Morphological and diet variation in *Chrysophrys auratus* populations

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Abstract

Unrecognised intraspecific variation within a fishery can have sustainability consequences. *Chrysophrys auratus* (snapper) are an important species for many New Zealand stakeholders, but there is evidence that management units don't line up with biological populations around the country, which could result in a loss of intraspecific biodiversity and localised depletions. This thesis aimed to better understand the biological population structure and intraspecific biodiversity of *C. auratus* to help to conserve the species in the face of fishing pressure and better understand how they may respond to environmental changes. To do this, geometric morphometric techniques were used on photographs of 329 New Zealand and 79 Australian *C. auratus*. Otolith morphology measurements were also used for population delineation. Jaw morphology and diet analysis of the stomach contents were then used to understand the functional feeding morphology of *C. auratus.* Significant differences between populations in external body morphology were observed, with differences most pronounced in the head curvature, body depth, eye size and caudal peduncle width. Otolith morphology was a less successful technique for population delineation than external morphology in *C. auratus,* but there were still significant differences in otolith shape between populations. *C. auratus* consumed a diverse diet spanning many functional groups, but crustaceans, polychaetes, echinoderms, molluscs and teleosts made up most of the diet. Proportions of different prey varied by region, with a more pelagic diet recorded in the Hauraki Gulf and Bay of Plenty populations and a harder, more crustacean dominant diet in East Northland and on the East Coast of the North Island around Gisborne and Hawkes Bay. The hardness of the diet was weakly linked to jaw and head morphology, especially the jaw and tooth width variables, which determine the crushing strength of a fish's jaw. The generalist nature of *C. auratus* meant that any jaw adaptations still enabled the consumption of a variety of prey. The polymorphism and functional morphology identified in *C. auratus* has implications for fisheries compliance, ecological effects of population recovery and how the species will respond to environmental change. The ecomorphological insight should be utilised with appropriate fisheries management units to preserve their valuable, intraspecific variation.

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Chapter One. General Introduction

1.1 The importance of intraspecific variation

Biodiversity loss at the species level is one of science's biggest concerns, but far less discussed is the impact of diversity loss within species (Des Roches et al., 2018). Anthropogenic pressure such as climate change and overfishing can cause small-scale, localised depletions of populations and threaten intraspecific variety. Intraspecific variation is defined as the difference between individuals of the same species caused by a variety of intrinsic (e.g. genetics) and extrinsic (e.g. environmental) factors (Harding et al., 2019). Variation can be expressed both in the phenotype and genotype and be heritable or non-heritable (Harding et al., 2019).

There are many examples of intraspecific variation being as extreme as interspecific variation, meaning ecosystem function is not only dependent on species biodiversity but within species biodiversity as well (Albert et al., 2010; Palkovacs & Post., 2009). In a meta-analysis comparing intraspecific and species variation effects on the ecosystem, indirect effects on the ecosystem were equal to, or more strongly affected by intraspecific effects (Des Roches et al., 2018). The indirect interactions of predators on primary producers through trophic cascades can have wider ecosystem implications (Des Roches et al., 2018). Overall, intraspecific and species effects have roughly similar impacts on most ecological responses, and this may be underestimated due to the usually implicit reporting of intraspecific effects (Des Roches et al., 2018).

When intraspecific variation that is expressed phenotypically is repeatedly inherited, it can lead to separate morphs (West-Eberhard, 2008). Morphs are groups of individuals with similar body shape or form. The term morph is used because morphological information alone cannot distinguish between groups within a population, separate populations or separate species; that is determined by geographic distribution and the degree of sexual isolation (West-Eberhard, 2008). Multiple morphs that aren't sexually isolated and share a habitat, are known as a polymorphic population. Human blood types are an example of polymorphism. If there is significant sexual isolation, and/or geographic separation, the morphs are known as separate populations (West-Eberhard, 2008). Sexual isolation in a polymorphic population with advantageous niche differentiation can sympatrically speciate to form entirely new species (Smith, 1962).

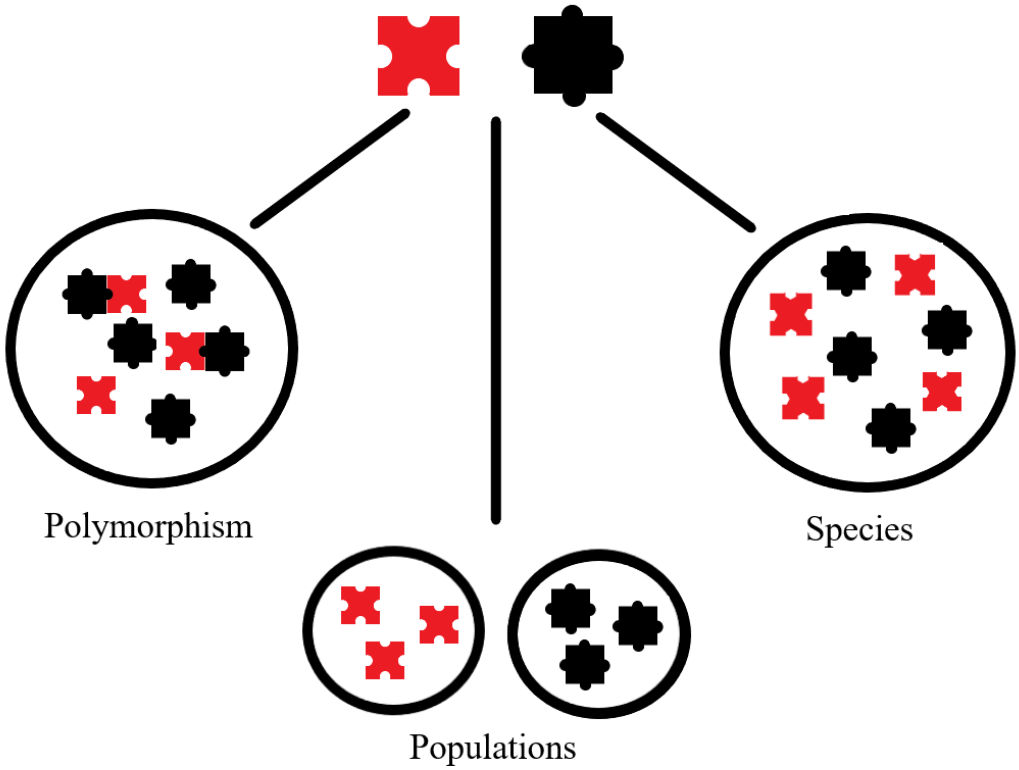

Figure 1.1 Red and black morphs either sexually mix in a polymorphic population, are reproductively and geographically isolated as separate populations or are incapable of interbreeding as separate species

1.2 The impact of repeated inherited intraspecific variation

Epigenetic responses are alterations in gene expression due to non-genetic influences e.g. habitat. Heritable epigenetic responses are selectable, intraspecific, phenotypic variation, whereas non-heritable responses are known as phenotypic plasticity (Thorson et al., 2017). Phenotypically plastic individuals are able to change their morphology, physiological state, behaviour or any combination of these in response to a change in environment without a change in genotype (West-Eberhard, 2008). Thus, you could put two genetically identical individuals in different environmental conditions and observe varied phenotypes. Although phenotypic plasticity is not genetically driven, some individuals may have genotypes that result in a more advantageous response (West-Eberhard, 2008).

In many groups of animals, similar morphological features can be used as an indicator of similar ecologies. Examples include bird beaks that fill identical feeding niches, lizard body plans adapted to certain habitats and independent evolution of wings as a transport mechanism (McGhee, 2011; Ord & Klomp, 2014). Understanding and studying the links between form and function, is known as functional morphology (Wainwright, 1994).

Pairs of African cichlid species from sister lakes Malawi and Tanganyika not only demonstrate identical functional morphologies, but ecomorphological equivalence. Where functional morphology looks solely at the relationship between form and function, ecomorphology studies the effect of the environment on morphological specialisations (Wainwright, 1991). Rapid evolution in each of the lakes separated one common ancestor into many cichlid species. Niche partitioning occurred due to natural selection and competition driving different patterns of resource use. Now distantly related, ecomorphological equivalence can be observed in cichlids occupying identical niches in each sister lake (Kocher et al., 1993; Kassam et al., 2003). For example, two rock dwelling cichlids, *Petrochromis fasciolatus* and *Petrotilapia spp.* are both epilithic algal grazers with remarkably similar gapes, feeding ecology and body shape (Kassam et al., 2003). Other parallel similarities observed in cichlids include jaw morphology, fleshy lips, nuchal hump, horizontal striping and the overall body shape- depth, width, length and caudal peduncle (Kocher et al., 1993; Elmer et al., 2010).

