitive ability and its high predation and consumption rates of small endemic fishes (Albins & Hixon, 2008; Albins & Hixon, 2011). These impacts on the food chain and ecosystem function cannot be predicted using our analyses, but are also important to understand in order to predict which tropical and subtropical species are most likely to impact NZ’s fish fauna, other biodiversity, and marine ecosystems.

The frequency of novel species arrivals in lower latitudes will continue to increase as global climate change drives marine taxa to extend their ranges (Melbourne-Thomas et al., 2022; Poloczanska et al., 2016; Wernberg et al., 2012). While NZ has remained relatively unimpacted by climate change to date, this will not always be the case. In a depauperate system with a high level of endemic and specialist species, the establishment of generalist range-extending species increases the potential for native species displacement, biotic homogenisation, the loss of biodiversity and ultimately, functional changes to ecosystems. Through species morphology and ecological niche (habitat and trophic group) we can start to understand potential species interactions and their likely competition as well as the impact of novel species on ecosystem function. Our approach informs morphological and ecological niche overlap for NZ native and out-of-range tropical, subtropical and rare fishes, indicating the potential for interspecific competition and displacement of NZ native species, should focal species continue to arrive and establish in NZ.

3.6 Supplementary Data

3.6.1 Supplement 1 – Full dataset

Raw data for 244 marine fishes used in this analysis including 139 focal species and 105 NZ native species, their trophic groups, habitat groups and morphological measurements. The “Terms” tab provides an explanation of the column headers, descriptions and vocabulary used in the “SpeciesList”. The “SpeciesList" tab contains the raw data for each of the 224 marine fishes used in this analysis.

https://1drv.ms/x/s!AoI1vxSjocLhhIZm2snqlYot0u2AtA?e=5oBW57

3.6.2 Supplement 2 – Trophic group additional data

Table S2.1: ANOVA tables comparing the ten inter-landmark distances across the four trophic groups of lower trophic (including herbivores and omnivores), invertivore, mixed carnivore and carnivore between NZ native and focal fishes. Significant *P* values are bold and italicised.

Total length (TL)	Estimate	Std Error	t value	df	P value
Grand Mean	692.69	45.11	15.36	1	<0.001
Lower trophic	-221.59	142.10	-1.56	1	0.120
Invertivore	-76.78	64.39	-1.19	1	0.234
Mixed Carnivore	6.573	94.9	0.069	1	0.945
Carnivore	-39.28	93.26	-0.42	1	0.674

Standard length (SL)	Estimate	Std Error	t value	df	P value
Grand Mean	591.51	40.07	14.76	1	<0.001
Lower trophic	-196.05	126.19	-1.55	1	0.122
Invertivore	-64.73	57.20	-1.13	1	0.259
Mixed Carnivore	0.09	84.29	0.001	1	0.999
Carnivore	-53.85	82.84	-0.65	1	0.516

Fork length (FL)	Estimate	Std Error	t value	df	P value
Grand Mean	660.45	42.18	15.66	1	<0.001
Lower trophic	-210.31	132.83	-1.58	1	0.115
Invertivore	-70.95	60.21	-1.18	1	0.240
Mixed Carnivore	9.58	88.74	0.11	1	0.914
Carnivore	-49.08	87.20	-0.56	1	0.574

Head length (HL)	Estimate	Std Error	t value	df	P value
Grand Mean	177.93	15.29	11.64	1	<0.001
Lower trophic	-64.46	48.13	-1.34	1	0.182
Invertivore	-18.95	21.82	-0.87	1	0.386
Mixed Carnivore	7.71	32.16	0.24	1	0.811
Carnivore	-25.64	31.60	-0.81	1	0.418

Pre-anal length (PAL)	Estimate	Std Error	t value	df	P value
Grand Mean	376.84	28.60	13.17	1	<0.001
Lower trophic	-154.46	90.08	-1.72	1	***0.088***
Invertivore	-30.23	40.83	-0.74	1	0.460
Mixed Carnivore	11.09	60.18	0.18	1	0.854
Carnivore	-18.76	59.14	-0.32	1	0.751

Pre-dorsal length (PDL)	Estimate	Std Error	t value	df	P value
Grand Mean	243.04	21.35	11.39	1	<0.001
Mixed Omnivore	-107.66	67.22	-1.60	1	0.111
Invertivore	-13.15	30.47	-0.43	1	0.667
Mixed Carnivore	23.53	44.91	0.52	1	0.601
Carnivore	-32.41	44.13	-0.73	1	0.463

Pre-pectoral fin length (PPEL)	Estimate	Std Error	t value	df	P value
Grand Mean	185.29	15.64	11.85	1	<0.001
Lower trophic	-70.12	49.25	-1.42	1	0.156
Invertivore	-20.87	22.33	-0.94	1	0.351
Mixed Carnivore	5.78	32.90	0.18	1	0.861
Carnivore	-26.16	32.34	-0.81	1	0.419

Eye diameter (ED)	Estimate	Std Error	t value	df	P value
Grand Mean	30.83	1.62	19.08	1	<0.001
Lower Trophic	-7.02	5.09	-1.38	1	0.169
Invertivore	-2.72	2.31	-1.18	1	0.239
Mixed Carnivore	1.89	3.39	0.56	1	0.579
Carnivore	-3.50	3.34	-1.05	1	0.295

Pre-orbital length (POL)	Estimate	Std Error	t value	df	P value
Grand Mean	67.21	9.83	6.84	1	<0.001
Lower trophic	-21.65	30.97	-0.69	1	0.485
Invertivore	-4.71	14.04	-0.34	1	0.738
Mixed Carnivore	8.11	20.69	0.39	1	0.695
Carnivore	-23.15	20.33	-1.14	1	0.256

Body Depth (BD)	Estimate	Std Error	t value	df	P value
Grand Mean	191.62	15.04	12.75	1	<0.001
Lower trophic	-29.17	47.35	-0.62	1	0.538
Invertivore	-30.03	21.46	-1.39	1	0.163
Mixed Carnivore	-2.47	31.63	-0.09	1	0.938
Carnivore	-27.65	31.08	-0.89	1	0.375

Table S2.2: ANOVA tables comparing the nine inter-landmark distances scaled by standard length (SL) across the four trophic groups of lower trophic (including herbivores and omnivores), invertivore, mixed carnivore and carnivore between NZ native and focal fishes. Significant *P* values are bold and italicised.

Total length (TL)	Estimate	Std Error	t value	df	P value
Grand Mean	1.19	0.01	261.61	1	<0.001
Lower trophic	0.03	0.01	2.34	1	***0.020***
Invertivore	0.01	0.01	1.33	1	0.185
Mixed Carnivore	0.01	0.01	0.64	1	0.520
Carnivore	0.01	0.01	0.72	1	0.475

Head length (HL)	Estimate	Std Error	t value	df	P value
Grand Mean	0.29	0.00	70.11	1	<0.001
Lower trophic	-0.01	0.01	-0.62	1	0.536
Invertivore	0.00	0.01	0.26	1	0.798
Mixed Carnivore	0.01	0.01	1.16	1	0.246
Carnivore	0.01	0.01	1.12	1	0.265

Fork length (FL)	Estimate	Std Error	t value	df	P value
Grand Mean	1.15	0.01	231.72	1	<0.001
Lower trophic	0.01	0.02	0.78	1	0.438
Invertivore	0.01	0.01	1.59	1	0.111
Mixed Carnivore	0.01	0.01	0.88	1	0.382
Carnivore	-0.00	0.01	-0.24	1	0.808

Pre-dorsal length (PDL)	Estimate	Std Error	t value	df	P value
Grand Mean	0.39	0.01	30.84	1	<0.001
Mixed Omnivore	-0.05	0.04	-1.34	1	0.181
Invertivore	0.01	0.01	0.79	1	0.430
Mixed Carnivore	0.02	0.03	0.89	1	0.370
Carnivore	-0.02	0.03	-0.66	1	0.508

Pre-anal length (PAL)	Estimate	Std Error	t value	df	P value
Grand Mean	0.62	0.01	66.93	1	<0.001
Lower trophic	-0.05	0.03	-1.65	1	0.100
Invertivore	0.03	0.01	1.97	1	***0.050***
Mixed Carnivore	0.01	0.02	0.70	1	0.484
Carnivore	0.03	0.02	1.56	1	0.120

Eye diameter (ED)	Estimate	Std Error	t value	df	P value
Grand Mean	0.06	0.00	40.28	1	<0.001
Lower Trophic	0.01	0.00	1.86	1	***0.065***
Invertivore	0.00	0.00	0.68	1	0.500
Mixed Carnivore	0.00	0.00	0.83	1	0.408
Carnivore	-0.00	0.00	-1.04	1	0.298

Pre-pectoral fin length (PPEL)	Estimate	Std Error	t value	df	P value
Grand Mean	0.30	0.01	67.13	1	<0.001
Lower trophic	-0.02	0.01	-1.14	1	0.255
Invertivore	-0.00	0.01	-0.27	1	0.785
Mixed Carnivore	0.01	0.01	1.18	1	0.238
Carnivore	0.01	0.01	0.97	1	0.332

Body Depth (BD)	Estimate	Std Error	t value	df	P value
Grand Mean	0.34	0.01	36.98	1	<0.001
Lower trophic	0.09	0.03	3.27	1	***0.001***
Invertivore	-0.01	0.01	-0.79	1	0.428
Mixed Carnivore	0.01	0.02	0.72	1	0.470
Carnivore	-0.01	0.02	-0.65	1	0.515

Pre-orbital length (POL)	Estimate	Std Error	t value	df	P value
Grand Mean	0.09	0.00	25.24	1	<0.001
Lower trophic	0.00	0.01	0.34	1	0.735
Invertivore	0.01	0.01	1.27	1	0.204
Mixed Carnivore	0.01	0.01	1.69	1	***0.091***
Carnivore	-0.00	0.01	-0.22	1	0.823

Table S2.3: LDA Classification success based on the ten inter-landmark distances for NZ native species across the four trophic groups of lower trophic (herbivores and omnivores), invertivore, mixed carnivore and carnivore.

Prediction	**Mixed omnivore**	**Invertivore**	**Mixed carnivore**	**Carnivore**
Lower trophic	1	3	1	0
Invertivore	0	50	3	0
Mixed Carnivore	1	21	5	1
Carnivore	0	6	1	12
Accuracy (%)	73	75	63	92

Table S2.4: The 139 Focal species and the NZ native species that are most morphologically similar based on the ten inter-landmark distances, and the most morphologically similar NZ native species that also shares the same trophic group. Species are ordered from most similar in morphology (i.e., the focal and NZ native species pair with the minimum Euclidean distance) to the least similar in morphology (i.e., the focal and NZ native species pair with the maximum Euclidean distance).

Focal Species			**Most morphologically similar NZ native species**			**Most morphologically similar NZ native species from the same trophic group**	
Common name	**Scientific name**	**Trophic group**	**Common name**	**Scientific name**	**Trophic group**	**Common name**	**Scientific name**
Elongate green wrasse	*Pseudojuloides elongatus*	Invertivore	Black rockfish	*Acanthoclinus littoreus*	Invertivore	Olive rockfish	*Acanthoclinus littoreus*
Pacific Redstripe hogfish	*Bodianus masudai*	Invertivore	Northern bastard cod	*Pseudophycis breviuscula*	Invertivore	Northern bastard cod	*Pseudophycis breviuscula*
Tilefish	*Malacanthus brevirostris*	Invertivore	Lemon sole	*Pelotretis flavilatus*	Invertivore	Lemon sole	*Pelotretis flavilatus*
Mado	*Atypichthys latus*	Invertivore	Blue warehou	*Seriolella brama*	Mixed Carnivore	Butterfly perch	*Caesioperca lepidoptera*
Blunthead wrasse	*Thalassoma amblycephalum*	Invertivore	Sandagers wrasse	*Coris sandeyeri*	Mixed Carnivore	Spotty	*Notolabrus celidotus*
Two-spot wrasse	*Oxycheilinus bimaculatus*	Invertivore	Slender roughy	*Optivus elongatus*	Invertivore	Slender roughy	*Optivus elongatus*
Redbanded grubfish	*Parapercis binivirgata*	Invertivore	Sweep	*Scorpis lineolata*	Invertivore	Sweep	*Scorpis lineolata*
Longnose butterflyfish	*Forcipiger flavissimus*	Invertivore	Snipefish	*Macroramphosus scolopax*	Invertivore	Snipefish	*Macroramphosus scolopax*
Kermadec scalyfin	*Parma kermadecensis*	Mixed Omnivore	Blue Maomao	*Scorpis violacea*	Invertivore	Olive rockfish	*Aldrichetta forsteri*
Spotfin porcupinefish	*Diodon hystrix*	Mixed Carnivore	Hake	*Merluccius australis*	Carnivore	Jock Stewart	*Helicolenus percoides*
Yellow demoiselle	*Chromis fumea*	Invertivore	Ruffe	*Tubbia tasmanica*	Mixed Carnivore	Sweep	*Scorpis lineolata*
Parore	*Girella tricuspidata*	Mixed Omnivore	Blue striped mullet	*Upeneichthys porosus*	Invertivore	Black rockfish	*Aldrichetta forsteri*
Cheekspot scorpionfish	*Scorpaenodes evides*	Carnivore	Spotty	*Notolabrus celidotus*	Invertivore	Redbanded perch	*Hypoplectrodes huntii*
Yellowfin foxfish	*Bodianus flavipinnis*	Invertivore	Blue warehou	*Seriolella brama*	Mixed Carnivore	Butterfly perch	*Caesioperca lepidoptera*
Vanderbilts chromis	*Chromis vanderbilti*	Invertivore	Spotty	*Notolabrus celidotus*	Invertivore	Spotty	*Notolabrus celidotus*
Sharksucker	*Echeneis naucrates*	Mixed Carnivore	Spotted gurnard	*Pterygotrigla andertoni*	Mixed Carnivore	Spotted gurnard	*Pterygotrigla andertoni*

Bluestriped fangblenny	*Plagiotremus rhinorhynchos*	Carnivore	Slender roughy	*Optivus elongatus*	Invertivore	Redbanded perch	*Hypoplectrodes huntii*
Easter Island demoiselle	*Chrysiptera rapanui*	Mixed Omnivore	Northern bastard cod	*Pseudophycis breviuscula*	Invertivore	Black rockfish	*Aldrichetta forsteri*
Gunthers butterflyfish	*Chaetodon guentheri*	Invertivore	Rockling	*Gaidropsarus novaezelandiae*	Mixed Carnivore	Rock cod	*Lotella rhacina*
Striped pigfish	*Bodianus izuensis*	Invertivore	Northern bastard cod	*Pseudophycis breviuscula*	Invertivore	Northern bastard cod	*Pseudophycis breviuscula*
Boxfish	*Ostracion cubicus*	Invertivore	Red cod	*Pseudophycis bachus*	Mixed Carnivore	Red rock cod	*Scorpaena cardinalis*
Twostripe goby	*Valenciennea helsdingenii*	Invertivore	Spotty	*Notolabrus celidotus*	Invertivore	Spotty	*Notolabrus celidotus*
Mimic blenny	*Plagiotremus tapeinosoma*	Mixed Carnivore	Twospot demoiselle	*Chromis dispila*	Invertivore	New Zealand halfbanded perch	*Hypoplectrodes dimidius*
Oblong sunfish	*Ranzania laevis*	Mixed Carnivore	Silver drummer	*Kyphosus sydneyanus*	Mixed Omnivore	Jock Stewart	*Helicolenus percoides*
Doubleheader	*Coris bulbifrons*	Invertivore	Trevally	*Pseudocaranx dentex*	Mixed Carnivore	Porae	*Nemadactylus douglasii*
Painted moki	*Morwong ephippium*	Invertivore	Trumpeter	*Latris lineata*	Invertivore	Trumpeter	*Latris lineata*
Confused goby	*Acentrogobius pflaumii*	Invertivore	Slender roughy	*Optivus elongatus*	Invertivore	Slender roughy	*Optivus elongatus*
Starry toado	*Arothron firmamentum*	Invertivore	Blue warehou	*Seriolella brama*	Mixed Carnivore	Butterfly perch	*Caesioperca lepidoptera*
Kermadec scorpionfish	*Maxillicosta raoulensis*	Invertivore	Pilchard	*Sardinops sagax*	Invertivore	Pilchard	*Sardinops sagax*
Grey drummer	*Kyphosus bigibbus*	Mixed Omnivore	Pink maomao	*Caprodon longimanus*	Mixed Carnivore	Greenbone butterfish	*Odax pullus*
Lavender lizardfish	*Synodus similis*	Carnivore	Rock cod	*Lotella rhacina*	Invertivore	Redbanded perch	*Hypoplectrodes huntii*
Jughead puffer	*Lagocephalus*	Mixed Carnivore	Golden snapper	*Centroberyx affinis*	Mixed Carnivore	Golden snapper	*Centroberyx affinis*
Threadfin butterflyfish	*Chaetodon auriga*	Mixed Carnivore	Rockling	*Gaidropsarus novaezelandiae*	Mixed Carnivore	Rockling	*Gaidropsarus novaezelandiae*
Pinklined coris	*Coris dorsomacula*	Invertivore	Olive rockfish	*Acanthoclinus fuscus*	Mixed Carnivore	Spotty	*Notolabrus celidotus*
White remora	*Remora albescens*	Invertivore	Pilchard	*Sardinops sagax*	Invertivore	Pilchard	*Sardinops sagax*
Southern damselfish	*Chrysiptera notialis*	Mixed Omnivore	Slender roughy	*Optivus elongatus*	Invertivore	Olive rockfish	*Aldrichetta forsteri*
Painted Lizardfish	*Trachinocephalus trachinus*	Carnivore	Ruffe	*Tubbia tasmanica*	Mixed Carnivore	Red scorpionfish	*Scorpaena papillosa*
Pelagic puffer	*Pelagocephalus marki*	Invertivore	Pilchard	*Sardinops sagax*	Invertivore	Pilchard	*Sardinops sagax*
Marbled parrotfish	*Leptoscarus vaigiensis*	Mixed Omnivore	Red scorpionfish	*Scorpaena papillosa*	Carnivore	Yelloweye mullet	*Aldrichetta forsteri*
Bartailed goatfish	*Upeneus francisi*	Invertivore	Rock cod	*Lotella rhacina*	Invertivore	Rock cod	*Lotella rhacina*
Rainbowfish	*Suezichthys arquatus*	Invertivore	Sandagers wrasse	*Coris sandeyeri*	Mixed Carnivore	Slender roughy	*Optivus elongatus*
Bluefish	*Girella cyanea*	Mixed Omnivore	Silver warehou	*Seriolella punctata*	Invertivore	Grey mullet	*Mugil cephalus*
Masked foxfish	*Bodianus flavifrons*	Mixed Carnivore	Banded wrasse	*Notolabrus fucicola*	Mixed Carnivore	Banded wrasse	*Notolabrus fucicola*
Elegant wrasse	*Anampses elegans*	Invertivore	Olive rockfish	*Acanthoclinus fuscus*	Mixed Carnivore	Spotty	*Notolabrus celidotus*
Green wrasse	*Notolabrus inscriptus*	Mixed Carnivore	Red cod	*Pseudophycis bachus*	Mixed Carnivore	Red cod	*Pseudophycis bachus*
Blackspot goatfish	*Parupeneus spilurus*	Invertivore	Telescope fish	*Mendosoma lineatum*	Mixed Carnivore	Sweep	*Scorpis lineolata*
Onespot demoiselle	*Chromis hypsilepis*	Mixed Omnivore	Girdled wrasse	*Notolabrus cinctus*	Mixed Carnivore	Olive rockfish	*Aldrichetta forsteri*