1.3 Variation in feeding morphology

Niche partitioning can also lead to binary morphs, such as the alternate morphs of the threespine stickleback, *Gasterosteus spp.* Endemic to coastal, postglacial lakes *Gasterosteus spp.* exhibits clear niche partitioning with distinct benthic and limnetic morphs (McPhail, 1984). The benthic morph has a deeper, larger body with a wider mouth and a few short gill rakers, suited for littoral feeding on invertebrates (Day, Pritchard & Schluter., 1994). The limnetic morph contrasts this, with a long, slender body, shorter, upturned mouth and numerous, long gill rakers specialised for zooplankton feeding in the water-column (Day et al., 1994). In some small lakes, an intermediate morph exists as niche partitioning doesn't occur, but if this morph was transferred to a lake with the binary morphs, it would be selected against and likely outcompeted (Schluter et al., 2010). This is because the intermediate morph has a poorer foraging efficiency than either the benthic or limnetic form in their respective niches, but in a small lake with limited resources, can feed on both zooplankton and invertebrates successfully (Schluter, 1993). To determine if the stickleback traits were a plastic response to their environment, Day et al. (1994) experimentally switched the diet of the benthic morph and the limnetic morph. A corresponding shift in stickleback morphology was observed, becoming more phenotypically aligned with the diet they were eating, proving a degree of phenotypic plasticity (Day et al., 1994).

Phenotypic diversity can also be affected by food abundance according to the Optimal Foraging Theory (Prado et al., 2016). The Optimal Foraging Theory predicts that in certain circumstances, foraging species with an abundance of resources may fit into a specific, selective feeding niche, while when resources become scarce, are forced to occupy a wider niche (MacArthur & Pianka, 1966). Gray snapper, *Lutjanus griseus* and schoolmaster snapper *L. apodus* are two coastal species that feed in accordance with the optimal foraging theory, at the subpopulation level. Within populations, groups of fish make repeated movements to certain areas to forage and $\delta^{13}C$ values indicate feeding on different prey types (Hammerschlag-Peyer & Layman, 2010). 'Home' sites experienced higher competition and depleted $\delta^{13}C$ values but less risk of predation, while the further afield foraging sites had better resource availability, and enriched $\delta^{13}C$ values but higher risk of predation (Hammerschlag-Peyer & Layman, 2010). The behavioural decisions involved in this choice are aligned with the 'shyness or boldness' dichotomy, observed in a variety of fish species (Gosling & John, 1999). Shyer fish are more likely to stay in close proximity to home sites, while bolder fish venture to other habitats and areas. In this case, the two snapper species had subpopulations which differed phenotypically in behaviour, but differences in morphology are also possible.

Pumpkinseed sunfish *Lepomis gibbosus* demonstrate polymorphism of feeding specialisations in response to repeated differences in resource use, aligned with optimal foraging theory. Gastropod molluscs make up the primary diet component of pumpkinseed sunfish, crushing the shells with their pharyngeal jaws (Wainwright, 1991). In areas with prosperous snail abundance, the muscles associated with pharyngeal jaw movement in *L. gibbosus* were significantly larger than in areas with low snail abundance (Wainwright, 1991). All three pharyngeal bones in snail dense areas were enlarged and shaped to maximise crushing forces, which caused worn down, short teeth (Wainwright, 1991).

Understanding the degree of intraspecific variation in a species is important because it affects an individual's ability to respond to environmental and anthropogenic stressors. Geometric morphometrics (GM) is a technique that can be used to understand morphological variation. GM analyses the position of features in relation to one another using landmarks, going far beyond the information linear calliper measurements provide. When used in conjunction with other information, GM can identify the degree of functional morphology or ecomorphology of a group, significantly advancing the understanding of the ecology of a population or species.

1.4 Intraspecific variation in a fisheries context

Understanding intraspecific variation becomes crucial when stressors are applied to a population, such as fishery extractions pressure. Fished species are typically separated into distinct units for management purposes, known as stocks (Burkenroad, 1953). Despite being essential for the management of an exploited resource, identifying appropriate stock boundaries is difficult as biology usually fails to abide by lines on a map (Berger et al., 2021). A population or biological stock is defined as a group of interbreeding individuals cohabitating in a given area. The definition of a stock, conceived by Russell (1931), is a reproductively isolated population, with young fish entirely spawned from adults within the population. It's usually assumed that a stock has demographic independence with homogenous recruitment, mortality, growth and age composition (Cadrin, 2020). The 'perfect' stock is well-mixed, randomly mated, with homogenous life history and spatial distribution (Hilborn et al., 2003). However, stocks can consist of either multiple populations, a metapopulation or a portion of a population (Cadrin et al., 2014). Stocks usually have limited connectivity with neighbouring populations outside the management boundaries and may even have recruitment subsidies, but it is unusual for a stock assessment model to take this into consideration.

1.5 Implications of not understanding intraspecific variation in a fishery

If there is unrecognised spatial population structure with significant intraspecific variation within a stock, unintentional overfishing can lead to localised depletion or even complete stock collapse (Cadrin, 2020). One of the most famous examples of stock depletion is the Atlantic cod, *Gadus morhua* in the late 1990s. Although multiple factors contributed to its collapse, stock structure played a part (Kerr et al., 2014). Both the northern stock around Canada and the US stock off New England were more biologically complex than their 'single stock' management unit accounted for. The US and Canadian Atlantic cod stocks were each made up of multiple separate populations, with different growth rates, dispersal patterns, genetics and morphologies (Morgan & Brattey, 2005; Kerr et al., 2014). While increasing Catch Per Unit Effort (CPUE) suggested the stock was doing well, this was driven by aggregations in certain areas, obscuring the severe declines of other population components (Rose & Kulka, 1999; Kerr et al., 2014). To this day, Atlantic cod populations remain well below target levels emphasising the importance of accurate stock definition in effective fisheries management (Northeast Fisheries Science Center, 2020).

The presence of discrete morphological groups does not always necessitate stock differentiation for management purposes. For example, if each morph doesn't interact with fisheries differently, and expresses identical productivity and environmental responses, there is no need for stock division. Morphs can indicate separate populations with incomplete reproductive mixing, but functionality and separation shouldn't be assumed.

The importance of understanding morphs and having corresponding fishing restrictions is especially important for net caught species. Designing fishing gear with fish morphology in mind is key to maximising selectivity. Girth and body depth determines whether a fish will be retained in a net (Stergiou & Karpouzi, 2003). The mesh size should be matched with morphological dimensions so the minimum legal size can be caught while not retaining undersize fish. If there is variation in body depth for fish of the same FL (either through polymorphism, sexual dimorphism or population variation) the fish with deeper bodies will get caught in the net at a smaller FL and potentially be undersize (Broadhurst et al., 2006).

1.6 Quantifying intraspecific variation in fish

There are three types of information that are often used to identify a stock; distribution, dispersal and geographic variation (Cadrin, 2020). Distribution information can come from seasonal and spatial fisheries data, or fisheries independent surveys (Cadrin, 2020). Dispersal information can include data on connectivity between nursery and spawning areas, individual migrations and spawning dynamics (Cadrin, 2020). Geographic variation represents a wide variety of intraspecific variation including morphology, meristics, life history characteristics, genetics, size and age composition (Cadrin, 2020). Phenotypic characters, even without genetic backing, are a good measure as they indicate prolonged separation (Leslie & Grant, 1990). Genetics techniques aren't always useful in differentiating fish stocks as their sensitivity means it only takes a few individuals to interbreed to be classed as one stock. Phenotypic stock delineation techniques include body morphometrics, meristics, biological tagging, otolith microchemistry and otolith shape analysis (Rogers, 2014). Productivity parameters such as year class strength, age structure and recruitment patterns are frequently compared between stocks to assess whether stock delineation is accurate (Marsh et al., 2021).

Technological advancements have made some of these stock identification techniques very time and cost-effective, particularly GM. GM is a non-invasive technique, only requiring a photograph of the fish that software uses to analyse external morphology. There are numerous examples of GM being used to identify stocks, such as the separation of three

stocks of *Harpadon nehereus* in India (Rawat, 2017). It's also possible to use GM on microfeatures like scales. Ibáñez (2015) correctly identified which population a fish was from using just the scales with 83% accuracy or 100% accuracy if adjacent geographical areas were included.

There is no one correct method to decide on stock boundaries, but spatial heterogeneity should be considered for heavily exploited stocks (Cadrin et al., 2020). If complex spatial stock structure isn't considered, it can lead to overexploitation of the more vulnerable population components (Ying et al., 2011). Localised depletions contribute to damaging biodiversity loss within species and prevents species' ability to adapt to stressors such as climate change (Bestion et al., 2015). If stocks are low information, they should be managed precautionarily to account for unknown intraspecific variation.

1.7 New Zealand Fisheries management

Following concerns of depleting fish stocks, Aotearoa New Zealand introduced the Quota Management System (QMS) in 1986 (Clark et al., 1988). The QMS is a single-species management framework that sets annual total allowable catches (TAC) for individual species, divided between stocks, called Quota Management Areas (QMA). Like many other countries, stock boundaries were primarily designed for simplicity rather than accurately reflecting population boundaries (McCormack, 2017). Some stocks have as many as three known populations (Fisheries NZ, 2020).

In New Zealand, the TAC is split between recreational, commercial and customary sectors. All the total allowable catch allocated to commercial stakeholders (TACC) is owned proportionally, as Individually Transferrable Quota (ITQ) which grants ITQ owners or leasers the right to fish (Clark et al., 1988). The Ministry of Primary Industries assesses fish stocks annually and adjusts TAC when necessary.

New Zealand adopted the QMS more enthusiastically than anywhere else in the world and gained a lot of attention and praise (Bess, 2005). Since its introduction, various challenges have come to light, such as discards, relationships with recreational fishers and consequences for Maori (Hersoug, 2018). Failure to address these and other issues means the QMS isn't as prestigious as the more comprehensive ecosystem-based management other countries are adopting (Hersoug, 2018).

1.8. The Australasian snapper, *Chrysophrys auratus*

1.8.1 Life History and Ecology

Snapper/ tāmure, *Chrysophrys auratus* are the most heavily recreationally fished species in New Zealand (Fisheries NZ, 2020). They belong to the family Sparidae, which includes many species prevalent in fisheries and aquaculture (Antonucci et al., 2009). Within this family, the trophic position of a species can be classified based on functional morphology adapted for a feeding niche (Antonucci et al., 2009). Ecomorphologically, *C. auratus* have been labelled as a low-predator because of their dentition, reddish colouration and scales on the head in the interorbital region (Antonucci et al., 2009).

C. auratus are one of the most abundant inshore fish in New Zealand but are also found in Australia, Norfolk and Lord Howe Islands (Parsons et al., 2014). A demersal fish, *C. auratus* occupy a wide variety of habitats to 200 m depth but are usually found between 15-60 m (Parsons et al., 2014). A relatively long-lived species, *C. auratus* can live up to 60 years, growing to 1000 mm fork length (FL) and 17 kg (Parsons et al., 2014). As protogynous hermaphrodites, all *C. auratus* begin as immature females and sexually develop into males and females. *C. auratus* are serial, broadcast spawners, initiated with surface water temperatures between 14.8 °C and 16 °C, peaking typically in early summer (Scott & Pankhurst, 1992). As seen in most fish, the larger the individual, the more fecund it is. Crossland (1977) found that in the Hauraki Gulf, 250mm FL *C. auratus* produced between 80,000-300,000 eggs in a season, while a *C. auratus* 500mm FL produced 4.5-6 million eggs in a season.

C. auratus eggs are approximately 1mm in diameter and successful eggs hatch after 28-48 hours (Cassie, 1956). Around 83% of eggs die before hatching and a further 98% in the initial 8 days after hatching, primarily caused by predation (Zeldis et al., 2005). Four to six days after hatching, the larvae are 3-4 mm long and begin selective, exogenous feeding on zooplankton (Parsons et al., 2014). Water temperature has a significant impact on the survival, food consumption and growth rates of *C. auratus* larvae. Temperatures between 15 and 24 °C have a positive impact on growth, with temperatures less than 20 °C causing decreases in food consumption and high mortality when spawned colder than 18 °C (Fielder et al., 2005; Parsons et al., 2014).

Most *C. auratus* larvae metamorphose into juveniles after 18-25 days, at roughly 8.6 mm (Battaglene & Talbot, 1992; Sim-Smith et al., 2012). Habitats with a biogenic structure, such

as sponge gardens, seagrass and mussel beds are the most common settling areas for *C. auratus* (Parsons et al., 2014). Sheltered, estuarine environments are preferred but not essential (Walsh et al., 2012). Within these estuarine habitats, juvenile *C. auratus* diets are made up of pelagic prey such as mysids and copepods (Parsons et al., 2014).

From 70 mm FL, *C. auratus* begin to disperse from estuarine environments to shallow, coastal environments and then onto various habitats, including muddy sediment, rocky reef, coralline turf or sandy substrates (Compton et al., 2012). Dietary breadth expands to include small, brachyuran crabs, Caridea (shrimp), molluscs, polychaetes and small teleosts (Usmar, 2012).

C. auratus reach sexual maturity between 200-300 mm FL or 2 to 5+ years, depending on the growth rate of the area (Walsh et al., 2012; Walsh et al., 2011). Growth on the West Coast of the North Island, for example, can be twice that of the East Coast of the North Island (Walsh et al., 2011). Differences in growth rates in *C. auratus* are linked to genetics, environmental and density-dependent factors, as has been observed throughout nature (Irving, 2021; Bernal-Ramírez et al., 2003; Lorenzen & Enberg 2002). The Hauraki Gulf population has shown a deceleration in growth as population biomass has increased and is now believed to be the slowest growing population while the southern and western populations are the fastest (Walsh et al., 2019).

As generalists, their dietary breadth increases ontogenetically but remains dominated by crustaceans. Strong jaw development and dentition allow the inclusion of pelagic fishes and larger, harder-bodied prey such as paguroidea, *Haliotis virginea* and *Jasus edwardsii* (Colman, 1972; Usmar, 2012). Polychaetes also form an important part of adult *C. auratus* (Parsons et al., 2014). *Evechinus chloroticus* are predated on by large *C. auratus*, who have a role in regulating *E. chloroticus* population sizes (Shears et al., 2008). If *C. auratus* populations are significantly reduced, it can result in an increase in *E. chloroticus* biomass, which overgraze macroalgal beds creating urchin barrens (Shears et al., 2008). All the present knowledge on *C. auratus* diet comes from specific areas in the Northern North Island, primarily in the Hauraki Gulf (Godfriaux, 1969; Colman, 1972; Russell, 1983; Usmar, 2012; Drummond, 2020). To understand intraspecific variation in *C. auratus* diets and their interactions with various ecosystems around the country, further research is needed. Dietary research paired with morphological data would provide excellent insight into *C. auratus* ecomorphology across various regions and populations.

1.8.2 Intraspecific variation in *C. auratus*

C. auratus movement can be highly variable, with habitat and spawning migrations contributing to this variation. In the Hauraki Gulf, tagging studies have demonstrated that shallow, rocky reef fish tend to be highly philopatric, moving as little as a few hundred meters, while *C. auratus* associated with deeper, soft-sediment habitats moved tens of kilometers on average (Parsons et al., 2011). One fish travelled over 400km from the tagging location (Parsons et al., 2011). There is a long-held anecdotal belief that these differences in migration are the result of a distinct spawning group, that only enters the gulf seasonally (Cassie, 1956). These fish supposedly have sharper teeth and different colouration than the resident fish (Cassie, 1956). Parsons et al. (2015) provided scientific evidence of polymorphism within the *C. auratus* species as the migrating fish displayed both ecomorphological and meristic differences. This distinct morph was labelled the "spawning stratum" and had morphological features, such as an elongated head length, consistent with a more pelagic life history (Parsons et al., 2015; Antonucci et al., 2009).

C. auratus in West Australia exhibit similar patterns of polymorphism, with different populations displaying unique morphologies (Moran et al., 1998). Although they are the same species, Australian *C. auratus* look quite different to those found in New Zealand. Australian *C. auratus* have large, fleshy lips, prominent humps on the head, and pronounced sexual dimorphism in areas (Moran et al., 1998). The state of South Australia has numerous phenotypically distinct populations with unique head shapes (Rogers, 2014). Within a much smaller area in the Shark Bay region of Western Australia, genetic, tagging and morphometric studies have found three distinct populations of *C. auratus* (Moran et al., 1998). These findings successfully resulted in a respective stock differentiation to prevent population depletion (Moran et al., 1998). Despite it being unusual for marine teleosts to have distinct populations within a small geographical area, *C. auratus* exhibit fine-scale population structure (Moran et al., 1998; Parsons et al., 2015).

There is anecdotal evidence that other areas around New Zealand, beyond the Hauraki Gulf, also have discrete *C. auratus* morphologies. For example, it has been said that fish from the Hawkes Bay have deeper body profiles compared to those in the Bay of Plenty (E. Jones, personal communication, May 2021). Reduced trawl gear selectivity of *C. auratus* has been observed in the Hawkes Bay region and differing morphologies in this area could explain the difference in fishing selectivity (E. Jones, personal communication, May 2021). Until now,

there has been no quantitative investigation of morphological differences in New Zealand *C. auratus* outside of the Hauraki Gulf, and no study into whether these differences reflect altered diet and trophic interactions. Investigating morphological differences of *C. auratus* in various New Zealand regions to identify any separate phenotypic populations will inform and assist sustainable management of *C. auratus*.