Notchhead marblefish	*Aplodactylus etheridgii*	Mixed Omnivore	Balloonfish	*Sphoeroides pachygaster*	Carnivore	Greenbone butterfish	*Odax pullus*
Bridled goby	*Arenigobius bifrenatus*	Invertivore	Slender roughy	*Optivus elongatus*	Invertivore	Slender roughy	*Optivus elongatus*
Sunset wrasse	*Thalassoma lutescens*	Mixed Carnivore	Olive rockfish	*Acanthoclinus fuscus*	Mixed Carnivore	Olive rockfish	*Acanthoclinus fuscus*
Lyretail hawkfish	*Cyprinocirrhites polyactis*	Invertivore	Scarlet wrasse	*Pseudolabrus miles*	Mixed Carnivore	Koheru	*Decapterus koheru*
Caramel drummer	*Girella fimbriata*	Mixed Omnivore	Blue warehou	*Seriolella brama*	Mixed Carnivore	Greenbone butterfish	*Odax pullus*
Red lionfish	*Pterois volitans*	Carnivore	Kahawai	*Arripis trutta*	Carnivore	Kahawai	*Arripis trutta*
Yellowspot demoiselle	*Chromis flavomaculata*	Invertivore	Blue warehou	*Seriolella brama*	Mixed Carnivore	Butterfly perch	*Caesioperca lepidoptera*
Spotted sawtail	*Prionurus maculatus*	Mixed Omnivore	Sandfish	*Gonorynchus forsteri*	Mixed Omnivore	Sandfish	*Gonorynchus forsteri*
Sargassum fish	*Histrio*	Mixed Carnivore	Graham's gudgeon	*Grahamichthys radiata*	Invertivore	New Zealand halfbanded perch	*Hypoplectrodes dimidius*
Scad	*Decapterus muroadsi*	Invertivore	Yellow boarfish	*Pentaceros decacanthus*	Invertivore	Yellow boarfish	*Pentaceros decacanthus*
Grey knifefish	*Bathystethus cultratus*	Invertivore	Ruffe	*Tubbia tasmanica*	Mixed Carnivore	Blue Maomao	*Scorpis violacea*
Crimson cleanerfish	*Suezichthys aylingi*	Invertivore	New Zealand halfbanded perch	*Hypoplectrodes dimidius*	Mixed Carnivore	Speckled sole	*Peltorhamphus latus*
Latchet	*Pterygotrigla polyommata*	Mixed Carnivore	Silver drummer	*Kyphosus sydneyanus*	Mixed Omnivore	Jock Stewart	*Helicolenus percoides*
Velifer	*Metavelifer multiradiatus*	Mixed Carnivore	Chilean mackerel	*Trachurus murphyi*	Invertivore	Golden snapper	*Centroberyx affinis*
Flying gurnard	*Dactyloptena orientalis*	Mixed Carnivore	Kingfish	*Seriola lalandi*	Carnivore	Rudderfish	*Centrolophus niger*
Bronze bream	*Xenobrama microlepis*	Carnivore	Trevally	*Pseudocaranx dentex*	Mixed Carnivore	Skipjack tuna	*Katsuwonus pelamis*
Clown toado	*Canthigaster callisterna*	Invertivore	Snipefish	*Macroramphosus scolopax*	Invertivore	Snipefish	*Macroramphosus scolopax*
Moorish idol	*Zanclus cornutus*	Mixed Omnivore	Snipefish	*Macroramphosus scolopax*	Invertivore	Black rockfish	*Aldrichetta forsteri*
Beaked drummer	*Kyphosus sectatrix*	Mixed Omnivore	Telescope fish	*Mendosoma lineatum*	Mixed Carnivore	Yelloweye mullet	*Aldrichetta forsteri*
Rainbow runner	*Elagatis bipinnulata*	Carnivore	Pomfret	*Taractichthys longipinnis*	Carnivore	Pomfret	*Taractichthys longipinnis*
Blunthead platax	*Platax teira*	Carnivore	Rays bream	*Brama*	Carnivore	Rays bream	*Brama*
Doaks lizardfish	*Synodus doaki*	Carnivore	Witch	*Arnoglossus scapha*	Mixed Carnivore	Redbanded perch	*Hypoplectrodes huntii*
Red morwong	*Morwong fuscus*	Invertivore	Skipjack tuna	*Katsuwonus pelamis*	Carnivore	Chilean mackerel	*Trachurus murphyi*
Combfish	*Coris picta*	Invertivore	Rock cod	*Lotella rhacina*	Invertivore	Rock cod	*Lotella rhacina*
Orange wrasse	*Pseudolabrus luculentus*	Invertivore	Rock cod	*Lotella rhacina*	Invertivore	Rock cod	*Lotella rhacina*
Blue knifefish	*Labracoglossa nitida*	Invertivore	Blue Maomao	*Scorpis violacea*	Invertivore	Blue Maomao	*Scorpis violacea*
Slender remora	*Phtheirichthys lineatus*	Mixed Carnivore	Sandfish	*Gonorynchus forsteri*	Mixed Omnivore	Red gurnard	*Chelidonichthys kumu*
Common lizardfish	*Synodus variegatus*	Carnivore	Rock cod	*Lotella rhacina*	Invertivore	Redbanded perch	*Hypoplectrodes huntii*
Goldstripe groper	*Aulacocephalus temminckii*	Carnivore	Red cod	*Pseudophycis bachus*	Mixed Carnivore	Red scorpionfish	*Scorpaena papillosa*
Blue wrasse	*Thalassoma lunare*	Invertivore	Rock cod	*Lotella rhacina*	Invertivore	Rock cod	*Lotella rhacina*

Knifejaw	*Oplegnathus woodwardi*	Invertivore	Red moki	*Chirodactylus spectabilis*	Invertivore	Red moki	*Chirodactylus spectabilis*
Northern kelpfish	*Chironemus microlepis*	Invertivore	Blue warehou	*Seriolella brama*	Mixed Carnivore	Butterfly perch	*Caesioperca lepidoptera*
Grey marlinsucker	*Remora brachyptera*	Invertivore	Snipefish	*Macroramphosus scolopax*	Invertivore	Snipefish	*Macroramphosus scolopax*
Banded scalyfin	*Parma polylepis*	Mixed Omnivore	Banded wrasse	*Notolabrus fucicola*	Mixed Carnivore	Yelloweye mullet	*Aldrichetta forsteri*
Striped beakfish	*Oplegnathus fasciatus*	Mixed Carnivore	Rudderfish	*Centrolophus niger*	Mixed Carnivore	Rudderfish	*Centrolophus niger*
Pilotfish	*Naucrates ductor*	Invertivore	Trumpeter	*Latris lineata*	Invertivore	Trumpeter	*Latris lineata*
IndoPacific sergeant	*Abudefduf vaigiensis*	Mixed Omnivore	Banded wrasse	*Notolabrus fucicola*	Mixed Carnivore	Black rockfish	*Aldrichetta forsteri*
Bullet tuna	*Auxis rochei*	Carnivore	Trevally	*Pseudocaranx dentex*	Mixed Carnivore	Skipjack tuna	*Katsuwonus pelamis*
Striped boarfish	*Evistias acutirostris*	Invertivore	Giant boarfish	*Paristiopterus labiosus*	Invertivore	Giant boarfish	*Paristiopterus labiosus*
Eyebrow perch	*Hypoplectrodes coronatus*	Mixed Carnivore	Red moki	*Chirodactylus spectabilis*	Invertivore	Slender tuna	*Allothunnus fallai*
Brassy drummer	*Kyphosus vaigiensis*	Mixed Omnivore	Rays bream	*Brama*	Carnivore	Silver drummer	*Kyphosus sydneyanus*
Magpie perch	*Pseudogoniistius nigripes*	Invertivore	Spotted gurnard	*Pterygotrigla andertoni*	Mixed Carnivore	Giant boarfish	*Paristiopterus labiosus*
Darkvent leatherjacket	*Thamnaconus analis*	Invertivore	Leatherjacket	*Meuschenia scaber*	Invertivore	Leatherjacket	*Meuschenia scaber*
Pineapplefish	*Monocentris japonica*	Invertivore	Banded wrasse	*Notolabrus fucicola*	Mixed Carnivore	Lemon sole	*Pelotretis flavilatus*
Cheesemans puffer	*Lagocephalus cheesemanii*	Mixed Carnivore	Red gurnard	*Chelidonichthys kumu*	Mixed Carnivore	Red gurnard	*Chelidonichthys kumu*
Twospot hogfish	*Bodianus bimaculatus*	Invertivore	Albacore	*Thunnus alalunga*	Carnivore	NZ Brill	*Colistium guntheri*
Remora	*Remora*	Invertivore	Sandfish	*Gonorynchus forsteri*	Mixed Omnivore	Leatherjacket	*Meuschenia scaber*
Silverspot	*Chironemus maculosus*	Invertivore	Southern bastard cod	*Pseudophycis barbata*	Invertivore	Southern bastard cod	*Pseudophycis barbata*
Lord Howe coralfish	*Amphichaetodon howensis*	Invertivore	Telescope fish	*Mendosoma lineatum*	Mixed Carnivore	Blue striped mullet	*Upeneichthys porosus*
Northern kahawai	*Arripis xylabion*	Carnivore	Trevally	*Pseudocaranx dentex*	Mixed Carnivore	Skipjack tuna	*Katsuwonus pelamis*
Hardfin marlinsucker	*Remora osteochir*	Invertivore	Yelloweye mullet	*Aldrichetta forsteri*	Mixed Omnivore	Koheru	*Decapterus koheru*
Sharptail sunfish	*Masturus lanceolatus*	Mixed Carnivore	Bluenose	*Hyperoglyphe antarctica*	Carnivore	Sunfish	*Mola alexandrini*
Almacojack	*Seriola rivoliana*	Carnivore	Pomfret	*Taractichthys longipinnis*	Carnivore	Pomfret	*Taractichthys longipinnis*
Pacific seabream	*Acanthopagrus pacificus*	Mixed Carnivore	Red moki	*Chirodactylus spectabilis*	Invertivore	Slender tuna	*Allothunnus fallai*
Yellowbanded perch	*Acanthistius cinctus*	Carnivore	Southern bastard cod	*Pseudophycis barbata*	Invertivore	Kahawai	*Arripis trutta*
Yellowfin bream	*Acanthopagrus australis*	Invertivore	Hake	*Merluccius australis*	Carnivore	NZ Brill	*Colistium guntheri*
Orange bellowsfish	*Notopogon xenosoma*	Invertivore	Yelloweye mullet	*Aldrichetta forsteri*	Mixed Omnivore	Koheru	*Decapterus koheru*
Frigate tuna	*Auxis thazard*	Carnivore	Trevally	*Pseudocaranx dentex*	Mixed Carnivore	Skipjack tuna	*Katsuwonus pelamis*
Kermadec barracuda	*Sphyraena waitii*	Carnivore	Red gurnard	*Chelidonichthys kumu*	Mixed Carnivore	Balloonfish	*Sphoeroides pachygaster*
Whitefingered angler	*Antennatus nummifer*	Carnivore	Olive rockfish	*Acanthoclinus fuscus*	Mixed Carnivore	Redbanded perch	*Hypoplectrodes huntii*
Cowfish	*Lactoria diaphana*	Invertivore	Red gurnard	*Chelidonichthys kumu*	Mixed Carnivore	Yellow boarfish	*Pentaceros decacanthus*

Ruby snapper	*Etelis carbunculus*	Carnivore	Bass	*Polyprion americanus*	Carnivore	Bass	*Polyprion americanus*
Toadstool groper	*Trachypoma macracanthus*	Invertivore	Rays bream	*Brama*	Carnivore	Porae	*Nemadactylus douglasii*
Greys sandfish	*Gonorynchus greyi*	Mixed Omnivore	Red gurnard	*Chelidonichthys kumu*	Mixed Carnivore	Sandfish	*Gonorynchus forsteri*
Wingfish	*Pteraclis velifera*	Carnivore	Slender tuna	*Allothunnus fallai*	Mixed Carnivore	Kahawai	*Arripis trutta*
Clown coris	*Coris aygula*	Mixed Carnivore	Southern bastard cod	*Pseudophycis barbata*	Invertivore	Red cod	*Pseudophycis bachus*
Slender boxfish	*Polyplacapros tyleri*	Invertivore	Sandfish	*Gonorynchus forsteri*	Mixed Omnivore	Leatherjacket	*Meuschenia scaber*
Eyestripe surgeonfish	*Acanthurus dussumieri*	Mixed Omnivore	Spotted gurnard	*Pterygotrigla andertoni*	Mixed Carnivore	Grey mullet	*Mugil cephalus*
Blackfin barracuda	*Sphyraena qenie*	Carnivore	Hoki	*Macruronus novaezelandiae*	Carnivore	Hoki	*Macruronus novaezelandiae*
Commersons frogfish	*Antennarius commerson*	Carnivore	New Zealand turbot	*Colistium nudipinnis*	Invertivore	Red scorpionfish	*Scorpaena papillosa*
Samsonfish	*Seriola hippos*	Carnivore	Hake	*Merluccius australis*	Carnivore	Hake	*Merluccius australis*
Spotfin burrfish	*Chilomycterus reticulatus*	Invertivore	Yellowfin tuna	*Thunnus albacares*	Carnivore	NZ Brill	*Colistium guntheri*
Australian bonito	*Sarda australis*	Carnivore	Hake	*Merluccius australis*	Carnivore	Hake	*Merluccius australis*
silver cheeked toadfish	*Lagocephalus sceleratus*	Mixed Carnivore	Sunfish	*Mola alexandrini*	Mixed Carnivore	Sunfish	*Mola alexandrini*
Halfmoon groper	*Epinephelus rivulatus*	Mixed Carnivore	Hake	*Merluccius australis*	Carnivore	Trevally	*Pseudocaranx dentex*
Astronomers toado	*Arothron stellatus*	Mixed Carnivore	Hoki	*Macruronus novaezelandiae*	Carnivore	Rudderfish	*Centrolophus niger*
Barred leatherjacket	*Cantherhines dumerilii*	Invertivore	Piper	*Hyporhamphus ihi*	Invertivore	Piper	*Hyporhamphus ihi*
Bluespine unicornfish	*Naso unicornis*	Mixed Omnivore	Blue marlin	*Makaira nigricans*	Carnivore	Grey mullet	*Mugil cephalus*
Wahoo	*Acanthocybium solandri*	Carnivore	Snapper	*Chrysophrys auratus*	Mixed Carnivore	Hoki	*Macruronus novaezelandiae*
Striped angler	*Antennarius striatus*	Carnivore	Slender tuna	*Allothunnus fallai*	Mixed Carnivore	Skipjack tuna	*Katsuwonus pelamis*
Trumpetfish	*Aulostomus chinensis*	Carnivore	Leatherjacket	*Meuschenia scaber*	Invertivore	Redbanded perch	*Hypoplectrodes huntii*
Amberjack	*Seriola dumerili*	Carnivore	Bass	*Polyprion americanus*	Carnivore	Bass	*Polyprion americanus*
Mahimahi	*Coryphaena hippurus*	Carnivore	Bass	*Polyprion americanus*	Carnivore	Bass	*Polyprion americanus*
Convict groper	*Hyporthodus octofasciatus*	Carnivore	Hapuku groper	*Polyprion oxygeneios*	Carnivore	Hapuku groper	*Polyprion oxygeneios*
Tailor	*Pomatomus saltatrix*	Carnivore	Hapuku groper	*Polyprion oxygeneios*	Carnivore	Hapuku groper	*Polyprion oxygeneios*
Smooth leatherjacket	*Aluterus monoceros*	Mixed Carnivore	Blue marlin	*Makaira nigricans*	Carnivore	Spotted gurnard	*Pterygotrigla andertoni*
Spotted black groper	*Epinephelus daemelii*	Carnivore	Hapuku groper	*Polyprion oxygeneios*	Carnivore	Hapuku groper	*Polyprion oxygeneios*
Scrawled leatherjacket	*Aluterus scriptus*	Invertivore	Piper	*Hyporhamphus ihi*	Invertivore	Piper	*Hyporhamphus ihi*
Sailfish	*Istiophorus platypterus*	Carnivore	Swordfish	*Xiphias gladius*	Carnivore	Swordfish	*Xiphias gladius*
Cornetfish	*Fistularia commersonii*	Carnivore	Swordfish	*Xiphias gladius*	Carnivore	Swordfish	*Xiphias gladius*
Red cornetfish	*Fistularia petimba*	Carnivore	Piper	*Hyporhamphus ihi*	Invertivore	Swordfish	*Xiphias gladius*
Queensland groper	*Epinephelus lanceolatus*	Carnivore	New Zealand turbot	*Colistium nudipinnis*	Invertivore	Hapuku groper	*Polyprion oxygeneios*