1.8.3 *C. auratus* fisheries management

C. auratus quota is split over six QMAs, with the majority of this quota associated with four of these QMAs (Table 1.1). The most fished QMA is SNA 1, with nearly five times more commercial allowance than any other QMA (Table 1.1). The main commercial fishing methods are bottom trawling, bottom long-line, set net and Danish seine, the proportions of which vary by QMA. There is also substantial recreational rod and line fishing of *C. auratus* (Fisheries NZ, 2020).

Table 1.1 Total allowable catch and recreational allowance of *C. auratus* from each stock as at 2022. Data sourced from Fisheries NZ, 2020

QMA	SNA 1	SNA 2	SNA 3	SNA 7	SNA 8	SNA 10
TAC	8050 t	450 t	32 t	645 t	1785 t	10 t
Recreational allowance	3050 t	90 t	-	250 t	312 t	-

SNA 1, the most commercially and recreationally important QMA spans the length of the Northeast coast of the North Island and is spread over three known *C. auratus* populations, one around East Northland (ENLD), one in the Hauraki Gulf (HAGU) and one in the Bay of Plenty (BPLE) (Figure 1.3; Fisheries NZ, 2020). There is limited mixing between the three populations, with the most interaction between HAGU and BPLE (Fisheries NZ, 2020). The Hauraki Gulf population itself is polymorphic, with evidence of at least two subpopulations, the shallow reef and spawning groups (Parsons et al., 2015). In SNA 2 there are thought to be two biological populations, with uncertainty over whether the northern population is connected to the BPLE population or not (Fisheries NZ, 2020). Lastly, SNA 7 is also thought to have two biological populations, one in the Marlborough Sounds and one in Tasman/Golden Bay (Fisheries NZ, 2020).

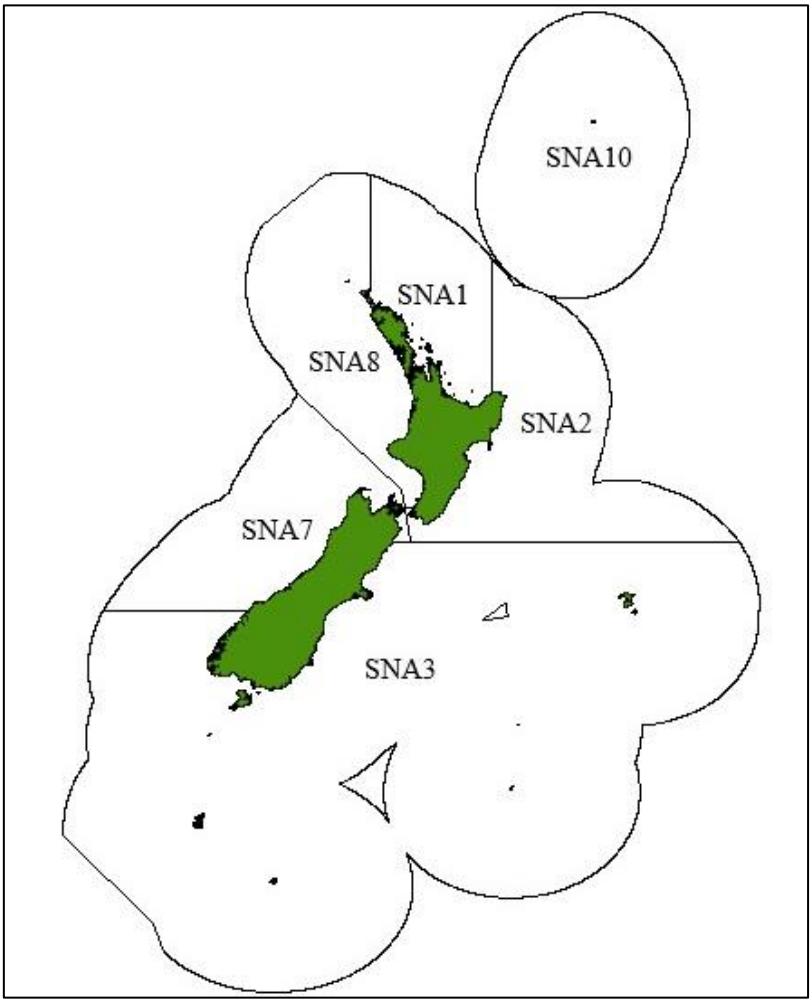

Figure 1.2 Overview of New Zealand *C. auratus* QMA boundaries

While the status of the multiple populations within SNA 1 and SNA 2 are assessed individually, decisions affecting the TAC are made at the whole QMA scale. As such, if one of the component stocks within a QMA has a poor status that suggests management intervention is required, the resulting management decision would have implications for other stocks within that QMA, even if their status was in a better state.

1.9 Study aims

This thesis aims to advance knowledge of *C. auratus* ecomorphology and fine-scale population structure to help the preservation of intraspecific biodiversity in the face of fishing pressure.

Despite *C. auratus* being a crucial ecological, economic and cultural species, there is still much to learn. There is local and international evidence of fine-scale population structure in *C. auratus*, which suggests that preserving biodiversity within species will be essential for wider ecosystem health. This research will evaluate regional *C. auratus* morphology as an indicator of separate populations. Chapter two will scientifically quantify body and otolith polymorphism within *C. auratus* and use GM to understand the morphological differences between the hypothesised biological populations. Understanding biological stock structure will help fisheries managers better assess and manage *C. auratus* as a prominently fished species. Although the focus is on New Zealand *C. auratus* populations, this study will also contrast New Zealand *C. auratus* morphology with some Australian *C. auratus* stocks.

There have been multiple studies of *C. auratus* diet in specific areas, but to date there is no documentation or comparison of nationwide *C. auratus* diets (Godfriaux, 1969; Colman, 1972; Russell, 1983; Usmar, 2012; Drummond, 2020). Additionally, there has been very little research on *C. auratus* ecomorphology. *C. auratus* are typically characterised as a generalist species, but it's unknown if there is niche partitioning contributing to unique functional morphologies at the individual level. Chapter three will explore *C. auratus* functional morphology, comparing prey choice and corresponding morphology between and within stocks which will provide insight into *C. auratus* ecomorphology.

Chapter Two. Intraspecific variation in *C. auratus* morphology

2.1 Introduction

The biodiversity crisis has highlighted the ecosystem services provided by biodiversity and the consequences of extinctions on humans and ecosystems (Worm et al., 2006). Not only the loss of species, but the loss of biodiversity within species, known as "intraspecific variation", is cause for serious concern. Due to anthropogenic interruptions, intraspecific variation loss is more accelerated than species loss (Des Roches et al., 2021). Humans can introduce artificial selection pressures on species, directly through fishing or indirectly through climate change, habitat modification, invasive species introduction and pollution that prevents the reproductive success of diverse individuals (Singh, 2002). Documenting, monitoring, maintaining and restoring intraspecific variation is vital for ecosystem resilience and preventing biodiversity loss (Des Roches et al., 2021). This need is heightened for species whose diversity is directly threatened by fishing.

Intraspecific diversity can be broadly separated into genetic and phenotypic diversity. In a review of studies that mentioned the ecosystem services provided by intraspecific variation, it was primarily genetic variation that was described or quantified (Des Roches et al., 2021). The value of phenotypic studies need not be forgotten, as valuable phenotypic diversity is not always apparent at the genotypic level (Oostra et al., 2018). Phenotypic diversity can come in various forms, including colouration, external morphology and internal morphology and may or may not be functionally important.

An individual's success is determined by the junction between its environment and its phenotype (Koehl, 1996). Measuring external phenotypes and how these change across environments can be done easily and cost-effectively (Des Roches et al., 2018). The trophic position of an individual or population can be affected by this interaction between habitat and morphology, to the point where external similarity can be used as a proxy for habitat use for many fish species (Fugi, Agostinho & Hahn, 2001). The alternate morphs of three-spined stickleback is a common example, as it clearly demonstrates many of these ecomorphological features (Mckinnon & Rundle, 2002). The limnetic form of the three-spined stickleback has larger eyes and more and longer gill rakers (McPhail, 1983; McKinnon & Rundle, 2002). Gill rakers project from the branchial gill arch and serve to protect the gills from large debris and trap food (Hyatt, 1979). The number of inner, and outer gill rakers is widely used in meristics

and stock identification (Chase, 2014). As with different classes of sieves, the number and density of gill-rakers can relate to prey choice, with less gill rakers typically associated with more benthic and/or larger prey and more gill rakers for a pelagic, planktivorous diet (Hyatt, 1979). Eye size can be a reflection of water chemistry and clarity and also impacts food acquisition and predator evasion (Shuai et al., 2018).