Table S2.5: LDA Classification success based on the nine inter-landmark distances scaled by standard length (SL) for NZ native species across the four trophic groups of lower trophic (herbivores and omnivores), invertivore, mixed carnivore and carnivore.

Prediction	**Mixed omnivore**	**Invertivore**	**Mixed carnivore**	**Carnivore**
Lower trophic	1	3	1	0
Invertivore	0	43	7	3
Mixed Carnivore	0	15	11	2
Carnivore	0	7	5	7
Accuracy (%)	98	68	62	73

Table S2.6: The 139 Focal species and the NZ native species that are most morphologically similar based on the nine inter-landmark distances scaled by standard length (SL), and the most morphologically similar NZ native species that also shares the same trophic group. Species are ordered from most similar in morphology (i.e., the focal and NZ native species pair with the minimum Euclidean distance) to the least similar in morphology (i.e., the focal and NZ native species pair with the maximum Euclidean distance).

Focal species			**Most morphologically similar NZ native species**			**Most morphologically similar NZ native species from the same trophic group**	
Common name	**Scientific name**	**Trophic group**	**Common name**	**Scientific name**	**Trophic group**	**Common name**	**Scientific name**
Bronze bream	*Xenobrama microlepis*	Carnivore	Rays bream	*Brama*	Carnivore	Rays bream	*Brama*
Silverspot	*Chironemus maculosus*	Invertivore	Red moki	*Chirodactylus spectabilis*	Invertivore	Red moki	*Chirodactylus spectabilis*
Spotfin porcupinefish	*Diodon hystrix*	Mixed Carnivore	Sweep	*Scorpis lineolata*	Invertivore	Hiwihiwi	*Chironemus marmoratus*
Northern kahawai	*Arripis xylabion*	Carnivore	Olive rockfish	*Acanthoclinus fuscus*	Mixed Carnivore	Kahawai	*Arripis trutta*
Gunthers butterflyfish	*Chaetodon guentheri*	Invertivore	Splendid perch	*Callanthias australis*	Invertivore	Splendid perch	*Callanthias australis*
Wingfish	*Pteraclis velifera*	Carnivore	Spotty	*Notolabrus celidotus*	Invertivore	Albacore	*Thunnus alalunga*
Rainbowfish	*Suezichthys arquatus*	Invertivore	Yellowbelly flounder	*Rhombosolea leporina*	Invertivore	Yellowbelly flounder	*Rhombosolea leporina*
Almacojack	*Seriola rivoliana*	Carnivore	Blue cod	*Parapercis colias*	Mixed Carnivore	Kahawai	*Arripis trutta*
Painted moki	*Morwong ephippium*	Invertivore	Yellowbelly flounder	*Rhombosolea leporina*	Invertivore	Yellowbelly flounder	*Rhombosolea leporina*
Magpie perch	*Pseudogoniistius nigripes*	Invertivore	Slender sprat	*Sprattus antipodum*	Invertivore	Slender sprat	*Sprattus antipodum*

Threadfin butterflyfish	*Chaetodon auriga*	Mixed Carnivore	Rays bream	*Brama*	Carnivore	Bigeye ruffe	*Tubbia stewarti*
Twostripe goby	*Valenciennea helsdingenii*	Invertivore	Sand flounder	*Rhombosolea plebeia*	Invertivore	Sand flounder	*Rhombosolea plebeia*
Bluefish	*Girella cyanea*	Mixed Omnivore	Blue Maomao	*Scorpis violacea*	Invertivore	Silver drummer	*Kyphosus sydneyanus*
Pacific Redstripe hogfish	*Bodianus masudai*	Invertivore	Yellowbelly flounder	*Rhombosolea leporina*	Invertivore	Yellowbelly flounder	*Rhombosolea leporina*
Amberjack	*Seriola dumerili*	Carnivore	Chilean mackerel	*Trachurus murphyi*	Invertivore	John Dory	*Zeus faber*
Brassy drummer	*Kyphosus vaigiensis*	Mixed Omnivore	Pomfret	*Taractichthys longipinnis*	Carnivore	Silver drummer	*Kyphosus sydneyanus*
Bluestriped fangblenny	*Plagiotremus rhinorhynchos*	Carnivore	Red gurnard	*Chelidonichthys kumu*	Mixed Carnivore	Rays bream	*Brama*
Australian bonito	*Sarda australis*	Carnivore	Slender tuna	*Allothunnus fallai*	Mixed Carnivore	Skipjack tuna	*Katsuwonus pelamis*
Samsonfish	*Seriola hippos*	Carnivore	Skipjack tuna	*Katsuwonus pelamis*	Carnivore	Skipjack tuna	*Katsuwonus pelamis*
Sunset wrasse	*Thalassoma lutescens*	Mixed Carnivore	Southern bastard cod	*Pseudophycis barbata*	Invertivore	Trevally	*Pseudocaranx dentex*
Pinklined coris	*Coris dorsomacula*	Invertivore	Hake	*Merluccius australis*	Carnivore	Trumpeter	*Latris lineata*
Two-spot wrasse	*Oxycheilinus bimaculatus*	Invertivore	Horse mackerel	*Trachurus novaezelandiae*	Invertivore	Horse mackerel	*Trachurus novaezelandiae*
Mimic blenny	*Plagiotremus tapeinosoma*	Mixed Carnivore	Grey mullet	*Mugil cephalus*	Mixed Omnivore	Rudderfish	*Centrolophus niger*
Striped pigfish	*Bodianus izuensis*	Invertivore	Yellowbelly flounder	*Rhombosolea leporina*	Invertivore	Yellowbelly flounder	*Rhombosolea leporina*
Orange wrasse	*Pseudolabrus luculentus*	Invertivore	Spotty	*Notolabrus celidotus*	Invertivore	Spotty	*Notolabrus celidotus*
Blackfin barracuda	*Sphyraena qenie*	Carnivore	Hake	*Merluccius australis*	Carnivore	Hake	*Merluccius australis*
Blue wrasse	*Thalassoma lunare*	Invertivore	Piper	*Hyporhamphus ihi*	Invertivore	Piper	*Hyporhamphus ihi*
Bullet tuna	*Auxis rochei*	Carnivore	Olive rockfish	*Acanthoclinus fuscus*	Mixed Carnivore	Kahawai	*Arripis trutta*
Yellowfin bream	*Acanthopagrus australis*	Invertivore	Pink maomao	*Caprodon longimanus*	Mixed Carnivore	Red moki	*Chirodactylus spectabilis*
Bridled goby	*Arenigobius bifrenatus*	Invertivore	Lemon sole	*Pelotretis flavilatus*	Invertivore	Lemon sole	*Pelotretis flavilatus*

Astronomers toado	*Arothron stellatus*	Mixed Carnivore	Yellow cod	*Parapercis gilliesii*	Invertivore	Spotted gurnard	*Pterygotrigla andertoni*
Elongate green wrasse	*Pseudojuloides elongatus*	Invertivore	Sand flounder	*Rhombosolea plebeia*	Invertivore	Sand flounder	*Rhombosolea plebeia*
Yellowfin foxfish	*Bodianus flavipinnis*	Invertivore	Giant boarfish	*Paristiopterus labiosus*	Invertivore	Giant boarfish	*Paristiopterus labiosus*
Longnose butterflyfish	*Forcipiger flavissimus*	Invertivore	Yellow boarfish	*Pentaceros decacanthus*	Invertivore	Yellow boarfish	*Pentaceros decacanthus*
Kermadec barracuda	*Sphyraena waitii*	Carnivore	Yellowbelly flounder	*Rhombosolea leporina*	Invertivore	Rays bream	*Brama*
silver cheeked toadfish	*Lagocephalus sceleratus*	Mixed Carnivore	Yellow boarfish	*Pentaceros decacanthus*	Invertivore	Golden snapper	*Centroberyx affinis*
Crimson cleanerfish	*Suezichthys aylingi*	Invertivore	Grey mullet	*Mugil cephalus*	Mixed Omnivore	Rock cod	*Lotella rhacina*
Cheekspot scorpionfish	*Scorpaenodes evides*	Carnivore	Slender roughy	*Optivus elongatus*	Invertivore	Pomfret	*Taractichthys longipinnis*
Sharptail sunfish	*Masturus lanceolatus*	Mixed Carnivore	Skipjack tuna	*Katsuwonus pelamis*	Carnivore	Sandagers wrasse	*Coris sandeyeri*
Parore	*Girella tricuspidata*	Mixed Omnivore	Greenbone butterfish	*Odax pullus*	Mixed Omnivore	Greenbone butterfish	*Odax pullus*
Blue knifefish	*Labracoglossa nitida*	Invertivore	Rockling	*Gaidropsarus novaezelandiae*	Mixed Carnivore	Twospot demoiselle	*Chromis dispila*
Scad	*Decapterus muroadsi*	Invertivore	Koheru	*Decapterus koheru*	Invertivore	Koheru	*Decapterus koheru*
Eyebrow perch	*Hypoplectrodes coronatus*	Mixed Carnivore	Olive rockfish	*Acanthoclinus fuscus*	Mixed Carnivore	Olive rockfish	*Acanthoclinus fuscus*
Painted Lizardfish	*Trachinocephalus trachinus*	Carnivore	Olive rockfish	*Acanthoclinus fuscus*	Mixed Carnivore	Kahawai	*Arripis trutta*
Boxfish	*Ostracion cubicus*	Invertivore	Olive rockfish	*Acanthoclinus fuscus*	Mixed Carnivore	Koheru	*Decapterus koheru*
Blackspot goatfish	*Parupeneus spilurus*	Invertivore	Red moki	*Chirodactylus spectabilis*	Invertivore	Red moki	*Chirodactylus spectabilis*
Spotted sawtail	*Prionurus maculatus*	Mixed Omnivore	Red gurnard	*Chelidonichthys kumu*	Mixed Carnivore	Silver drummer	*Kyphosus sydneyanus*
Northern kelpfish	*Chironemus microlepis*	Invertivore	Speckled sole	*Peltorhamphus latus*	Invertivore	Speckled sole	*Peltorhamphus latus*
Grey knifefish	*Bathystethus cultratus*	Invertivore	Sand flounder	*Rhombosolea plebeia*	Invertivore	Sand flounder	*Rhombosolea plebeia*
Clown toado	*Canthigaster callisterna*	Invertivore	Slender sprat	*Sprattus antipodum*	Invertivore	Slender sprat	*Sprattus antipodum*

Tilefish	*Malacanthus brevirostris*	Invertivore	Yelloweye mullet	*Aldrichetta forsteri*	Mixed Omnivore	Rock cod	*Lotella rhacina*
Blunthead wrasse	*Thalassoma amblycephalum*	Invertivore	Blue cod	*Parapercis colias*	Mixed Carnivore	Twospot demoiselle	*Chromis dispila*
Red morwong	*Morwong fuscus*	Invertivore	Chilean mackerel	*Trachurus murphyi*	Invertivore	Chilean mackerel	*Trachurus murphyi*
Beaked drummer	*Kyphosus sectatrix*	Mixed Omnivore	Greenbone butterfish	*Odax pullus*	Mixed Omnivore	Greenbone butterfish	*Odax pullus*
Marbled parrotfish	*Leptoscarus vaigiensis*	Mixed Omnivore	Spotty	*Notolabrus celidotus*	Invertivore	Yelloweye mullet	*Aldrichetta forsteri*
IndoPacific sergeant	*Abudefduf vaigiensis*	Mixed Omnivore	Southern burrfish	*Allomycterus pilatus*	Mixed Carnivore	Silver drummer	*Kyphosus sydneyanus*
Kermadec scalyfin	*Parma kermadecensis*	Mixed Omnivore	Pomfret	*Taractichthys longipinnis*	Carnivore	Silver drummer	*Kyphosus sydneyanus*
Twospot hogfish	*Bodianus bimaculatus*	Invertivore	Red pigfish	*Bodianus unimaculatus*	Invertivore	Red pigfish	*Bodianus unimaculatus*
Confused goby	*Acentrogobius pflaumii*	Invertivore	Ahuru	*Auchenoceros punctatus*	Invertivore	Ahuru	*Auchenoceros punctatus*
Masked foxfish	*Bodianus flavifrons*	Mixed Carnivore	Blue cod	*Parapercis colias*	Mixed Carnivore	Blue cod	*Parapercis colias*
Combfish	*Coris picta*	Invertivore	Hake	*Merluccius australis*	Carnivore	Trumpeter	*Latris lineata*
Mahimahi	*Coryphaena hippurus*	Carnivore	Piper	*Hyporhamphus ihi*	Invertivore	Kahawai	*Arripis trutta*
Elegant wrasse	*Anampses elegans*	Invertivore	Skipjack tuna	*Katsuwonus pelamis*	Carnivore	New Zealand turbot	*Colistium nudipinnis*
Pilotfish	*Naucrates ductor*	Invertivore	Piper	*Hyporhamphus ihi*	Invertivore	Piper	*Hyporhamphus ihi*
Red cornetfish	*Fistularia petimba*	Carnivore	Spotty	*Notolabrus celidotus*	Invertivore	Albacore	*Thunnus alalunga*
Green wrasse	*Notolabrus inscriptus*	Mixed Carnivore	Speckled sole	*Peltorhamphus latus*	Invertivore	Pink maomao	*Caprodon longimanus*
Pacific seabream	*Acanthopagrus pacificus*	Mixed Carnivore	Chilean mackerel	*Trachurus murphyi*	Invertivore	Pink maomao	*Caprodon longimanus*
Jughead puffer	*Lagocephalus*	Mixed Carnivore	Sunfish	*Mola alexandrini*	Mixed Carnivore	Sunfish	*Mola alexandrini*
Doubleheader	*Coris bulbifrons*	Invertivore	Red rock cod	*Scorpaena cardinalis*	Invertivore	Red rock cod	*Scorpaena cardinalis*

Doaks lizardfish	*Synodus doaki*	Carnivore	Slender tuna	*Allothunnus fallai*	Mixed Carnivore	Kingfish	*Seriola lalandi*
Sargassum fish	*Histrio*	Mixed Carnivore	Kingfish	*Seriola lalandi*	Carnivore	Sandagers wrasse	*Coris sandeyeri*
Frigate tuna	*Auxis thazard*	Carnivore	Slender tuna	*Allothunnus fallai*	Mixed Carnivore	Skipjack tuna	*Katsuwonus pelamis*
Rainbow runner	*Elagatis bipinnulata*	Carnivore	New Zealand sole	*Peltorhamphus novaezeelandiae*	Invertivore	Kahawai	*Arripis trutta*
Smooth leatherjacket	*Aluterus monoceros*	Mixed Carnivore	Ahuru	*Auchenoceros punctatus*	Invertivore	Spotted gurnard	*Pterygotrigla andertoni*
Red lionfish	*Pterois volitans*	Carnivore	Butterfly perch	*Caesioperca lepidoptera*	Invertivore	Pomfret	*Taractichthys longipinnis*
Trumpetfish	*Aulostomus chinensis*	Carnivore	Skipjack tuna	*Katsuwonus pelamis*	Carnivore	Skipjack tuna	*Katsuwonus pelamis*
Toadstool groper	*Trachypoma macracanthus*	Invertivore	Snipefish	*Macroramphosus scolopax*	Invertivore	Snipefish	*Macroramphosus scolopax*
Notchhead marblefish	*Aplodactylus etheridgii*	Mixed Omnivore	Grey mullet	*Mugil cephalus*	Mixed Omnivore	Grey mullet	*Mugil cephalus*
Banded scalyfin	*Parma polylepis*	Mixed Omnivore	Splendid perch	*Callanthias australis*	Invertivore	Silver drummer	*Kyphosus sydneyanus*
Knifejaw	*Oplegnathus woodwardi*	Invertivore	Redbanded perch	*Hypoplectrodes huntii*	Carnivore	Porae	*Nemadactylus douglasii*
Ruby snapper	*Etelis carbunculus*	Carnivore	Yellow boarfish	*Pentaceros decacanthus*	Invertivore	Red scorpionfish	*Scorpaena papillosa*
Cheesemans puffer	*Lagocephalus cheesemanii*	Mixed Carnivore	Northern bastard cod	*Pseudophycis breviuscula*	Invertivore	Witch	*Arnoglossus scapha*
Grey drummer	*Kyphosus bigibbus*	Mixed Omnivore	Rock cod	*Lotella rhacina*	Invertivore	Grey mullet	*Mugil cephalus*
Cornetfish	*Fistularia commersonii*	Carnivore	Grey mullet	*Mugil cephalus*	Mixed Omnivore	Hoki	*Macruronus novaezelandiae*
Striped beakfish	*Oplegnathus fasciatus*	Mixed Carnivore	John Dory	*Zeus faber*	Carnivore	Pink maomao	*Caprodon longimanus*
Mado	*Atypichthys latus*	Invertivore	Spotted gurnard	*Pterygotrigla andertoni*	Mixed Carnivore	Splendid perch	*Callanthias australis*
Moorish idol	*Zanclus cornutus*	Mixed Omnivore	Red scorpionfish	*Scorpaena papillosa*	Carnivore	Silver drummer	*Kyphosus sydneyanus*

Clown coris	*Coris aygula*	Mixed Carnivore	Slender tuna	*Allothunnus fallai*	Mixed Carnivore	Slender tuna	*Allothunnus fallai*
Starry toado	*Arothron firmamentum*	Invertivore	Lemon sole	*Pelotretis flavilatus*	Invertivore	Lemon sole	*Pelotretis flavilatus*
Yellow demoiselle	*Chromis fumea*	Invertivore	Red scorpionfish	*Scorpaena papillosa*	Carnivore	Globefish	*Contusus richei*
Sharksucker	*Echeneis naucrates*	Mixed Carnivore	Hoki	*Macruronus novaezelandiae*	Carnivore	Red cod	*Pseudophycis bachus*
Hardfin marlinsucker	*Remora osteochir*	Invertivore	Hoki	*Macruronus novaezelandiae*	Carnivore	Rock cod	*Lotella rhacina*
Orange bellowsfish	*Notopogon xenosoma*	Invertivore	Yellow boarfish	*Pentaceros decacanthus*	Invertivore	Yellow boarfish	*Pentaceros decacanthus*
Vanderbilts chromis	*Chromis vanderbilti*	Invertivore	Longfin boarfish	*Zanclistius elevatus*	Invertivore	Longfin boarfish	*Zanclistius elevatus*
Southern damselfish	*Chrysiptera notialis*	Mixed Omnivore	Wavyline perch	*Lepidoperca tasmanica*	Invertivore	Silver drummer	*Kyphosus sydneyanus*
Tailor	*Pomatomus saltatrix*	Carnivore	Trevally	*Pseudocaranx dentex*	Mixed Carnivore	Hapuku groper	*Polyprion oxygeneios*
Greys sandfish	*Gonorynchus greyi*	Mixed Omnivore	Rudderfish	*Centrolophus niger*	Mixed Carnivore	Grey mullet	*Mugil cephalus*
Latchet	*Pterygotrigla polyommata*	Mixed Carnivore	Splendid perch	*Callanthias australis*	Invertivore	Spotted gurnard	*Pterygotrigla andertoni*
Bluespine unicornfish	*Naso unicornis*	Mixed Omnivore	Ahuru	*Auchenoceros punctatus*	Invertivore	Silver drummer	*Kyphosus sydneyanus*
Bartailed goatfish	*Upeneus francisi*	Invertivore	Spotted gurnard	*Pterygotrigla andertoni*	Mixed Carnivore	Slender roughy	*Optivus elongatus*
Lavender lizardfish	*Synodus similis*	Carnivore	Yellowfin tuna	*Thunnus albacares*	Carnivore	Yellowfin tuna	*Thunnus albacares*
Remora	*Remora*	Invertivore	Sandfish	*Gonorynchus forsteri*	Mixed Omnivore	Rock cod	*Lotella rhacina*
Cowfish	*Lactoria diaphana*	Invertivore	Leatherjacket	*Meuschenia scaber*	Invertivore	Leatherjacket	*Meuschenia scaber*
Goldstripe groper	*Aulacocephalus temminckii*	Carnivore	Red rock cod	*Scorpaena cardinalis*	Invertivore	Balloonfish	*Sphoeroides pachygaster*
Caramel drummer	*Girella fimbriata*	Mixed Omnivore	Red gurnard	*Chelidonichthys kumu*	Mixed Carnivore	Silver drummer	*Kyphosus sydneyanus*
Grey marlinsucker	*Remora brachyptera*	Invertivore	Rudderfish	*Centrolophus niger*	Mixed Carnivore	Rock cod	*Lotella rhacina*

White remora	*Remora albescens*	Invertivore	Ruffe	*Tubbia tasmanica*	Mixed Carnivore	Trumpeter	*Latris lineata*
Yellowspot demoiselle	*Chromis flavomaculata*	Invertivore	Jock Stewart	*Helicolenus percoides*	Mixed Carnivore	Wavyline perch	*Lepidoperca tasmanica*
Convict groper	*Hyporthodus octofasciatus*	Carnivore	Blue marlin	*Makaira nigricans*	Carnivore	Blue marlin	*Makaira nigricans*
Pelagic puffer	*Pelagocephalus marki*	Invertivore	Red scorpionfish	*Scorpaena papillosa*	Carnivore	Globefish	*Contusus richei*
Blunthead platax	*Platax teira*	Carnivore	Splendid perch	*Callanthias australis*	Invertivore	Bluenose	*Hyperoglyphe antarctica*
Oblong sunfish	*Ranzania laevis*	Mixed Carnivore	Blue marlin	*Makaira nigricans*	Carnivore	Trevally	*Pseudocaranx dentex*
Striped boarfish	*Evistias acutirostris*	Invertivore	Longfin boarfish	*Zanclistius elevatus*	Invertivore	Longfin boarfish	*Zanclistius elevatus*
Redbanded grubfish	*Parapercis binivirgata*	Invertivore	Ahuru	*Auchenoceros punctatus*	Invertivore	Ahuru	*Auchenoceros punctatus*
Eyestripe surgeonfish	*Acanthurus dussumieri*	Mixed Omnivore	Leatherjacket	*Meuschenia scaber*	Invertivore	Silver drummer	*Kyphosus sydneyanus*
Flying gurnard	*Dactyloptena orientalis*	Mixed Carnivore	Longfin boarfish	*Zanclistius elevatus*	Invertivore	Spotted gurnard	*Pterygotrigla andertoni*
Slender remora	*Phtheirichthys lineatus*	Mixed Carnivore	Sandfish	*Gonorynchus forsteri*	Mixed Omnivore	Rudderfish	*Centrolophus niger*
Velifer	*Metavelifer multiradiatus*	Mixed Carnivore	Splendid perch	*Callanthias australis*	Invertivore	Spotted gurnard	*Pterygotrigla andertoni*
Lyretail hawkfish	*Cyprinocirrhites polyactis*	Invertivore	Splendid perch	*Callanthias australis*	Invertivore	Splendid perch	*Callanthias australis*
Sailfish	*Istiophorus platypterus*	Carnivore	Trevally	*Pseudocaranx dentex*	Mixed Carnivore	Blue marlin	*Makaira nigricans*
Halfmoon groper	*Epinephelus rivulatus*	Mixed Carnivore	Balloonfish	*Sphoeroides pachygaster*	Carnivore	Sunfish	*Mola alexandrini*
Common lizardfish	*Synodus variegatus*	Carnivore	Slender tuna	*Allothunnus fallai*	Mixed Carnivore	Yellowfin tuna	*Thunnus albacares*
Onespot demoiselle	*Chromis hypsilepis*	Mixed Omnivore	Longfin boarfish	*Zanclistius elevatus*	Invertivore	Silver drummer	*Kyphosus sydneyanus*
Yellowbanded perch	*Acanthistius cinctus*	Carnivore	Blue marlin	*Makaira nigricans*	Carnivore	Blue marlin	*Makaira nigricans*
Kermadec scorpionfish	*Maxillicosta raoulensis*	Invertivore	Longfin boarfish	*Zanclistius elevatus*	Invertivore	Longfin boarfish	*Zanclistius elevatus*

Wahoo	*Acanthocybium solandri*	Carnivore	Ruffe	*Tubbia tasmanica*	Mixed Carnivore	Yellowfin tuna	*Thunnus albacares*
Pineapplefish	*Monocentris japonica*	Invertivore	Snipefish	*Macroramphosus scolopax*	Invertivore	Snipefish	*Macroramphosus scolopax*
Barred leatherjacket	*Cantherhines dumerilii*	Invertivore	Ahuru	*Auchenoceros punctatus*	Invertivore	Ahuru	*Auchenoceros punctatus*
Spotted black groper	*Epinephelus daemelii*	Carnivore	Blue marlin	*Makaira nigricans*	Carnivore	Blue marlin	*Makaira nigricans*
Darkvent leatherjacket	*Thamnaconus analis*	Invertivore	Leatherjacket	*Meuschenia scaber*	Invertivore	Leatherjacket	*Meuschenia scaber*
Whitefingered angler	*Antennatus nummifer*	Carnivore	Swordfish	*Xiphias gladius*	Carnivore	Swordfish	*Xiphias gladius*
Spotfin burrfish	*Chilomycterus reticulatus*	Invertivore	Balloonfish	*Sphoeroides pachygaster*	Carnivore	Snipefish	*Macroramphosus scolopax*
Easter Island demoiselle	*Chrysiptera rapanui*	Mixed Omnivore	Leatherjacket	*Meuschenia scaber*	Invertivore	Silver drummer	*Kyphosus sydneyanus*
Lord Howe coralfish	*Amphichaetodon howensis*	Invertivore	Leatherjacket	*Meuschenia scaber*	Invertivore	Leatherjacket	*Meuschenia scaber*
Slender boxfish	*Polyplacapros tyleri*	Invertivore	Leatherjacket	*Meuschenia scaber*	Invertivore	Leatherjacket	*Meuschenia scaber*
Commersons frogfish	*Antennarius commerson*	Carnivore	Swordfish	*Xiphias gladius*	Carnivore	Swordfish	*Xiphias gladius*
Striped angler	*Antennarius striatus*	Carnivore	Balloonfish	*Sphoeroides pachygaster*	Carnivore	Balloonfish	*Sphoeroides pachygaster*
Scrawled leatherjacket	*Aluterus scriptus*	Invertivore	Leatherjacket	*Meuschenia scaber*	Invertivore	Leatherjacket	*Meuschenia scaber*
Queensland groper	*Epinephelus lanceolatus*	Carnivore	Swordfish	*Xiphias gladius*	Carnivore	Swordfish	*Xiphias gladius*

3.6.3 Supplement 3 – Habitat group additional data

Table S3.1: ANOVA tables comparing the ten inter-landmark distances across the four habitat groups of true benthic, benthopelagic, coastal pelagic and oceanic pelagic. Significant *P* values are bold and italicised.

Total length (TL)	Estimate	Std Error	t value	df	P value
Grand Mean	690.29	45.26	15.25	1	0
True benthic	-40.40	89.80	-0.45	1	0.653
Benthopelagic	-66.67	64.77	-1.03	1	0.304
Coastal pelagic	15.59	107.02	0.15	1	0.884
Oceanic pelagic	-228.15	131.81	-1.73	1	***0.085***

Standard length (SL)	Estimate	Std Error	t value	df	P value
Grand Mean	588.61	40.21	14.64	1	0
True benthic	-34.30	79.78	-0.43	1	0.668
Benthopelagic	-63.61	57.53	-1.11	1	0.27
Coastal pelagic	0.162	95.07	0.00	1	0.999
Oceanic pelagic	-199.60	117.09	-1.71	1	***0.09***

Fork length (FL)	Estimate	Std Error	t value	df	P value
Grand Mean	656.53	42.37	15.49	1	0
True benthic	-45.38	84.06	-0.54	1	0.59
Benthopelagic	-63.04	60.63	-1.04	1	0.299
Coastal pelagic	5.51	100.19	0.06	1	0.956
Oceanic pelagic	-195.85	123.38	-1.59	1	0.114

Head length (HL)	Estimate	Std Error	t value	df	P value
Grand Mean	176.62	15.19	11.62	1	0
True benthic	-3.63	30.15	-0.12	1	0.904
Benthopelagic	-13.03	21.74	-0.59	1	***0.55***
Coastal pelagic	9.44	35.93	0.26	1	0.793
Oceanic pelagic	-121.93	44.24	-2.76	1	***0.006***

Pre-anal length (PAL)	Estimate	Std Error	t value	df	P value
Grand Mean	375.14	28.68	13.08	1	0
True benthic	11.14	56.89	0.19	1	0.845
Benthopelagic	-36.16	41.03	-0.88	1	0.379
Coastal pelagic	7.49	67.81	0.11	1	0.912
Oceanic pelagic	-155.81	83.51	-1.87	1	***0.063***

Pre-dorsal length (PDL)	Estimate	Std Error	t value	df	P value
Grand Mean	236.75	21.43	11.05	1	0
True benthic	-2.63	42.51	-0.06	1	0.951
Benthopelagic	-5.51	30.66	-0.18	1	0.858
Coastal pelagic	-11.45	50.67	-0.23	1	0.821
Oceanic pelagic	-116.39	62.39	-1.87	1	***0.063***

Pre-pectoral fin length (PPEL)	Estimate	Std Error	t value	df	P value
Grand Mean	183.73	15.56	11.81	1	0
True benthic	-6.38	30.88	-0.21	1	0.837
Benthopelagic	-14.48	22.27	-0.65	1	0.516
Coastal pelagic	6.68	36.80	0.18	1	0.856
Oceanic pelagic	-123.02	45.32	-2.71	1	***0.007***

Eye diameter (ED)	Estimate	Std Error	t value	df	P value
Grand Mean	30.88	1.62	19.13	1	0
True benthic	-0.87	3.20	-0.27	1	0.786
Benthopelagic	-3.31	2.31	-1.43	1	0.153
Coastal pelagic	3.06	3.82	0.80	1	0.423
Oceanic pelagic	-9.51	4.70	-2.02	1	***0.044***

Pre-orbital length (POL)	Estimate	Std Error	t value	df	P value
Grand Mean	65.61	9.75	6.73	1	0
True benthic	0.01	19.35	0.00	1	1
Benthopelagic	1.43	13.95	0.10	1	0.918
Coastal pelagic	3.72	23.06	0.16	1	0.872
Oceanic pelagic	-80.38	28.39	-2.83	1	***0.005***

Body Depth (BD)	Estimate	Std Error	t value	df	P value
Grand Mean	193.67	14.95	12.96	1	0
True benthic	-17.74	29.66	-0.59	1	0.55
Benthopelagic	-24.06	21.39	-1.13	1	0.262
Coastal pelagic	22.44	35.34	0.64	1	0.526
Oceanic pelagic	-106.09	43.53	-2.44	1	***0.016***

Table S3.2: ANOVA tables comparing the nine inter-landmark distances scaled by standard length (SL) across the four habitat groups of true benthic, benthopelagic, coastal pelagic and oceanic pelagic. Significant *P* values are bold and italicised.