Other functional phenotypic traits that can vary intraspecifically in fish include the mouth, tail and overall body shape. The size of the mouth gape determines the maximum sized prey a fish can eat, and the size of the gape can be predicted by mouth length (Wainwright, 1995). The position of the mouth also provides insight into the ecomorphology of a fish. A superior mouth has an upturned jaw and is typically found on surface feeding fishes, an inferior mouth is downturned and best adapted for bottom-dwelling species, and terminal mouths, the most common orientation, are usually found on species that feed in the mid-water but can eat either pelagically or benthically (Keppeler et al., 2020). Variation in the body profile and tail region can affect the drag a fish is exposed to in the water as well as its manoeuvrability (Blake, 2004). The most streamlined fish have tapered bodies with a narrow, shallow caudal peduncle region (Blake, 2004). Antonucci et al. (2009) conducted a meta-analysis within the Sparidae family of fish, quantitatively describing ecomorphological interactions of morphology, habitat use and trophic level. For this group, stouter body profiles, smaller mouths and thicker caudal peduncles were associated with fish in lower trophic positions, while top-level predators had larger head regions, smaller eyes and longer, more slender bodies (Antonucci et al., 2009). The narrower caudal peduncle for the top predators allows faster burst starts, powerful turns, and propulsion necessary for prey gathering at the highest trophic levels (Antonucci et al., 2009).

Parsons et al. (2015) found evidence of groups with distinct life histories within the *C. auratus* species, and their morphology reflected the hypothesised trophic positions according to Antonucci et al. (2009). A subpopulation of *C. auratus* collected from a known spawning area had narrower bodies, smaller inter-orbit width and an increased number of gill rakers. The hypothesis that this group of *C. auratus* had a higher trophic position than other *C. auratus* groups was corroborated by enriched nitrogen and depleted carbon from stable isotope analysis, consistent with a more pelagic diet (Parsons et al., 2015).

Shape comparisons are done in many types of scientific, engineering and archaeological studies (Zeldicth et al., 2012). In biology, shape analysis can explain a variety of processes

such as ontogeny, evolution, mutation or growth, and GM is a tool that can quantify these shape changes. Landmark-based GM methods put landmarks on biologically discrete, homologous loci, that is, a clearly defined structure that can be found repeatedly and reliably (Zeldicth et al., 2012). Landmarks are identified across an image, creating a series of *x y* coordinates to capture shape. For example, a good landmark is the insertion point of a fin, which is a clear, unambiguous point, whereas a bad landmark might be the middle point of a curve. However, there are often features of interest, important to the overall shape that don't have clear landmarks, such as the curvature of the head. To quantify this information without discrete, homologous loci, semilandmarks can be used, which capture information about curvature (Mitteroecker & Gunz, 2009). A set number of semilandmarks are positioned an equal distance apart along a structure, usually spanning between two discrete points. There should be enough semi-landmarks to capture all the desired information on the curve, but not so many that the data is overcomplicated (Zeldicth et al., 2012). The TPS series of software by Rohlf (2015) utilises the GM method and performs Procrustes superimposition that overlays, centres, scales and rotates the landmarks, enabling quantifiable analysis of shape changes.

Otoliths are routinely collected and used in stock assessments, utilising the alternating bands which form a permanent record of age and growth (Begg et al., 2005). Otoliths are of great utility because they contain a wealth of information about the individual, including age, growth rate, movement patterns and the environmental conditions it lived in (Nazir & Khan, 2021). Otoliths can also delineate species, stocks and populations through otolith shape or chemistry (Avigliano et al., 2017; Jemaa et al., 2015; Miyan et al., 2016). The shape of an otolith has been labelled as a more stable population delineation tool than external morphology, which can demonstrate plastic changes in response to environmental and dietary variation (Nazir & Khan, 2021). This isn't to say that a combination of exogenous and endogenous factors doesn't affect otolith shape, but rather that changes are exhibited over more extended periods. Environmental conditions such as the levels of CO_2 in the water affect the deposition of the calcium carbonate structure of the otolith, and even dietary composition can affect the proteins responsible for biomineralization (Nazir & Khan, 2021). In the Sparidae family, Kikuchi et al. (2020) identified four potential stocks of *Pagrus pagrus* using otolith shape. Otolith shape analysis has been successfully used to distinguish Australian *C. auratus* populations using Fourier analysis (Rogers, 2014) and population variation in *C. auratus* otolith microchemistry has been analysed in the Hauraki Gulf region

of New Zealand (Parsons et al., 2015), but no studies examining New Zealand *C. auratus* otolith morphology have been conducted.

Fourier analysis & GM are two highly useful techniques for quantifying differences in otolith morphology but come at a cost of time and energy. Comprehensive shape techniques require otolith extraction, photography and then digitisation of the images. Calliper measurements capture much less information on otolith shape but are a much quicker technique. For certain species, population discrimination is just as successful with four simple measurements: otolith length, width, thickness and weight (Wakefield et al., 2014). If the simplest technique can successfully answer the proposed research question, it should be utilised.

Using morphological analyses and other techniques to ensure management units align with biological population structure is key for the sustainable management of a species (Cadrin et al., 2020). Fishing pressure on a region with unrecognised population structure can result in a misconception of the species' productivity and biomass (Kerr et al., 2014). If fishing continues under the guise that harvest is occurring at sustainable levels, it can lead to localised depletion and stock collapse, which causes a significant loss in intraspecific biodiversity (Ying et al., 2011; Cadrin et al., 2020). Intraspecific biodiversity supports ecological functioning, including environmental regulation that is of critical value to humans (Des Roches et al., 2021). Despite the human and ecosystem reliance on rich intraspecific biodiversity, the International Union for the Conservation of Nature only evaluates 1.1% of species at the intraspecific level (Des Roches et al., 2021). As a result, there is a call to document and conserve intraspecific biodiversity with optimal sustainable management practices.

This chapter aims to identify any polymorphism in *C. auratus* between and within New Zealand and Australia to advance understanding of population structure. Intraspecific variation in external body morphology will be quantified, as well as differences in otolith morphology and meristics. As fish populations are impacted by fishing and other anthropogenic factors, strong knowledge of *C. auratus* population structure will help inform the management of the species in the face of these pressures, contributing to its sustainability.

2.2 Methods and materials

2.2.1 Study area and collection

2.2.1.1 New Zealand

Between March 2013 and July 2021, 329 *C. auratus* were collected from around New Zealand. Sample areas covered East Northland, West Coast of the North Island, the Hauraki Gulf, Bay of Plenty, Gisborne, Hawkes Bay and Nelson regions (Table 2.1; Figure 2.1). *C. auratus* between 300mm and 400mm FL were targeted to minimise any ontogenetic effects on morphology (Parsons et al., 2014). *C. auratus* were predominantly obtained from NIWA trawl surveys, but spatial gaps in the distribution of samples were filled by obtaining whole fish that were commercially caught. Once fish were captured, they were placed on ice and subsequently frozen at -20 °C until analysis. It was important that all fish were frozen as studies have shown water loss due to preservation can affect length, weight and morphometric measurements (Wessels et al., 2010). Samples were processed in a random order, blinding the collection area to minimise bias. Because of the random order, and temporal spread of samples, some fish were frozen longer than others, but there is no evidence to suggest the variation in freezing duration would have a significant impact on measurements (Wessels et al., 2010).

Table 2.1 Number of *C. auratus* collected from each population. Note that not all specimens were used in all analyses e.g. when otoliths were broken and unable to be measured.

Population	Number of specimens collected
SNA1ENLD	71
SNA1HAGU	68
SNA1BOP	48
SNA2N	47
SNA2S	39
SNA7	8
SNA8	48