Total length (TL)	Estimate	Std Error	t value	df	P value
Grand Mean	1.19	0.01	261.61	1	0
True benthic	0.01	0.01	0.96	1	0.341
Benthopelagic	0.01	0.01	1.75	1	***0.082***
Coastal pelagic	0.02	0.01	2.05	1	***0.041***
Oceanic pelagic	-0.01	0.01	-0.95	1	0.343

Fork length (FL)	Estimate	Std Error	t value	df	P value
Grand Mean	1.15	0.01	231.54	1	0
True benthic	-0.01	0.01	-0.60	1	0.546
Benthopelagic	0.01	0.01	1.53	1	0.127
Coastal pelagic	0.02	0.01	1.68	1	***0.094***
Oceanic pelagic	0.01	0.01	0.49	1	0.628

Pre-anal length (PAL)	Estimate	Std Error	t value	df	P value
Grand Mean	0.62	0.01	68.07	1	0
True benthic	0.08	0.02	4.28	1	0
Benthopelagic	-0.00	0.01	-0.33	1	0.745
Coastal pelagic	0.04	0.02	0.30	1	0.764
Oceanic pelagic	-0.01	0.03	-0.28	1	0.782

Pre-pectoral fin length (PPEL)	Estimate	Std Error	t value	df	P value
Grand Mean	0.30	0.01	67.46	1	0
True benthic	0.02	0.01	1.79	1	***0.075***
Benthopelagic	0.00	0.01	0.19	1	0.844
Coastal pelagic	0.00	0.01	0.36	1	0.719
Oceanic pelagic	-0.03	0.01	-2.09	1	***0.037***

Pre-orbital length (POL)	Estimate	Std Error	t value	df	P value
Grand Mean	0.09	0.01	24.86	1	0
True benthic	0.01	0.01	0.86	1	0.39
Benthopelagic	0.01	0.01	2.33	1	***0.021***
Coastal pelagic	0.00	0.01	0.02	1	0.982
Oceanic pelagic	-0.01	0.01	-1.12	1	0.265

Head length (HL)	Estimate	Std Error	t value	df	P value
Grand Mean	0.29	0.00	71.82	1	0
True benthic	0.02	0.01	2.38	1	***0.018***
Benthopelagic	0.00	0.01	0.33	1	0.741
Coastal pelagic	0.01	0.01	1.34	1	0.181
Oceanic pelagic	-0.03	0.01	-2.74	1	***0.007***

Pre-dorsal length (PDL)	Estimate	Std Error	t value	df	P value
Grand Mean	0.39	0.01	30.10	1	0
True benthic	0.01	0.03	0.55	1	0.583
Benthopelagic	0.01	0.02	0.34	1	0.732
Coastal pelagic	-0.02	0.03	-0.75	1	0.457
Oceanic pelagic	0.01	0.04	0.19	1	0.845

Eye diameter (ED)	Estimate	Std Error	t value	df	P value
Grand Mean	0.06	0.00	40.29	1	0
True benthic	0.00	0.00	0.73	1	0.469
Benthopelagic	0.00	0.00	0.67	1	0.503
Coastal pelagic	0.01	0.00	1.35	1	0.177
Oceanic pelagic	-0.01	0.00	-1.47	1	0.143

Body Depth (BD)	Estimate	Std Error	t value	df	P value
Grand Mean	0.35	0.01	37.35	1	0
True benthic	-0.01	0.02	-0.28	1	0.778
Benthopelagic	0.01	0.01	0.81	1	0.419
Coastal pelagic	0.05	0.02	2.12	1	***0.035***
Oceanic pelagic	-0.07	0.03	-2.61	1	***0.01***

Table S3.3: LDA Classification success based on the ten inter-landmark distances for NZ native species across the four habitat types of true benthic, benthopelagic, coastal pelagic and oceanic pelagic

Prediction	**True benthic**	**Benthopelagic**	**Coastal pelagic**	**Oceanic pelagic**
True benthic	21	8	2	0
Benthopelagic	4	30	5	0
Coastal pelagic	2	6	14	2
Oceanic pelagic	0	2	2	7
Accuracy (%)	82	75	74	87

Table S3.4: The 139 Focal species and the NZ native species that are most morphologically similar based on the ten inter-landmark distances, and the most morphologically similar NZ native species that also shares the same habitat group. Species are ordered from most similar in morphology (i.e., the focal and NZ native species pair with the minimum Euclidean distance) to the least similar in morphology (i.e., the focal and NZ native species pair with the maximum Euclidean distance).

Focal Species			**Most morphologically similar NZ native species**			**Most morphologically similar NZ native species from the same habitat type**	
Common name	**Scientific name**	**Habitat type**	**Common name**	**Scientific name**	**Habitat type**	**Common name**	**Scientific name**
Scad	*Decapterus muroadsi*	oceanic pelagic	Spotted gurnard	*Pterygotrigla andertoni*	true benthic	Balloonfish	*Sphoeroides pachygaster*
Pacific Redstripe hogfish	*Bodianus masudai*	benthopelagic	Black rockfish	*Acanthoclinus littoreus*	true benthic	Twospot demoiselle	*Chromis dispila*
Parore	*Girella tricuspidata*	benthopelagic	Banded wrasse	*Notolabrus fucicola*	benthopelagic	Banded wrasse	*Notolabrus fucicola*
Blue knifefish	*Labracoglossa nitida*	coastal pelagic	Blue striped mullet	*Upeneichthys porosus*	true benthic	Telescope fish	*Mendosoma lineatum*
Elegant wrasse	*Anampses elegans*	benthopelagic	Olive rockfish	*Acanthoclinus fuscus*	true benthic	Twospot demoiselle	*Chromis dispila*
Kermadec scalyfin	*Parma kermadecensis*	benthopelagic	Bigeye	*Pempheris adspersa*	true benthic	Splendid perch	*Callanthias australis*
Bluefish	*Girella cyanea*	benthopelagic	Blue moki	*Latridopsis ciliaris*	benthopelagic	Blue moki	*Latridopsis ciliaris*
Twostripe goby	*Valenciennea helsdingenii*	true benthic	Rock cod	*Lotella rhacina*	true benthic	Rock cod	*Lotella rhacina*
Elongate green wrasse	*Pseudojuloides elongatus*	benthopelagic	Northern bastard cod	*Pseudophycis breviuscula*	true benthic	Twospot demoiselle	*Chromis dispila*
Easter Island demoiselle	*Chrysiptera rapanui*	benthopelagic	Rock cod	*Lotella rhacina*	true benthic	Wavyline perch	*Lepidoperca tasmanica*
Yellowfin foxfish	*Bodianus flavipinnis*	benthopelagic	Ruffe	*Tubbia tasmanica*	benthopelagic	Ruffe	*Tubbia tasmanica*
Longnose butterflyfish	*Forcipiger flavissimus*	benthopelagic	Crested blenny	*Parablennius laticlavius*	true benthic	Leatherjacket	*Meuschenia scaber*
Cowfish	*Lactoria diaphana*	benthopelagic	Yelloweye mullet	*Aldrichetta forsteri*	coastal pelagic	Wavyline perch	*Lepidoperca tasmanica*
Whitefingered angler	*Antennatus nummifer*	true benthic	New Zealand sole	*Peltorhamphus novaezeelandiae*	true benthic	New Zealand sole	*Peltorhamphus novaezeelandiae*

Pinklined coris	*Coris dorsomacula*	benthopelagic	Slender roughy	*Optivus elongatus*	benthopelagic	Slender roughy	*Optivus elongatus*
Sargassum fish	*Histrio*	true benthic	Snipefish	*Macroramphosus scolopax*	benthopelagic	New Zealand halfbanded perch	*Hypoplectrodes dimidius*
Spotfin burrfish	*Chilomycterus reticulatus*	coastal pelagic	Kingfish	*Seriola lalandi*	coastal pelagic	Kingfish	*Seriola lalandi*
Blackspot goatfish	*Parupeneus spilurus*	true benthic	Blue striped mullet	*Upeneichthys porosus*	true benthic	Blue striped mullet	*Upeneichthys porosus*
Lavender lizardfish	*Synodus similis*	true benthic	Red gurnard	*Chelidonichthys kumu*	true benthic	Red gurnard	*Chelidonichthys kumu*
Latchet	*Pterygotrigla polyommata*	true benthic	Grey mullet	*Mugil cephalus*	coastal pelagic	Jock Stewart	*Helicolenus percoides*
Orange wrasse	*Pseudolabrus luculentus*	benthopelagic	Pilchard	*Sardinops sagax*	coastal pelagic	Slender roughy	*Optivus elongatus*
Gunthers butterflyfish	*Chaetodon guentheri*	benthopelagic	Pilchard	*Sardinops sagax*	coastal pelagic	Girdled wrasse	*Notolabrus cinctus*
Pineapplefish	*Monocentris japonica*	true benthic	Southern bastard cod	*Pseudophycis barbata*	true benthic	Southern bastard cod	*Pseudophycis barbata*
Onespot demoiselle	*Chromis hypsilepis*	benthopelagic	Red scorpionfish	*Scorpaena papillosa*	true benthic	Splendid perch	*Callanthias australis*
Rainbowfish	*Suezichthys arquatus*	benthopelagic	Anchovy	*Engraulis australis*	coastal pelagic	Slender roughy	*Optivus elongatus*
Lyretail hawkfish	*Cyprinocirrhites polyactis*	true benthic	Red scorpionfish	*Scorpaena papillosa*	true benthic	Red scorpionfish	*Scorpaena papillosa*
Common lizardfish	*Synodus variegatus*	true benthic	Red scorpionfish	*Scorpaena papillosa*	true benthic	Red scorpionfish	*Scorpaena papillosa*
Green wrasse	*Notolabrus inscriptus*	benthopelagic	Common roughy	*Paratrachichthys trailli*	benthopelagic	Common roughy	*Paratrachichthys trailli*
Sunset wrasse	*Thalassoma lutescens*	benthopelagic	Rockling	*Gaidropsarus novaezelandiae*	benthopelagic	Rockling	*Gaidropsarus novaezelandiae*
Crimson cleanerfish	*Suezichthys aylingi*	benthopelagic	Northern bastard cod	*Pseudophycis breviuscula*	true benthic	Snipefish	*Macroramphosus scolopax*
Masked foxfish	*Bodianus flavifrons*	benthopelagic	Sand flounder	*Rhombosolea plebeia*	true benthic	Blue Maomao	*Scorpis violacea*
Doaks lizardfish	*Synodus doaki*	true benthic	Blue cod	*Parapercis colias*	true benthic	Blue cod	*Parapercis colias*
Starry toado	*Arothron firmamentum*	coastal pelagic	Red cod	*Pseudophycis bachus*	benthopelagic	Horse mackerel	*Trachurus novaezelandiae*
IndoPacific sergeant	*Abudefduf vaigiensis*	benthopelagic	Balloonfish	*Sphoeroides pachygaster*	oceanic pelagic	Pink maomao	*Caprodon longimanus*
Tilefish	*Malacanthus brevirostris*	true benthic	Yellow cod	*Parapercis gilliesii*	true benthic	Yellow cod	*Parapercis gilliesii*
Combfish	*Coris picta*	benthopelagic	Redbanded perch	*Hypoplectrodes huntii*	benthopelagic	Redbanded perch	*Hypoplectrodes huntii*
Striped pigfish	*Bodianus izuensis*	benthopelagic	Slender sprat	*Sprattus antipodum*	coastal pelagic	Twospot demoiselle	*Chromis dispila*
Goldstripe groper	*Aulacocephalus temminckii*	benthopelagic	Balloonfish	*Sphoeroides pachygaster*	oceanic pelagic	Ruffe	*Tubbia tasmanica*
Magpie perch	*Pseudogoniistius nigripes*	benthopelagic	Spotted gurnard	*Pterygotrigla andertoni*	true benthic	Red cod	*Pseudophycis bachus*
Wingfish	*Pteraclis velifera*	oceanic pelagic	Jock Stewart	*Helicolenus percoides*	true benthic	Chilean mackerel	*Trachurus murphyi*
Clown toado	*Canthigaster callisterna*	benthopelagic	Snipefish	*Macroramphosus scolopax*	benthopelagic	Snipefish	*Macroramphosus scolopax*
Two-spot wrasse	*Oxycheilinus bimaculatus*	benthopelagic	Rock cod	*Lotella rhacina*	true benthic	Wavyline perch	*Lepidoperca tasmanica*

Yellow demoiselle	*Chromis fumea*	benthopelagic	Blue striped mullet	*Upeneichthys porosus*	true benthic	Ruffe	*Tubbia tasmanica*
White remora	*Remora albescens*	oceanic pelagic	Spotty	*Notolabrus celidotus*	benthopelagic	Balloonfish	*Sphoeroides pachygaster*
Marbled parrotfish	*Leptoscarus vaigiensis*	benthopelagic	Banded wrasse	*Notolabrus fucicola*	benthopelagic	Banded wrasse	*Notolabrus fucicola*
Beaked drummer	*Kyphosus sectatrix*	benthopelagic	Sand flounder	*Rhombosolea plebeia*	true benthic	Sweep	*Scorpis lineolata*
Blunthead wrasse	*Thalassoma amblycephalum*	benthopelagic	Rockling	*Gaidropsarus novaezelandiae*	benthopelagic	Rockling	*Gaidropsarus novaezelandiae*
Southern damselfish	*Chrysiptera notialis*	benthopelagic	Rock cod	*Lotella rhacina*	true benthic	Rockling	*Gaidropsarus novaezelandiae*
Painted Lizardfish	*Trachinocephalus trachinus*	true benthic	Blue cod	*Parapercis colias*	true benthic	Blue cod	*Parapercis colias*
Blue wrasse	*Thalassoma lunare*	benthopelagic	Red gurnard	*Chelidonichthys kumu*	true benthic	Wavyline perch	*Lepidoperca tasmanica*
Cheekspot scorpionfish	*Scorpaenodes evides*	true benthic	Rock cod	*Lotella rhacina*	true benthic	Rock cod	*Lotella rhacina*
Pacific seabream	*Acanthopagrus pacificus*	benthopelagic	Silver drummer	*Kyphosus sydneyanus*	benthopelagic	Silver drummer	*Kyphosus sydneyanus*
Bluestriped fangblenny	*Plagiotremus rhinorhynchos*	benthopelagic	Rock cod	*Lotella rhacina*	true benthic	Wavyline perch	*Lepidoperca tasmanica*
Caramel drummer	*Girella fimbriata*	benthopelagic	Balloonfish	*Sphoeroides pachygaster*	oceanic pelagic	Ruffe	*Tubbia tasmanica*
Eyebrow perch	*Hypoplectrodes coronatus*	true benthic	Southern burrfish	*Allomycterus pilatus*	coastal pelagic	Jock Stewart	*Helicolenus percoides*
Halfmoon groper	*Epinephelus rivulatus*	true benthic	Trevally	*Pseudocaranx dentex*	coastal pelagic	Red rock cod	*Scorpaena cardinalis*
Bridled goby	*Arenigobius bifrenatus*	true benthic	Rock cod	*Lotella rhacina*	true benthic	Rock cod	*Lotella rhacina*
Darkvent leatherjacket	*Thamnaconus analis*	benthopelagic	Sand diver	*Tewara cranwellae*	true benthic	Leatherjacket	*Meuschenia scaber*
Sharksucker	*Echeneis naucrates*	oceanic pelagic	Yellow cod	*Parapercis gilliesii*	true benthic	Balloonfish	*Sphoeroides pachygaster*
Brassy drummer	*Kyphosus vaigiensis*	benthopelagic	Porae	*Nemadactylus douglasii*	benthopelagic	Porae	*Nemadactylus douglasii*
Banded scalyfin	*Parma polylepis*	benthopelagic	Southern bastard cod	*Pseudophycis barbata*	true benthic	Common roughy	*Paratrachichthys trailli*
Redbanded grubfish	*Parapercis binivirgata*	true benthic	Yellow cod	*Parapercis gilliesii*	true benthic	Yellow cod	*Parapercis gilliesii*
Red lionfish	*Pterois volitans*	true benthic	Horse mackerel	*Trachurus novaezelandiae*	coastal pelagic	Spotted gurnard	*Pterygotrigla andertoni*
Notchhead marblefish	*Aplodactylus etheridgii*	true benthic	Greenback flounder	*Rhombosolea tapirina*	true benthic	Greenback flounder	*Rhombosolea tapirina*
Mado	*Atypichthys latus*	benthopelagic	Southern bastard cod	*Pseudophycis barbata*	true benthic	Ruffe	*Tubbia tasmanica*
Grey drummer	*Kyphosus bigibbus*	benthopelagic	Copper moki	*Latridopsis forsteri*	benthopelagic	Copper moki	*Latridopsis forsteri*
Threadfin butterflyfish	*Chaetodon auriga*	benthopelagic	Scarlet wrasse	*Pseudolabrus miles*	benthopelagic	Scarlet wrasse	*Pseudolabrus miles*
Wahoo	*Acanthocybium solandri*	oceanic pelagic	Rays bream	*Brama*	oceanic pelagic	Rays bream	*Brama*
Orange bellowsfish	*Notopogon xenosoma*	benthopelagic	Rock cod	*Lotella rhacina*	true benthic	Wavyline perch	*Lepidoperca tasmanica*
Mimic blenny	*Plagiotremus tapeinosoma*	benthopelagic	Saury	*Scomberesox saurus*	coastal pelagic	Wavyline perch	*Lepidoperca tasmanica*
Hardfin marlinsucker	*Remora osteochir*	oceanic pelagic	Globefish	*Contusus richei*	coastal pelagic	Chilean mackerel	*Trachurus murphyi*
Yellowfin bream	*Acanthopagrus australis*	benthopelagic	Albacore	*Thunnus alalunga*	oceanic pelagic	Golden snapper	*Centroberyx affinis*