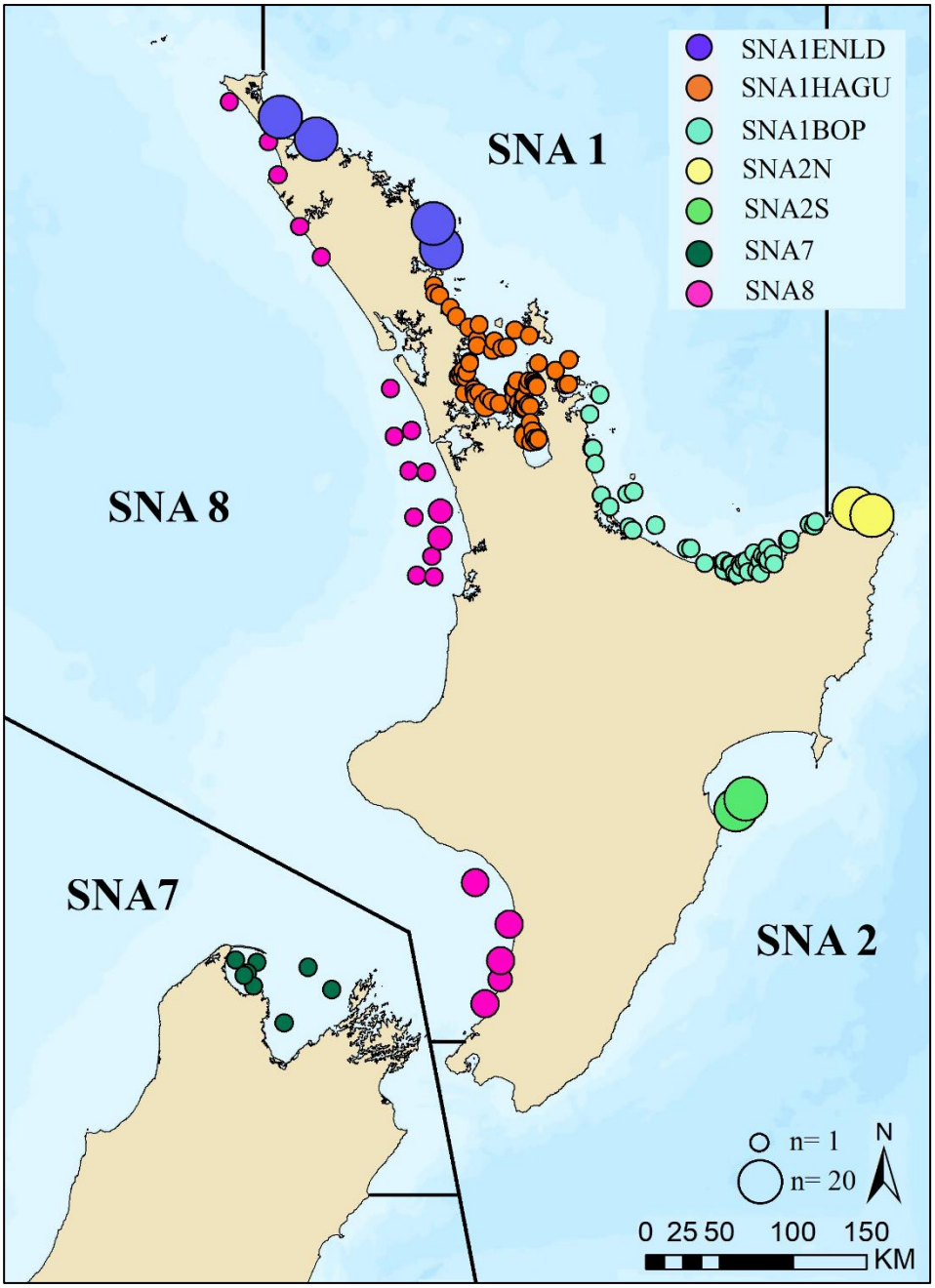

Figure 2.1 Map showing sample locations of 330 *C. auratus* from around New Zealand, spanning seven hypothesised populations and four stock boundaries shown in black. The size of the circle indicates the number of specimens collected in that location.

2.2.1.2 Australia

In addition to the samples of New Zealand *C. auratus*, photographs of 79 Australian *C. auratus* were also obtained. There were 23 individuals from New South Wales (NSW), 52 from West Australia (WA), and four from South Australia (SA). The fish from NSW were collected from the Eastern stock, the fish from SA were caught in the South East region, and the fish from WA were caught in the Gascoyne region north of Bernier island in the Oceanic

Shark Bay stock. Like the New Zealand *C. auratus,* all specimens were between 300mm and 400mm FL. Sex, meristic or otolith data was not collected for Australian *C. auratus*, so analyses were limited to external morphology.

2.2.2 Photography methods

Photographs were taken from a bird's eye position of each fish's lateral left side. Fins were splayed and out of their groove, so insertion points were visible. If the caudal or pectoral fin position had become skewed because of the freezing position, it was aligned to be in a natural orientation, with pins if necessary. All photos had a calliper or ruler in the image as a scale.

2.2.2.1 New Zealand

Trials were conducted to determine the best photography settings to see all the features of interest. For the New Zealand specimens, photos were taken on a Cannon EOS 550D mounted on a camera stand 60cm above the fish, with two lamps illuminating the subject. The camera was in Creative Shooting mode, maximum sharpness, with the brightness increased to four out of five and no flash.

2.2.2.2 Australia

Various cameras and settings were used for Australian fish, but the same general protocols of good lighting and no flash were replicated. The variation in specific photography methods was unavoidable as many different collaborators from each region were involved.

2.2.3 Digitising methods

There are multiple software options for GM, however, the TPS series of software was used for the present study as it's free, easy to navigate, covers the entire landmarking process and is widely used in the scientific community. *C. auratus* images were loaded into TPSUtil and converted into TPS files, the standard format for morphometric data (Rohlf, 2008). The TPS file was then inputted into digitising landmarking software TPSDig2 (Rohlf, 2008). Thirteen landmarks and twenty semilandmarks were digitised on each image (Table 2.2, Figure 2.2). The TPS file was run back through TPSUtil to convert the curve to sliding landmarks.

Table 2.2: Anatomical description of each landmark used in *C. auratus* geometric morphometric analysis. See Figure 2.2 for an illustration of the landmarks.

Landmark Number	Anatomical description of the landmark
1	Tip of snout
2	Anterior edge of orbit
3	Posterior edge of orbit
4	Termination of dorsal fin attachment
5	Upper insertion of caudal fin
6	Posterior margin in the medial region of the caudal peduncle/ end of vertebral column
7	Lower insertion of caudal fin
8	Posterior terminal attachment of anal fin
9	Anterior attachment of anal fin
10	Ventral insertion of pelvic fin
11	Dorsal insertion of pectoral fin
12	Most posterior point of operculum
13	Termination of upper jaw
Blue line	20 semilandmarks from the base of the brow bone, in front of the nostril to the insertion of the dorsal fin

Figure 2.2: Labelled landmark positions used in *C. auratus* geometric morphometric analysis in red dots. Blue line shows where 20 semilandmarks were placed equal distance apart. See Table 2.2 for descriptions of each landmark.

2.2.3.1 Landmark justification

The landmarks were chosen because of their homology, common use in the field, and representation of important traits for characterising fish in the Sparidae family (Zelditch et al., 2012, Antonucci et al., 2009 & Parsons et al., 2016). Landmark one represents the most

anterior point of the head, which serves as an important baseline to establish comparative body and head lengths with landmarks six and twelve, respectively. Landmarks two and three captured eye diameter which can reflect trophic position and habitat conditions (Blasina et al., 2016). Landmark pairs four and five and seven and eight, mark fin insertion points. These not only provide information on the overall post-cranial body shape but caudal peduncle morphology, which influences swimming performance (Rouleau et al., 2010). Landmarks nine, ten and eleven are also fin insertion points contributing to a picture of the overall shape. The final sliding semi-landmark at the insertion point of the dorsal fin can be paired with landmark ten to show body depth variation which has important management implications for selectivity (Stergiou & Karpouzi, 2003). The end of the cranial region is marked by landmark twelve. Although landmark thirteen is not directly on a bony structure, it serves as a proxy of the jaw length which has direct implications for feeding selectivity.

The contour of the cranial region can play a role in sex identification, species recognition, mate selection, predation evasion and prey choices (Nanami & Shimose, 2013; Takahashi., 2018). In *C. auratus* specifically, there is evidence of local and sexual variation in head morphology for a specific region in Western Australia (Moran et al., 1998). As there are a lack of homologous points on this part of the cranial region, twenty sliding semi-landmarks were placed along the cranial region, beginning at the nasal opening and ending at the beginning of the dorsal fin.

2.2.4 Otolith morphometrics

Sagittal otoliths were removed and cleaned with water. Once the otoliths had been patted dry, they were stored in a paper envelope until analysis. Performing GM on otoliths is a time-consuming process. There is evidence that calliper measurements of the otoliths can be just as efficient at population discrimination as GM, so this more rudimentary technique was used (Wakefield et al., 2014). Measurements of the left sagittal otolith were taken unless broken or chipped. Using metal callipers, measurements were taken of the length of the otolith from rostrum to postrostrum, the width at the widest point perpendicular to the length axis and the thickness of the otolith across the primordium, perpendicular to the sulcus acusticus (Wakefield et al., 2014; Figure 2.3).

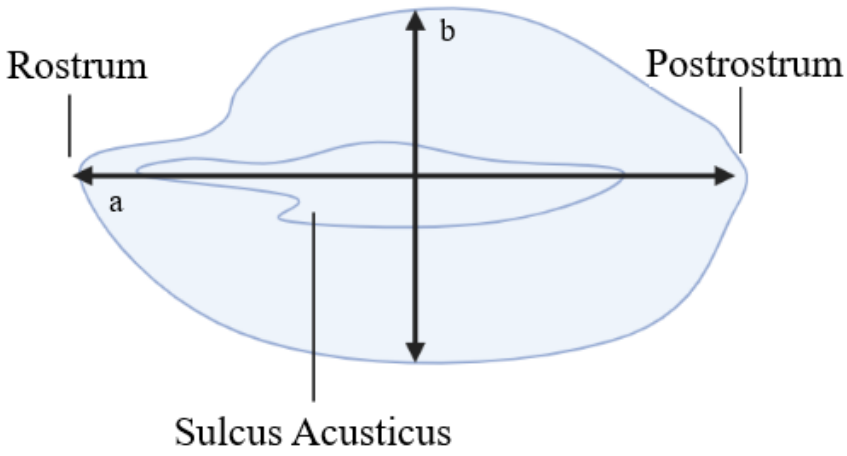

Figure 2.3: Two-dimensional diagram of an otolith. Length measurement is shown by line a, width measurement is shown by line b.