Flying gurnard	*Dactyloptena orientalis*	benthopelagic	Golden snapper	*Centroberyx affinis*	benthopelagic	Golden snapper	*Centroberyx affinis*
Boxfish	*Ostracion cubicus*	benthopelagic	Common roughy	*Paratrachichthys trailli*	benthopelagic	Common roughy	*Paratrachichthys trailli*
Bartailed goatfish	*Upeneus francisi*	true benthic	Yelloweye mullet	*Aldrichetta forsteri*	coastal pelagic	Red gurnard	*Chelidonichthys kumu*
Silverspot	*Chironemus maculosus*	true benthic	Blue warehou	*Seriolella brama*	coastal pelagic	Southern bastard cod	*Pseudophycis barbata*
Pelagic puffer	*Pelagocephalus marki*	coastal pelagic	Rock cod	*Lotella rhacina*	true benthic	Yelloweye mullet	*Aldrichetta forsteri*
Bullet tuna	*Auxis rochei*	coastal pelagic	NZ Brill	*Colistium guntheri*	true benthic	Silver warehou	*Seriolella punctata*
Red morwong	*Morwong fuscus*	benthopelagic	Blue moki	*Latridopsis ciliaris*	benthopelagic	Blue moki	*Latridopsis ciliaris*
Jughead puffer	*Lagocephalus*	coastal pelagic	Southern burrfish	*Allomycterus pilatus*	coastal pelagic	Southern burrfish	*Allomycterus pilatus*
Bronze bream	*Xenobrama microlepis*	coastal pelagic	Slender tuna	*Allothunnus fallai*	oceanic pelagic	Silver warehou	*Seriolella punctata*
Lord Howe coralfish	*Amphichaetodon howensis*	benthopelagic	Yelloweye mullet	*Aldrichetta forsteri*	coastal pelagic	Wavyline perch	*Lepidoperca tasmanica*
Vanderbilts chromis	*Chromis vanderbilti*	benthopelagic	Wavyline perch	*Lepidoperca tasmanica*	benthopelagic	Wavyline perch	*Lepidoperca tasmanica*
Knifejaw	*Oplegnathus woodwardi*	benthopelagic	Common roughy	*Paratrachichthys trailli*	benthopelagic	Common roughy	*Paratrachichthys trailli*
Grey knifefish	*Bathystethus cultratus*	coastal pelagic	Blue cod	*Parapercis colias*	true benthic	Yelloweye mullet	*Aldrichetta forsteri*
Cheesemans puffer	*Lagocephalus cheesemanii*	coastal pelagic	Yellow cod	*Parapercis gilliesii*	true benthic	Yelloweye mullet	*Aldrichetta forsteri*
Yellowspot demoiselle	*Chromis flavomaculata*	benthopelagic	Blue cod	*Parapercis colias*	true benthic	Ruffe	*Tubbia tasmanica*
Doubleheader	*Coris bulbifrons*	benthopelagic	Tarakihi	*Nemadactylus macropterus*	benthopelagic	Tarakihi	*Nemadactylus macropterus*
Eyestripe surgeonfish	*Acanthurus dussumieri*	benthopelagic	Scarlet wrasse	*Pseudolabrus miles*	benthopelagic	Scarlet wrasse	*Pseudolabrus miles*
Pilotfish	*Naucrates ductor*	oceanic pelagic	Hake	*Merluccius australis*	coastal pelagic	Chilean mackerel	*Trachurus murphyi*
Striped boarfish	*Evistias acutirostris*	benthopelagic	Tarakihi	*Nemadactylus macropterus*	benthopelagic	Tarakihi	*Nemadactylus macropterus*
Kermadec scorpionfish	*Maxillicosta raoulensis*	true benthic	Rock cod	*Lotella rhacina*	true benthic	Rock cod	*Lotella rhacina*
Grey marlinsucker	*Remora brachyptera*	oceanic pelagic	Sandfish	*Gonorynchus forsteri*	true benthic	Balloonfish	*Sphoeroides pachygaster*
Twospot hogfish	*Bodianus bimaculatus*	benthopelagic	Porae	*Nemadactylus douglasii*	benthopelagic	Porae	*Nemadactylus douglasii*
Confused goby	*Acentrogobius pflaumii*	true benthic	Sandfish	*Gonorynchus forsteri*	true benthic	Sandfish	*Gonorynchus forsteri*
Yellowbanded perch	*Acanthistius cinctus*	benthopelagic	Copper moki	*Latridopsis forsteri*	benthopelagic	Copper moki	*Latridopsis forsteri*
Remora	*Remora*	oceanic pelagic	Globefish	*Contusus richei*	coastal pelagic	Chilean mackerel	*Trachurus murphyi*
Painted moki	*Morwong ephippium*	benthopelagic	Red rock cod	*Scorpaena cardinalis*	true benthic	Red moki	*Chirodactylus spectabilis*
Toadstool groper	*Trachypoma macracanthus*	true benthic	Blue moki	*Latridopsis ciliaris*	benthopelagic	Red rock cod	*Scorpaena cardinalis*
Kermadec barracuda	*Sphyraena waitii*	oceanic pelagic	Yellow cod	*Parapercis gilliesii*	true benthic	Balloonfish	*Sphoeroides pachygaster*
Blackfin barracuda	*Sphyraena qenie*	coastal pelagic	Slender tuna	*Allothunnus fallai*	oceanic pelagic	Southern burrfish	*Allomycterus pilatus*
Slender boxfish	*Polyplacapros tyleri*	benthopelagic	Piper	*Hyporhamphus ihi*	coastal pelagic	Snipefish	*Macroramphosus scolopax*
Ruby snapper	*Etelis carbunculus*	benthopelagic	Bluenose	*Hyperoglyphe antarctica*	coastal pelagic	Snapper	*Chrysophrys auratus*

Frigate tuna	*Auxis thazard*	coastal pelagic	Rays bream	*Brama*	oceanic pelagic	Southern burrfish	*Allomycterus pilatus*
Spotted sawtail	*Prionurus maculatus*	benthopelagic	Sandagers wrasse	*Coris sandeyeri*	benthopelagic	Sandagers wrasse	*Coris sandeyeri*
Moorish idol	*Zanclus cornutus*	benthopelagic	Sandagers wrasse	*Coris sandeyeri*	benthopelagic	Sandagers wrasse	*Coris sandeyeri*
Northern kelpfish	*Chironemus microlepis*	true benthic	Yellow cod	*Parapercis gilliesii*	true benthic	Yellow cod	*Parapercis gilliesii*
Australian bonito	*Sarda australis*	coastal pelagic	Butterfly tuna	*Gasterochisma melampus*	oceanic pelagic	Trevally	*Pseudocaranx dentex*
Greys sandfish	*Gonorynchus greyi*	benthopelagic	Globefish	*Contusus richei*	coastal pelagic	Red cod	*Pseudophycis bachus*
Samsonfish	*Seriola hippos*	benthopelagic	Hapuku groper	*Polyprion oxygeneios*	benthopelagic	Hapuku groper	*Polyprion oxygeneios*
Rainbow runner	*Elagatis bipinnulata*	coastal pelagic	Bluenose	*Hyperoglyphe antarctica*	coastal pelagic	Bluenose	*Hyperoglyphe antarctica*
Northern kahawai	*Arripis xylabion*	coastal pelagic	Slender tuna	*Allothunnus fallai*	oceanic pelagic	Silver warehou	*Seriolella punctata*
Slender remora	*Phtheirichthys lineatus*	oceanic pelagic	Globefish	*Contusus richei*	coastal pelagic	Chilean mackerel	*Trachurus murphyi*
Commersons frogfish	*Antennarius commerson*	true benthic	Trumpeter	*Latris lineata*	benthopelagic	New Zealand turbot	*Colistium nudipinnis*
Spotfin porcupinefish	*Diodon hystrix*	benthopelagic	Snapper	*Chrysophrys auratus*	benthopelagic	Snapper	*Chrysophrys auratus*
Velifer	*Metavelifer multiradiatus*	benthopelagic	Blue moki	*Latridopsis ciliaris*	benthopelagic	Blue moki	*Latridopsis ciliaris*
Oblong sunfish	*Ranzania laevis*	oceanic pelagic	Snapper	*Chrysophrys auratus*	benthopelagic	Slender tuna	*Allothunnus fallai*
Clown coris	*Coris aygula*	benthopelagic	Greenback flounder	*Rhombosolea tapirina*	true benthic	Greenbone butterfish	*Odax pullus*
Almacojack	*Seriola rivoliana*	coastal pelagic	Pomfret	*Taractichthys longipinnis*	oceanic pelagic	Bluenose	*Hyperoglyphe antarctica*
Striped angler	*Antennarius striatus*	true benthic	Trevally	*Pseudocaranx dentex*	coastal pelagic	New Zealand turbot	*Colistium nudipinnis*
Bluespine unicornfish	*Naso unicornis*	benthopelagic	Sandagers wrasse	*Coris sandeyeri*	benthopelagic	Sandagers wrasse	*Coris sandeyeri*
Tailor	*Pomatomus saltatrix*	oceanic pelagic	Bass	*Polyprion americanus*	benthopelagic	Pomfret	*Taractichthys longipinnis*
Blunthead platax	*Platax teira*	coastal pelagic	Hapuku groper	*Polyprion oxygeneios*	benthopelagic	Trevally	*Pseudocaranx dentex*
Striped beakfish	*Oplegnathus fasciatus*	benthopelagic	Trevally	*Pseudocaranx dentex*	coastal pelagic	Hapuku groper	*Polyprion oxygeneios*
Trumpetfish	*Aulostomus chinensis*	benthopelagic	Sand diver	*Tewara cranwellae*	true benthic	Leatherjacket	*Meuschenia scaber*
Astronomers toado	*Arothron stellatus*	benthopelagic	Snapper	*Chrysophrys auratus*	benthopelagic	Snapper	*Chrysophrys auratus*
Barred leatherjacket	*Cantherhines dumerilii*	benthopelagic	Sandagers wrasse	*Coris sandeyeri*	benthopelagic	Sandagers wrasse	*Coris sandeyeri*
Sharptail sunfish	*Masturus lanceolatus*	oceanic pelagic	Sunfish	*Mola alexandrini*	oceanic pelagic	Sunfish	*Mola alexandrini*
silver cheeked toadfish	*Lagocephalus sceleratus*	benthopelagic	Bluenose	*Hyperoglyphe antarctica*	coastal pelagic	Snapper	*Chrysophrys auratus*
Amberjack	*Seriola dumerili*	coastal pelagic	Bluenose	*Hyperoglyphe antarctica*	coastal pelagic	Bluenose	*Hyperoglyphe antarctica*
Mahimahi	*Coryphaena hippurus*	oceanic pelagic	Sunfish	*Mola alexandrini*	oceanic pelagic	Sunfish	*Mola alexandrini*
Smooth leatherjacket	*Aluterus monoceros*	benthopelagic	Swordfish	*Xiphias gladius*	oceanic pelagic	John Dory	*Zeus faber*
Convict groper	*Hyporthodus octofasciatus*	benthopelagic	Blue marlin	*Makaira nigricans*	oceanic pelagic	Trumpeter	*Latris lineata*
Spotted black groper	*Epinephelus daemelii*	benthopelagic	Bass	*Polyprion americanus*	benthopelagic	Bass	*Polyprion americanus*

Red cornetfish	*Fistularia petimba*	benthopelagic	Sand diver	*Tewara cranwellae*	true benthic	Leatherjacket	*Meuschenia scaber*
Sailfish	*Istiophorus platypterus*	oceanic pelagic	Swordfish	*Xiphias gladius*	oceanic pelagic	Swordfish	*Xiphias gladius*
Scrawled leatherjacket	*Aluterus scriptus*	benthopelagic	Swordfish	*Xiphias gladius*	oceanic pelagic	Leatherjacket	*Meuschenia scaber*
Cornetfish	*Fistularia commersonii*	benthopelagic	Sand diver	*Tewara cranwellae*	true benthic	Leatherjacket	*Meuschenia scaber*
Queensland groper	*Epinephelus lanceolatus*	benthopelagic	Blue marlin	*Makaira nigricans*	oceanic pelagic	Bass	*Polyprion americanus*

Table S3.5: LDA Classification success based on the nine inter-landmark distances scaled by standard length (SL) for NZ native species across the four habitat groups of true benthic, benthopelagic, coastal pelagic and oceanic pelagic.

Prediction	**True benthic**	**Benthopelagic**	**Coastal pelagic**	**Oceanic pelagic**
True benthic	25	5	1	0
Benthopelagic	8	28	2	1
Coastal pelagic	2	2	19	1
Oceanic pelagic	0	3	5	3
Accuracy (%)	81	79	82	76

Table S3.6: The 139 Focal species and the NZ native species that are most morphologically similar based on the nine inter-landmark distances scaled by standard length (SL), and the most morphologically similar NZ native species that also shares the same habitat group. Species are ordered from most similar in morphology (i.e., the focal and NZ native species pair with the minimum Euclidean distance) to the least similar in morphology (i.e., the focal and NZ native species pair with the maximum Euclidean distance).

Focal Species			**Most morphologically similar NZ native species**			**Most morphologically similar NZ native species from the same habitat type**	
Common name	**Scientific name**	**Habitat type**	**Common name**	**Scientific name**	**Habitat type**	**Common name**	**Scientific name**
Pelagic puffer	*Pelagocephalus marki*	coastal pelagic	Speckled sole	*Peltorhamphus latus*	true benthic	Bluenose	*Hyperoglyphe antarctica*
Blue wrasse	*Thalassoma lunare*	benthopelagic	Jack mackerel	*Trachurus declivis*	coastal pelagic	White warehou	*Seriolella caerulea*
Magpie perch	*Pseudogoniistius nigripes*	benthopelagic	Slender sprat	*Sprattus antipodum*	coastal pelagic	Greenbone butterfish	*Odax pullus*
Red lionfish	*Pterois volitans*	true benthic	Yellowbelly flounder	*Rhombosolea leporina*	true benthic	Yellowbelly flounder	*Rhombosolea leporina*
Orange wrasse	*Pseudolabrus luculentus*	benthopelagic	Estuarine triplefin	*Forsterygion nigripenne*	true benthic	Silver drummer	*Kyphosus sydneyanus*
Remora	*Remora*	oceanic pelagic	Rock cod	*Lotella rhacina*	true benthic	Chilean mackerel	*Trachurus murphyi*
Mahimahi	*Coryphaena hippurus*	oceanic pelagic	Blue warehou	*Seriolella brama*	coastal pelagic	Butterfly tuna	*Gasterochisma melampus*
Bluefish	*Girella cyanea*	benthopelagic	Sand flounder	*Rhombosolea plebeia*	true benthic	Pink maomao	*Caprodon longimanus*
Spotted sawtail	*Prionurus maculatus*	benthopelagic	Banded wrasse	*Notolabrus fucicola*	benthopelagic	Banded wrasse	*Notolabrus fucicola*