2.2.5 Other morphology and meristics

Four external length measurements were taken with a measuring board and vernier callipers; Fork Length (FL) and Total Length (TL) were measured to the nearest millimetre, and maximum gape (G) and interorbital width (IOW) were measured to the nearest 0.02 mm. Total weight (TW) was measured to the nearest gram.

The first left gill arch was removed and rinsed with water to count the inner and outer gill rakers. An incision from the anus to above the ventral fin exposed the gut cavity, providing a view of the gonads. The shape, colouration and texture of the gonads were used to sex the specimens. While the gut cavity was exposed, the gastrointestinal tract was removed for the analysis in Chapter 3. Additionally, the head was baked and flesh removed from the jaw structure for analysis in Chapter 3

2.2.6 Statistical methods

2.2.6.1 External morphology

The TPS file containing the photo morphology data was inputted into MorphoJ for visualisation and analysis (Klingenberg, 2011). Any variation in orientation and zoom were equalised using a Procrustes superimposition, overlaying landmarks to achieve the best fit (Rohlf & Slice, 1990). Following this, a regression analysis used allometry to correct for the effects of size on morphology. To identify any differences in morphology based on the

population the fish was from, a Canonical Variate Analysis (CVA), a form of discriminant analysis was carried out. CVA assumes equal within-group covariance matrices (Albrecht, 1980). Permutation tests with 10,000 iterations were conducted on pairwise differences between populations, generating *p*-values to test differences in morphology across populations. Additionally, a Procrustes ANOVA tested the statistical differences between groups. Procrustes ANOVA requires fewer parameters than the similar MANOVA, allowing for smaller sample sizes and a more intuitive interpretation (Klingenberg, 2011). Using Euclidean distances, leave-one-out cross-validation was used to test whether body morphology could be used to discriminate between populations. Average body profiles of each population were generated, showing the landmarks that most contributed to the differences. Finally, population classification success was tested using leave-one-out analysis which omits a single sample at a time to reclassify, using the rest of the samples as a descriptor.

To compare New Zealand and Australian populations simultaneously the New Zealand populations were grouped into two larger groups according to the genetic evidence (Papa et al., 2021). The eastern genetic stock included *C. auratus* from SNA1ENLD, SNA1HAGU, SNA1BOP and SNA2N populations and the western genetic stock included *C. auratus* from SNA2S, SNA8 and SNA7 populations. All the multivariate analyses described above were repeated for the genetic stocks.

2.2.6.2 Otolith morphology

A multivariate linear discriminant analysis (LDA) used the otolith morphological data to predict the population each sample came from. LDA is robust to uneven sample sizes and violations of the equal covariance and normality assumptions. If it works well despite the violations, it is preferable over choosing a more complicated model such as quadratic discriminant analysis that may overfit. The data was split 60:40 into training and testing samples respectively.

2.2.6.3 Other Morphology and Meristics

Variation in inner and outer gill raker counts by population was individually tested using a two-way ANOVA with an interaction by sex. A linear model investigated the effect of sex on the relationship between FL and weight of snapper. A one-way ANOVA was used to test any significance of the linear model. After being allometrically adjusted for FL, a one-way ANOVA was also used to test any difference in interorbital width.

2.3 Results

2.3.1 External morphology

2.3.1.1 New Zealand

Of the 329 *C. auratus* collected, 305 individuals were photographed and inputted into the morphological software. The remaining fish were either outside of the size parameters or had been damaged in the freezing and thawing process.

Following Procrustes superimposition of the landmarks, no significant differences (*p*-value >0.05) were found between Procrustes coordinates and FL, indicating that the effect of body length was successfully corrected for. The one-way Procrustes ANOVA testing shape differences between males and females was also non-significant (*p*-value >0.05), meaning sex had no significant impact on shape. However, when performing this test by population, there was a significant difference (*p*-value <0.0001).

The CVA revealed that the first two canonical axes captured a significant proportion of the variance, together accounting for 71% of the overall variance in external snapper morphology (Figure 2.4). Despite some overlap, the CVA scatterplot showed clear groupings aligned with populations (Figure 2.4a). These groupings followed a horseshoe shape, largely aligned with the physical geography of the populations, with each branch of the horseshoe being loosely the East or West Coast of New Zealand (Figure 2.4). The 95% confidence ellipses of the mean showed no overlap, echoing the strong grouping pattern (Figure 2.4b).

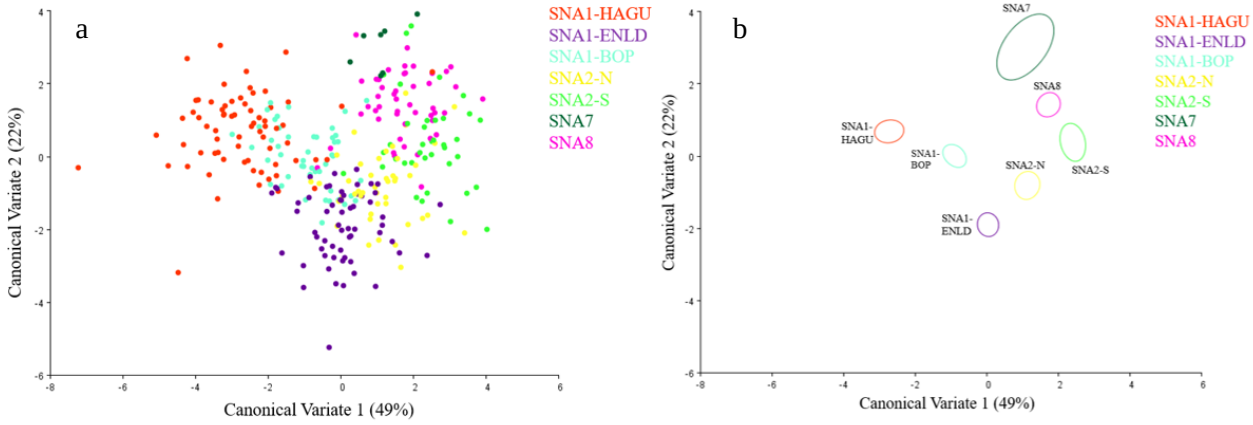

Figure 2.4: Canonical variation analysis (CVA) ordinations of *C. auratus* external body morphology as (a) scatterplot and (b) 95% confidence ellipses of the mean.

Pairwise *p*-values were obtained by performing permutation tests for Procrustes differences among groups. Of these, most groups had strong statistical evidence of significant differences, except for SNA1ENLD & SNA1BOP and SNA2S & SNA7 (Table 2.3).

Table 2.3: *p*-values from pairwise permutation tests (10,000 permutation rounds) for Procrustes distances among New Zealand *C. auratus* populations. Asterisks indicate statistically significant results.

	SNA1-ENLD	SNA1-HAGU	SNA1-BOP	SNA2-N	SNA2-S	SNA8
SNA1-HAGU	<.0001*					
SNA1-BOP	0.2485	0.0021*				
SNA2-N	0.0001*	<.0001*	0.0007*			
SNA2-S	<.0001*	<.0001*	<.0001*	<.0001*		
SNA8	<.0001*	<.0001*	<.0001*	0.0006*	<.0001*	
SNA7	<.0001*	<.0001*	<.0001*	0.0004*	0.0653	0.0013*

Using Euclidean distances, leave-one-out cross-validation allocated observations to groups. The overall allocation success was 64%, but where allocation failed, observations were usually classified into the adjacent populations. For example, SNA1HAGU and SNA2S had an allocation success of 71% and 66% respectively but increased to 91% and 84% when considering the adjacent populations (Table 2.4). SNA1ENLD was the exception, with the highest misclassification into SNA2N and SNA1BOP, not the adjacent SNA1HAGU or SNA8 (Table 2.4).

Table 2.4: Allocation success of the leave-one-out cross-validation test based on morphological landmarks for each New Zealand *C. auratus* population expressed as percentages accurately classified.