Doaks lizardfish	*Synodus doaki*	true benthic	Butterfly tuna	*Gasterochisma melampus*	oceanic pelagic	Southern bastard cod	*Pseudophycis barbata*
Bartailed goatfish	*Upeneus francisi*	true benthic	Slender sprat	*Sprattus antipodum*	coastal pelagic	Blue cod	*Parapercis colias*
Grey marlinsucker	*Remora brachyptera*	oceanic pelagic	Rudderfish	*Centrolophus niger*	coastal pelagic	Chilean mackerel	*Trachurus murphyi*
Green wrasse	*Notolabrus inscriptus*	benthopelagic	Olive rockfish	*Acanthoclinus fuscus*	true benthic	Bigeye ruffe	*Tubbia stewarti*
Banded scalyfin	*Parma polylepis*	benthopelagic	Spotted gurnard	*Pterygotrigla andertoni*	true benthic	Rockling	*Gaidropsarus novaezelandiae*
Parore	*Girella tricuspidata*	benthopelagic	Rays bream	*Brama*	oceanic pelagic	Sandagers wrasse	*Coris sandeyeri*
Latchet	*Pterygotrigla polyommata*	true benthic	Bigeye ruffe	*Tubbia stewarti*	benthopelagic	Olive rockfish	*Acanthoclinus fuscus*
Tilefish	*Malacanthus brevirostris*	true benthic	Rock cod	*Lotella rhacina*	true benthic	Rock cod	*Lotella rhacina*
Mado	*Atypichthys latus*	benthopelagic	Sand flounder	*Rhombosolea plebeia*	true benthic	Silver drummer	*Kyphosus sydneyanus*
Doubleheader	*Coris bulbifrons*	benthopelagic	Silver drummer	*Kyphosus sydneyanus*	benthopelagic	Silver drummer	*Kyphosus sydneyanus*
Kermadec scalyfin	*Parma kermadecensis*	benthopelagic	Slender sprat	*Sprattus antipodum*	coastal pelagic	Greenbone butterfish	*Odax pullus*
Pacific Redstripe hogfish	*Bodianus masudai*	benthopelagic	Sand flounder	*Rhombosolea plebeia*	true benthic	Silver drummer	*Kyphosus sydneyanus*
Amberjack	*Seriola dumerili*	coastal pelagic	Skipjack tuna	*Katsuwonus pelamis*	coastal pelagic	Skipjack tuna	*Katsuwonus pelamis*
Frigate tuna	*Auxis thazard*	coastal pelagic	Blue warehou	*Seriolella brama*	coastal pelagic	Blue warehou	*Seriolella brama*
Caramel drummer	*Girella fimbriata*	benthopelagic	Yelloweye mullet	*Acanthoclinus littoreus*	true benthic	Bigeye ruffe	*Tubbia stewarti*
Goldstripe groper	*Aulacocephalus temminckii*	benthopelagic	Red moki	*Chirodactylus spectabilis*	benthopelagic	Red moki	*Chirodactylus spectabilis*
Elongate green wrasse	*Pseudojuloides elongatus*	benthopelagic	Olive rockfish	*Acanthoclinus fuscus*	true benthic	Rockling	*Gaidropsarus novaezelandiae*
Clown toado	*Canthigaster callisterna*	benthopelagic	Girdled wrasse	*Notolabrus cinctus*	benthopelagic	Girdled wrasse	*Notolabrus cinctus*
Northern kahawai	*Arripis xylabion*	coastal pelagic	Kahawai	*Arripis trutta*	coastal pelagic	Kahawai	*Arripis trutta*
Kermadec barracuda	*Sphyraena waitii*	oceanic pelagic	Southern bastard cod	*Pseudophycis barbata*	true benthic	Rays bream	*Brama*
Sharptail sunfish	*Masturus lanceolatus*	oceanic pelagic	Piper	*Hyporhamphus ihi*	coastal pelagic	Albacore	*Thunnus alalunga*
Silverspot	*Chironemus maculosus*	true benthic	Yellowbelly flounder	*Rhombosolea leporina*	true benthic	Yellowbelly flounder	*Rhombosolea leporina*
Yellowfin bream	*Acanthopagrus australis*	benthopelagic	White warehou	*Seriolella caerulea*	benthopelagic	White warehou	*Seriolella caerulea*
Common lizardfish	*Synodus variegatus*	true benthic	Kingfish	*Seriola lalandi*	coastal pelagic	Southern bastard cod	*Pseudophycis barbata*
Yellow demoiselle	*Chromis fumea*	benthopelagic	Greenback flounder	*Rhombosolea tapirina*	true benthic	Girdled wrasse	*Notolabrus cinctus*
Ruby snapper	*Etelis carbunculus*	benthopelagic	Speckled sole	*Peltorhamphus latus*	true benthic	Butterfly perch	*Caesioperca lepidoptera*
Cornetfish	*Fistularia commersonii*	benthopelagic	Sweep	*Scorpis lineolata*	benthopelagic	Sweep	*Scorpis lineolata*
Jughead puffer	*Lagocephalus*	coastal pelagic	Skipjack tuna	*Katsuwonus pelamis*	coastal pelagic	Skipjack tuna	*Katsuwonus pelamis*
Grey knifefish	*Bathystethus cultratus*	coastal pelagic	Hake	*Merluccius australis*	coastal pelagic	Hake	*Merluccius australis*
Yellowfin foxfish	*Bodianus flavipinnis*	benthopelagic	Speckled sole	*Peltorhamphus latus*	true benthic	Bigeye ruffe	*Tubbia stewarti*
White remora	*Remora albescens*	oceanic pelagic	Skipjack tuna	*Katsuwonus pelamis*	coastal pelagic	Chilean mackerel	*Trachurus murphyi*

Notchhead marblefish	*Aplodactylus etheridgii*	true benthic	Slender sprat	*Sprattus antipodum*	coastal pelagic	Red gurnard	*Chelidonichthys kumu*
Grey drummer	*Kyphosus bigibbus*	benthopelagic	Southern bastard cod	*Pseudophycis barbata*	true benthic	Sandagers wrasse	*Coris sandeyeri*
IndoPacific sergeant	*Abudefduf vaigiensis*	benthopelagic	Red moki	*Chirodactylus spectabilis*	benthopelagic	Red moki	*Chirodactylus spectabilis*
Cheesemans puffer	*Lagocephalus cheesemanii*	coastal pelagic	Red gurnard	*Chelidonichthys kumu*	true benthic	Horse mackerel	*Trachurus novaezelandiae*
Brassy drummer	*Kyphosus vaigiensis*	benthopelagic	Bluenose	*Hyperoglyphe antarctica*	coastal pelagic	Twospot demoiselle	*Chromis dispila*
Painted moki	*Morwong ephippium*	benthopelagic	Blue Maomao	*Scorpis violacea*	benthopelagic	Kingfish	*Scorpis violacea*
Blunthead wrasse	*Thalassoma amblycephalum*	benthopelagic	Jack mackerel	*Trachurus declivis*	coastal pelagic	White warehou	*Seriolella caerulea*
Pineapplefish	*Monocentris japonica*	true benthic	Balloonfish	*Sphoeroides pachygaster*	oceanic pelagic	Red rock cod	*Scorpaena cardinalis*
Scad	*Decapterus muroadsi*	oceanic pelagic	Silver warehou	*Seriolella punctata*	coastal pelagic	Chilean mackerel	*Trachurus murphyi*
Pilotfish	*Naucrates ductor*	oceanic pelagic	Blue warehou	*Seriolella brama*	coastal pelagic	Butterfly tuna	*Gasterochisma melampus*
Marbled parrotfish	*Leptoscarus vaigiensis*	benthopelagic	Pomfret	*Taractichthys longipinnis*	oceanic pelagic	Golden snapper	*Centroberyx affinis*
Spotfin burrfish	*Chilomycterus reticulatus*	coastal pelagic	Girdled wrasse	*Notolabrus cinctus*	benthopelagic	Southern burrfish	*Allomycterus pilatus*
Blackspot goatfish	*Parupeneus spilurus*	true benthic	Skipjack tuna	*Katsuwonus pelamis*	coastal pelagic	Southern bastard cod	*Pseudophycis barbata*
Cheekspot scorpionfish	*Scorpaenodes evides*	true benthic	Crested blenny	*Parablennius laticlavius*	true benthic	Crested blenny	*Parablennius laticlavius*
Combfish	*Coris picta*	benthopelagic	Slender sprat	*Sprattus antipodum*	coastal pelagic	Banded wrasse	*Notolabrus fucicola*
Tailor	*Pomatomus saltatrix*	oceanic pelagic	Piper	*Hyporhamphus ihi*	coastal pelagic	Albacore	*Thunnus alalunga*
Masked foxfish	*Bodianus flavifrons*	benthopelagic	Butterfly perch	*Caesioperca lepidoptera*	benthopelagic	Butterfly perch	*Caesioperca lepidoptera*
Blue knifefish	*Labracoglossa nitida*	coastal pelagic	Jack mackerel	*Trachurus declivis*	coastal pelagic	Jack mackerel	*Trachurus declivis*
Onespot demoiselle	*Chromis hypsilepis*	benthopelagic	Bigeye ruffe	*Tubbia stewarti*	benthopelagic	Bigeye ruffe	*Tubbia stewarti*
Striped pigfish	*Bodianus izuensis*	benthopelagic	Butterfly perch	*Caesioperca lepidoptera*	benthopelagic	Butterfly perch	*Caesioperca lepidoptera*
Astronomers toado	*Arothron stellatus*	benthopelagic	Red gurnard	*Chelidonichthys kumu*	true benthic	Rockling	*Gaidropsarus novaezelandiae*
Barred leatherjacket	*Cantherhines dumerilii*	benthopelagic	Red moki	*Chirodactylus spectabilis*	benthopelagic	Red moki	*Chirodactylus spectabilis*
Samsonfish	*Seriola hippos*	benthopelagic	Albacore	*Thunnus alalunga*	oceanic pelagic	Blue moki	*Latridopsis ciliaris*
Twospot hogfish	*Bodianus bimaculatus*	benthopelagic	Common roughy	*Paratrachichthys trailli*	benthopelagic	Common roughy	*Paratrachichthys trailli*
Rainbow runner	*Elagatis bipinnulata*	coastal pelagic	Silver warehou	*Seriolella punctata*	coastal pelagic	Silver warehou	*Seriolella punctata*
Boxfish	*Ostracion cubicus*	benthopelagic	Slender sprat	*Sprattus antipodum*	coastal pelagic	Rockling	*Gaidropsarus novaezelandiae*
Eyebrow perch	*Hypoplectrodes coronatus*	true benthic	Slender sprat	*Sprattus antipodum*	coastal pelagic	Blue cod	*Parapercis colias*
Painted Lizardfish	*Trachinocephalus trachinus*	true benthic	Slender sprat	*Sprattus antipodum*	coastal pelagic	Blue cod	*Parapercis colias*
Lavender lizardfish	*Synodus similis*	true benthic	Blue warehou	*Seriolella brama*	coastal pelagic	Southern bastard cod	*Pseudophycis barbata*
Almacojack	*Seriola rivoliana*	coastal pelagic	Kahawai	*Arripis trutta*	coastal pelagic	Kahawai	*Arripis trutta*
Beaked drummer	*Kyphosus sectatrix*	benthopelagic	Skipjack tuna	*Katsuwonus pelamis*	coastal pelagic	Blue moki	*Latridopsis ciliaris*

Spotfin porcupinefish	*Diodon hystrix*	benthopelagic	Splendid perch	*Callanthias australis*	benthopelagic	Splendid perch	*Callanthias australis*
Lyretail hawkfish	*Cyprinocirrhites polyactis*	true benthic	Yellowbelly flounder	*Rhombosolea leporina*	true benthic	Yellowbelly flounder	*Rhombosolea leporina*
Greys sandfish	*Gonorynchus greyi*	benthopelagic	Sandfish	*Gonorynchus forsteri*	true benthic	Red cod	*Pseudophycis bachus*
Wingfish	*Pteraclis velifera*	oceanic pelagic	Grey mullet	*Mugil cephalus*	coastal pelagic	Chilean mackerel	*Trachurus murphyi*
Gunthers butterflyfish	*Chaetodon guentheri*	benthopelagic	Greenback flounder	*Rhombosolea tapirina*	true benthic	Scarlet wrasse	*Pseudolabrus miles*
Twostripe goby	*Valenciennea helsdingenii*	true benthic	White warehou	*Seriolella caerulea*	benthopelagic	Blue cod	*Parapercis colias*
Halfmoon groper	*Epinephelus rivulatus*	true benthic	Yellow boarfish	*Pentaceros decacanthus*	benthopelagic	Hiwihiwi	*Chironemus marmoratus*
Hardfin marlinsucker	*Remora osteochir*	oceanic pelagic	Rock cod	*Lotella rhacina*	true benthic	Chilean mackerel	*Trachurus murphyi*
Bullet tuna	*Auxis rochei*	coastal pelagic	Yelloweye mullet	*Aldrichetta forsteri*	coastal pelagic	Yelloweye mullet	*Aldrichetta forsteri*
Orange bellowsfish	*Notopogon xenosoma*	benthopelagic	Bass	*Polyprion americanus*	benthopelagic	Bass	*Polyprion americanus*
Rainbowfish	*Suezichthys arquatus*	benthopelagic	Bigeye ruffe	*Tubbia stewarti*	benthopelagic	Bigeye ruffe	*Tubbia stewarti*
Sharksucker	*Echeneis naucrates*	oceanic pelagic	Sandfish	*Gonorynchus forsteri*	true benthic	Chilean mackerel	*Trachurus murphyi*
Striped boarfish	*Evistias acutirostris*	benthopelagic	Redbanded perch	*Hypoplectrodes huntii*	benthopelagic	Redbanded perch	*Hypoplectrodes huntii*
Striped beakfish	*Oplegnathus fasciatus*	benthopelagic	Balloonfish	*Sphoeroides pachygaster*	oceanic pelagic	Hapuku groper	*Polyprion oxygeneios*
Mimic blenny	*Plagiotremus tapeinosoma*	benthopelagic	Rock cod	*Lotella rhacina*	true benthic	Red cod	*Pseudophycis bachus*
Red morwong	*Morwong fuscus*	benthopelagic	Sweep	*Scorpis lineolata*	benthopelagic	Sweep	*Scorpis lineolata*
Pinklined coris	*Coris dorsomacula*	benthopelagic	White warehou	*Seriolella caerulea*	benthopelagic	White warehou	*Seriolella caerulea*
Two-spot wrasse	*Oxycheilinus bimaculatus*	benthopelagic	Yellowbelly flounder	*Rhombosolea leporina*	true benthic	Leatherjacket	*Meuschenia scaber*
Clown coris	*Coris aygula*	benthopelagic	Southern bastard cod	*Pseudophycis barbata*	true benthic	Blue moki	*Latridopsis ciliaris*
Elegant wrasse	*Anampses elegans*	benthopelagic	Southern bastard cod	*Pseudophycis barbata*	true benthic	Tarakihi	*Nemadactylus macropterus*
Threadfin butterflyfish	*Chaetodon auriga*	benthopelagic	Balloonfish	*Sphoeroides pachygaster*	oceanic pelagic	Bass	*Polyprion americanus*
Spotted black groper	*Epinephelus daemelii*	benthopelagic	Trumpeter	*Latris lineata*	benthopelagic	Trumpeter	*Latris lineata*
Bronze bream	*Xenobrama microlepis*	coastal pelagic	Banded wrasse	*Notolabrus fucicola*	benthopelagic	Slender sprat	*Sprattus antipodum*
Blunthead platax	*Platax teira*	coastal pelagic	Southern burrfish	*Allomycterus pilatus*	coastal pelagic	Southern burrfish	*Allomycterus pilatus*
Australian bonito	*Sarda australis*	coastal pelagic	Slender tuna	*Allothunnus fallai*	oceanic pelagic	Kingfish	*Seriola lalandi*
Pacific seabream	*Acanthopagrus pacificus*	benthopelagic	Porae	*Nemadactylus douglasii*	benthopelagic	Porae	*Nemadactylus douglasii*
Smooth leatherjacket	*Aluterus monoceros*	benthopelagic	Butterfly perch	*Caesioperca lepidoptera*	benthopelagic	Butterfly perch	*Caesioperca lepidoptera*
Striped angler	*Antennarius striatus*	true benthic	Snipefish	*Macroramphosus scolopax*	benthopelagic	Red rock cod	*Scorpaena cardinalis*
Bluespine unicornfish	*Naso unicornis*	benthopelagic	Crested blenny	*Parablennius laticlavius*	true benthic	Bigeye ruffe	*Tubbia stewarti*
Blackfin barracuda	*Sphyraena qenie*	coastal pelagic	Slender tuna	*Allothunnus fallai*	oceanic pelagic	Piper	*Hyporhamphus ihi*
Velifer	*Metavelifer multiradiatus*	benthopelagic	Butterfly perch	*Caesioperca lepidoptera*	benthopelagic	Butterfly perch	*Caesioperca lepidoptera*

Sunset wrasse	*Thalassoma lutescens*	benthopelagic	Blue moki	*Latridopsis ciliaris*	benthopelagic	Blue moki	*Latridopsis ciliaris*
Flying gurnard	*Dactyloptena orientalis*	benthopelagic	Common roughy	*Paratrachichthys trailli*	benthopelagic	Common roughy	*Paratrachichthys trailli*
Trumpetfish	*Aulostomus chinensis*	benthopelagic	Trevally	*Pseudocaranx dentex*	coastal pelagic	Blue moki	*Latridopsis ciliaris*
silver cheeked toadfish	*Lagocephalus sceleratus*	benthopelagic	Speckled sole	*Peltorhamphus latus*	true benthic	Bigeye ruffe	*Tubbia stewarti*
Knifejaw	*Oplegnathus woodwardi*	benthopelagic	Crested blenny	*Parablennius laticlavius*	true benthic	Leatherjacket	*Meuschenia scaber*
Darkvent leatherjacket	*Thamnaconus analis*	benthopelagic	Common roughy	*Paratrachichthys trailli*	benthopelagic	Common roughy	*Paratrachichthys trailli*
Wahoo	*Acanthocybium solandri*	oceanic pelagic	Yellowfin tuna	*Thunnus albacares*	oceanic pelagic	Yellowfin tuna	*Thunnus albacares*
Southern damselfish	*Chrysiptera notialis*	benthopelagic	Common roughy	*Paratrachichthys trailli*	benthopelagic	Common roughy	*Paratrachichthys trailli*
Longnose butterflyfish	*Forcipiger flavissimus*	benthopelagic	John Dory	*Zeus faber*	benthopelagic	John Dory	*Zeus faber*
Moorish idol	*Zanclus cornutus*	benthopelagic	Snipefish	*Macroramphosus scolopax*	benthopelagic	Snipefish	*Macroramphosus scolopax*
Yellowbanded perch	*Acanthistius cinctus*	benthopelagic	Hapuku groper	*Polyprion oxygeneios*	benthopelagic	Hapuku groper	*Polyprion oxygeneios*
Convict groper	*Hyporthodus octofasciatus*	benthopelagic	Balloonfish	*Sphoeroides pachygaster*	oceanic pelagic	Hapuku groper	*Polyprion oxygeneios*
Yellowspot demoiselle	*Chromis flavomaculata*	benthopelagic	Common roughy	*Paratrachichthys trailli*	benthopelagic	Common roughy	*Paratrachichthys trailli*
Starry toado	*Arothron firmamentum*	coastal pelagic	Lemon sole	*Pelotretis flavilatus*	true benthic	Ahuru	*Auchenoceros punctatus*
Easter Island demoiselle	*Chrysiptera rapanui*	benthopelagic	Crested blenny	*Parablennius laticlavius*	true benthic	Leatherjacket	*Meuschenia scaber*
Eyestripe surgeonfish	*Acanthurus dussumieri*	benthopelagic	Jock Stewart	*Helicolenus percoides*	true benthic	Common roughy	*Paratrachichthys trailli*
Lord Howe coralfish	*Amphichaetodon howensis*	benthopelagic	Crested blenny	*Parablennius laticlavius*	true benthic	Leatherjacket	*Meuschenia scaber*
Crimson cleanerfish	*Suezichthys aylingi*	benthopelagic	Northern bastard cod	*Pseudophycis breviuscula*	true benthic	Splendid perch	*Callanthias australis*
Sargassum fish	*Histrio*	true benthic	Piper	*Hyporhamphus ihi*	coastal pelagic	Southern bastard cod	*Pseudophycis barbata*
Northern kelpfish	*Chironemus microlepis*	true benthic	Yelloweye mullet	*Acanthoclinus littoreus*	true benthic	Black rockfish	*Acanthoclinus littoreus*
Vanderbilts chromis	*Chromis vanderbilti*	benthopelagic	Northern bastard cod	*Pseudophycis breviuscula*	true benthic	Splendid perch	*Callanthias australis*
Scrawled leatherjacket	*Aluterus scriptus*	benthopelagic	Yellowbelly flounder	*Rhombosolea leporina*	true benthic	Common roughy	*Paratrachichthys trailli*
Bluestriped fangblenny	*Plagiotremus rhinorhynchos*	benthopelagic	Northern bastard cod	*Pseudophycis breviuscula*	true benthic	Splendid perch	*Callanthias australis*
Redbanded grubfish	*Parapercis binivirgata*	true benthic	Yellow cod	*Parapercis gilliesii*	true benthic	Yellow cod	*Parapercis gilliesii*
Confused goby	*Acentrogobius pflaumii*	true benthic	Yellow cod	*Parapercis gilliesii*	true benthic	Yellow cod	*Parapercis gilliesii*
Cowfish	*Lactoria diaphana*	benthopelagic	Yellowbelly flounder	*Rhombosolea leporina*	true benthic	Common roughy	*Paratrachichthys trailli*
Kermadec scorpionfish	*Maxillicosta raoulensis*	true benthic	Crested blenny	*Parablennius laticlavius*	true benthic	Crested blenny	*Parablennius laticlavius*
Slender remora	*Phtheirichthys lineatus*	oceanic pelagic	Rock cod	*Lotella rhacina*	true benthic	Chilean mackerel	*Trachurus murphyi*
Oblong sunfish	*Ranzania laevis*	oceanic pelagic	Sunfish	*Mola alexandrini*	oceanic pelagic	Sunfish	*Mola alexandrini*
Sailfish	*Istiophorus platypterus*	oceanic pelagic	Blue marlin	*Makaira nigricans*	oceanic pelagic	Blue marlin	*Makaira nigricans*
Slender boxfish	*Polyplacapros tyleri*	benthopelagic	Yellow cod	*Parapercis gilliesii*	true benthic	Common roughy	*Paratrachichthys trailli*

Whitefingered angler	*Antennatus nummifer*	true benthic	Snipefish	*Macroramphosus scolopax*	benthopelagic	Red rock cod	*Scorpaena cardinalis*
Bridled goby	*Arenigobius bifrenatus*	true benthic	Yellow cod	*Parapercis gilliesii*	true benthic	Yellow cod	*Parapercis gilliesii*
Toadstool groper	*Trachypoma macracanthus*	true benthic	Red scorpionfish	*Scorpaena papillosa*	true benthic	Red scorpionfish	*Scorpaena papillosa*
Queensland groper	*Epinephelus lanceolatus*	benthopelagic	Blue marlin	*Makaira nigricans*	oceanic pelagic	Trumpeter	*Latris lineata*
Commersons frogfish	*Antennarius commerson*	true benthic	Trumpeter	*Latris lineata*	benthopelagic	New Zealand turbot	*Colistium nudipinnis*
Red cornetfish	*Fistularia petimba*	benthopelagic	Blue marlin	*Makaira nigricans*	oceanic pelagic	Ruffe	*Tubbia tasmanica*

Chapter Four: General discussion

4.1 Overview

Climate change is causing significant changes to the physical, chemical and biological properties in the world's oceans, impacting marine life and ecosystem function. Species redistribution under climate change has been well documented with many marine taxa extending their ranges to track favourable environmental conditions, generally in a poleward direction (Burrows et al., 2014; Poloczanska et al., 2013). Species redistributions are altering species assemblages, biodiversity and ecosystem functioning, which ultimately impacts communities and industries reliant on them (e.g., cultural practices, recreational and commercial fishing, tourism; Pecl et al., 2017; Sweetman et al., 2017). Our knowledge of climate mediated range-shifts in Aotearoa New Zealand is limited (but refer to Middleton et al., 2021 and Middleton et al., *in press*), however the frequency and abundance of tropical and subtropical fishes in NZ's waters have increased in recent years, indicating that climate-mediated changes in NZ's fish biodiversity may already be taking place. Through monitoring range-extending species we can inform which of these species are most likely to impact the resident community and ecosystem functioning should they establish populations in NZ.

This thesis contributes to the understating of rare, tropical and subtropical fishes in Aotearoa New Zealand through monitoring occurrences, and analysing the morphology and ecological niche of rare, tropical and subtropical fishes to predict potential impacts to NZ's resident fauna and ecosystem function. I highlight the utility of citizen science in collecting occurrence and contextual data on tropical and subtropical fishes as well as outline the potential impacts of rare, tropical and subtropical fishes on NZ native and resident species. This chapter surmises the major results of this research, discusses the caveats of in these findings and outlines future directions in monitoring species redistribution under climate change.

4.2 Main findings

This thesis presents a novel approach to collecting occurrence data of tropical and subtropical fishes in NZ through citizen science, as well as predicts the potential impacts of arriving rare, tropical and subtropical taxa on NZ's native and resident fish fauna and ecosystem function, in particular, highlighting specific NZ native species at potential risk. Specifically, in *Chapter Two* I designed structured questionnaires with in-built quality controls to assess whether citizen scientists can collect reliable observations on rare, tropical and subtropical fishes without the need for photographic equipment. The results show a significantly high validation rate (83.33%) as well as a 93.38% completion rate, showing that not only can citizen scientists accurately provide occurrence data on tropical and subtropical fishes, but that completing questionnaires with a series of both multichoice and open text questions does not deter them from doing so. Moreover, my approach demonstrates the effectiveness of collecting contextual data alongside occurrence data, which is valuable in assessing the extent of individual species range-shifts and tracking biodiversity changes. In *Chapter Three* I demonstrate that by comparing the morphology, trophic niche and habitat preferences of rare, tropical and subtropical fishes to NZ native and resident species, we can gain valuable insight into potential novel species interactions, intra-specific competition and changes to ecosystem function. Specifically, this approach revealed a 74.37% overlap in morphology and ecological niche between arriving marine fishes and native marine fishes, suggesting a high potential for co-occurrence and competition should focal species establish and increase in abundance in Aotearoa New Zealand.

Monitoring the arrival and persistence of tropical and subtropical fishes using traditional scientific techniques can be an extremely labour intensive, expensive and time consuming (Delaney et al., 2007; McKinley et al., 2017; Pecl et al., 2019). Increasingly, scientists and managers are looking towards alternative methods to increase our understanding of range dynamics in the ocean (Pimm et al., 2014) and citizen-science can be a practical alternative. Citizen science has the potential to fill existing information gaps, expedite the collection of large amounts of data across large spatial and temporal scales and provide real-time data (Delaney et al., 2007; McKinley et al., 2017).

The approach used here successfully demonstrates the utility of citizen science to collect occurrence and contextual data on tropical and subtropical fishes in NZ. The addition of contextual data can be extremely valuable in monitoring species abundance and range changes over time, and has the potential to contribute to biodiversity monitoring. For example, the questionnaires designed in this project collected information on abundance, sex, life-stage and depth ranges, which can be used to predict abundance and range changes over time, track individual species establishment stages and their potential for reproduction. Similarly, by recording the behaviours observed and the resident species the individual was co-occurring with, we can increase our ecological understanding of these species, including their potential impacts on resident species and ecosystem function.

Moreover, citizens often require specialist (and often expensive) photographic equipment to contribute to citizen science projects in the marine realm. I demonstrate that through the use of structured questionnaires, we can make marine-based citizen science more inclusive, increasing the quantity of data collected without sacrificing data quality. This approach may lend particularly well in low socioeconomic and/or remote regions where access to photographic equipment and/or internet is limited. Overall, written records of species occurrences, like those presented in this thesis can provide a pragmatic and targeted approach for monitoring species whose occurrence and abundance changes are indicators of climate change impacts.

Tropical and subtropical species establishing in temperate systems have the potential to compete with resident species, increasing pressure on resident species and on ecosystem functions (Monaco et al., 2020; Munday, 2008). Globally, range extending tropical and subtropical species have been linked to the displacement of endemic and specialist taxa (Albins & Hixon, 2011; Azzurro et al., 2014; Smith et al., 2016), biotic homogenisation (Olden et al., 2016; Magurran et al., 2015) and ecosystem destruction (e.g., Bates et al., 2014; D. Booth et al., 2018; Delaney et al., 2007).

Morphology and ecological niche (including trophic and habitat niches) have been widely used to explain competition, niche partitioning and invasion success in many species and ecosystems (Azzurro et al., 2014; Clavel et al., 2010; Dominguez Almela et al., 2021; Monaco et al., 2020; Smith et al., 2016). This research provides the first attempt to analyse broadscale trophic niche, habitat preference and morphology to predict potential impacts of arriving tropical and subtropical species (‘focal species’) on native and resident species (‘NZ native species’) in Aotearoa New Zealand. By analysing the data using both univariate and multivariate analyses, this multifaceted approach confirms significant overlap in morphology, trophic group (74.37%) and habitat group (76.10%) between focal species and NZ native species. The high level of morphological similarity between focal species and NZ native species suggests a strong potential for focal species to impact the NZ native fauna through competition for diet items and habitat space, should they establish or increase in abundance in NZ waters. However, Aotearoa New Zealand’s marine realm is relatively depauperate, which may allow novel species the opportunity to occupy a new niche space, decreasing competition for resources and limiting the impacts to NZ native species.

One of the biggest concerns facing NZ’s marine realm, should tropical and subtropical species establish populations here, is the loss of biodiversity. In other regions the decline of specialist and endemic species due to novel generalist species has been well documented, with endemic species being unable to compete (e.g., Adamczuk, 2022; Albins & Hixon, 2011; Edelist et al., 2013). In NZ, approximately 22% of our fish fauna are endemic, thus putting them at a high risk for displacement if NZ tracks similarly to other temperate regions overseas. To better anticipate whether we will see similar patterns of species displacement in NZ, requires an understanding of which range-extending species pose an imminent threat based on their stage of establishment in Aotearoa New Zealand, as well as what specific NZ Native species they overlap with in habitat and geographical distribution.

This research demonstrates the potential to predict which focal species are most likely to impact specific NZ native species by identifying the focal and NZ native species that are most morphologically and ecologically (trophic and habitat niches) similar and combining this with their known NZ geographical distributions (Middleton et al., in press). Unfortunately, the geographical ranges of many of the focal species are still unknown therefore, inferences could only be made to several of the species in this dataset. Overall, the method and approach used in this research informs the morphological and ecological niche overlap for Focal and NZ native species and provides the means to predict potential impacts of increased establishment under climate change.

4.3 Caveats

In *Chapter Two*, I successfully created four data driven questionnaires, established and managed a mini citizen science project and analysed the data collected within these. However, the methods and approaches used in this research had some caveats. First, while we were able to collect 85 validated records for ten different tropical and subtropical fishes, it is likely that the inclusion of more observations could influence the patterns and results presented here. This citizen science project was launched during the COVID19 pandemic, which subsequently impacted the amount of data we could collect in the space of a masters thesis. Second, while we found no evidence that a species conspicuousness influenced the likelihood of a participant observing it, this result may be skewed due to the location of our citizen science project. Tawhiti Rahi is a pristine marine reserve and an iconic diving/snorkelling destination, therefore citizens visiting there are likely on the lookout for beautiful and unique marine taxa. Third, with an extremely high rate of divers completing our surveys (95.1%) it is likely that many of the participants had at least some fundamental knowledge of marine taxa. While not considered here, collecting information on participants age, education or profession may augment statistical analyses. Furthermore, because the surveys were anonymous we are unable to determine if divers completed multiple surveys. Accordingly, we were unable to correct for the possibility of repeated measures on individual divers. Finally, our results revealed that taxonomic confusion was high in inconspicuous species. While not included here, taxonomic confusion should be considered in future studies by either avoiding species that might be easily misidentified or by providing more information to participants to aid in correct taxonomic identification.

In *Chapter Three*, despite collecting and analysing trophic, habitat and morphological data on 244 reef fishes across 79 different taxonomic families, several caveats were identified. First, over 50 NZ native species were not included in this dataset due to the limited data available. It is likely that the morphology of these missing species could influence the patterns presented here. Second, the absolute linear and proportions measurements were generated using the maximum size of each species, opposed to the mean or median size, as these were often unavailable. Using the mean or median size should be considered for future analyses to provide results on the average size. Third, while ten morphological measures were analysed here, other measures should be considered. For example a measure of gape size would complement trophic group analyses and aid in inferences on dietary requirements. Finally, the 10 measurements and maximum sizes collected for each of the 105 NZ native species were gathered using literature and taxonomic images from Aotearoa New Zealand, thus providing regionally relevant data for the NZ native species. We were unable to do that for the focal species, therefore morphological variation that might naturally occur across the focal species ranges has not been considered here.

4.4 Future directions

The frequency and intensity of novel species arrivals will continue to increase as climate change drives species redistributions in the marine environment. Detecting range-extending tropical and subtropical fishes during the early stages of establishment will be the best defence to mitigating any negative impacts they may cause. The research and subsequent results within this thesis emphasise the need for continued monitoring of marine taxa, to provide a proactive response to biodiversity changes in Aotearoa New Zealand. There are several clear ways forward from here.

First, continued and increased effort should be placed on monitoring tropical and subtropical species in NZ's waters. While this thesis contributes to occurrences and impacts of tropical and subtropical species in NZ, our knowledge of range dynamics, establishment stage and potential impacts of many of these species is far from complete. To better anticipate whether we will see similar patterns of species displacement in NZ to those documented overseas, continued monitoring must be prioritised. Citizen science methods such as those used in *Chapter Two*, by WhatsThatFishNZ (Middleton et al., *in press*) or through alternative methods such as environmental DNA, will provide the information needed to help scientists and environmental managers proactively mitigate the impacts of climate induced biodiversity shifts. Second, while many of the results from *Chapter One* and *Chapter Two* cross inform each other, of particular interest is the NZ resident and native species identified as co-occurring (*Chapter Two*) and morphologically/ecologically similar (*Chapter three*) to the tropical and subtropical species I assessed. These results highlight the need to include NZ resident and native species in monitoring initiatives. By extending monitoring programmes to include high risk NZ native and resident species we can mitigate any negative impacts before it's too late. Additionally, poleward extension of several commercially and recreationally important temperate species (such as *Seriola lalandi* and *Chrysophrys auratus*) and has been documented both in NZ and in other temperate regions. Including these temperate species into monitoring efforts, will be informative for climate change monitoring. Finally, the methods presented here are effective for short-term projects (such as a thesis) but online platforms with automated pipelines will be better suited for long-term monitoring and should be considered in the future.

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