Original Group	SNA1ENLD	SNA1HAGU	SNA1BOP	SNA2N	SNA2S	SNA7	SNA8
SNA1ENLD	**62**	3	12	18	2	0	3
SNA1HAGU	4	**71**	16	1	0	4	3
SNA1BOP	13	19	**43**	19	2	0	4
SNA2N	18	0	11	**48**	11	5	7
SNA2S	5	0	3	18	**66**	8	0
SNA7	0	0	0	0	0	**86**	14
SNA8	4	0	6	6	6	4	**72**

In general, the *C. auratus* from the SNA1HAGU, SNA1BOP and SNA1ENLD population had a narrower body and caudal peduncle, larger eyes and mouths with a protruding snout (Figure 2.5). The fish from SNA2S, SNA7 and SNA8 populations had greater body depths, smaller mouths, eyes and wider caudal peduncles, and the *C. auratus* from the SNA2N population had a shape very similar to the overall average (Figure 6).

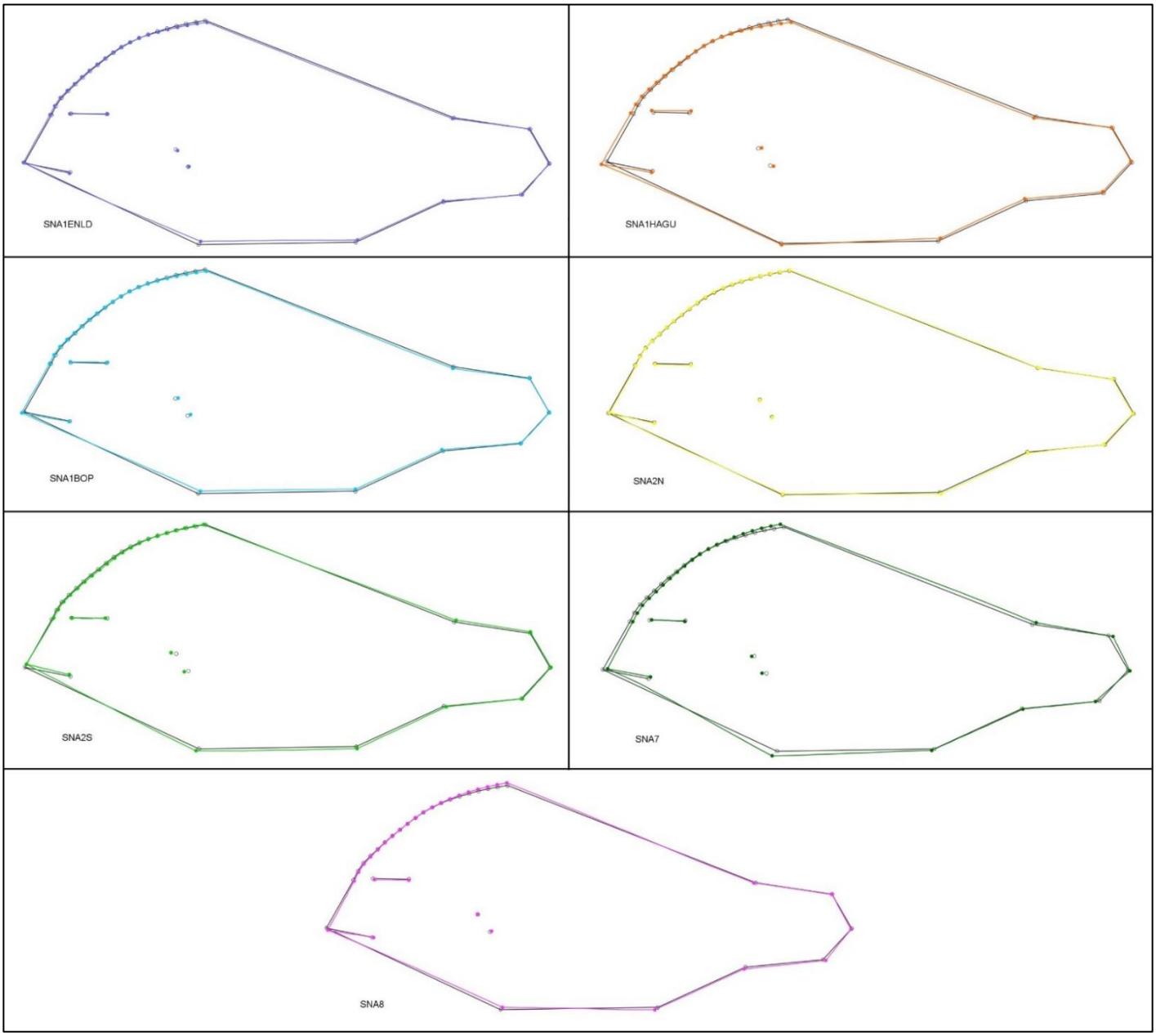

Figure 2.5: Average body profiles for each *C. auratus* population overlayed on the average *C. auratus* profile in black as calculated using landmarks in MorphoJ.

2.3.1.2 Australia

There were fewer *C. auratus* individuals photographed from Australian than New Zealand populations, but greater separation between stocks was observed. The Procrustes ANOVA testing differences in shape across regions was highly significant (*p*-value <0.0001), supplying strong evidence of differences in snapper body morphology between regions. The CVA ordination showed three clearly distinct groups, aligned with the three Australian stocks sampled. *C. auratus* from NSW and WA stocks were most separated along canonical variate axis one, while NSW and WA were separated from the SA stock along both canonical variate axis one and two (Figure 2.6).

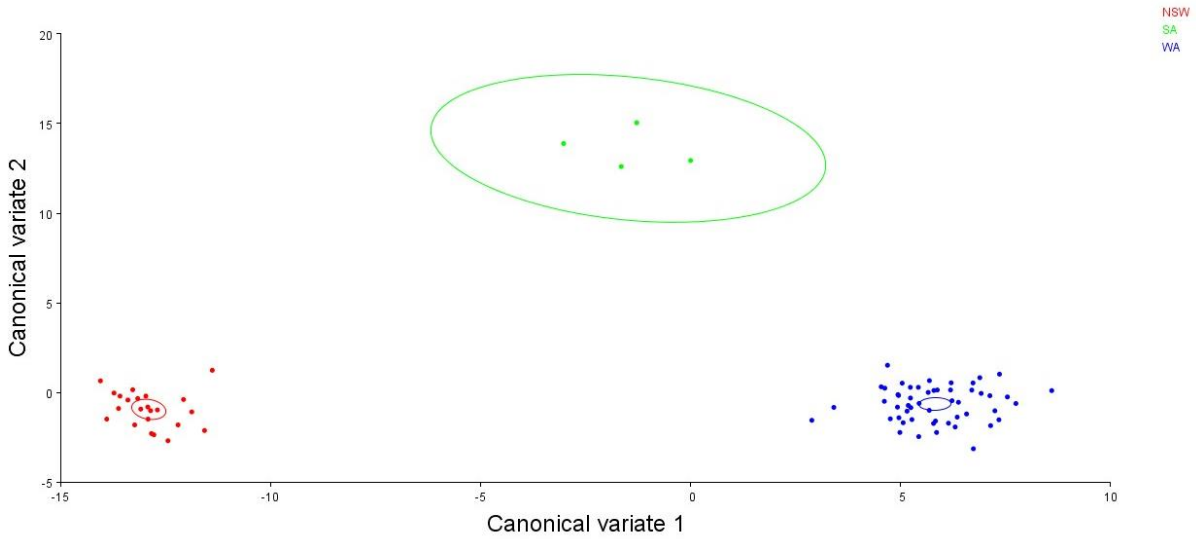

Figure 2.6 Ordination of Canonical Variate Analysis on the body morphology of *C. auratus* from three Australian populations

The differences between groups were investigated pairwise and all three populations were statistically significant from one another at the 5% level (*p*-value <0.05). The comparison between *C. auratus* in NSW and SA populations was slightly less significant than the other pairs, but still a highly significant difference (Table 2.5).

Table 2.5: *p*-values from pairwise permutation tests (10,000 permutation rounds) for Procrustes distances among Australian *C. auratus* populations.

	NSW	SA
SA	0.004	
WA	<0.0001	<0.0001

Leave one out cross-validation analysis successfully discriminated Australian *C. auratus* populations based solely on external morphology. *C. auratus* were most accurately assigned in the WA population at a rate of 96%, followed by NSW at 84% and then SA, which only had moderate allocation success at a rate of 63% accuracy (Table 2.6).

Table 2.6 Allocation success of the leave-one-out cross-validation analysis based on morphological landmarks for each Australian *C. auratus* population expressed as a percentage

Original Group	NSW	SA	WA
NSW	**84**	13	3
SA	13	**63**	25
WA	2	2	**96**

C. auratus from NSW had the most prominent hump on the head profile (Figure 2.7). SA *C. auratus* had the narrowest body profile with a prominent brow bone and high eye placement (Figure 2.7). The head profile for WA *C. auratus* was closest to average but had an elongated, downturned snout and the most upturned mouth

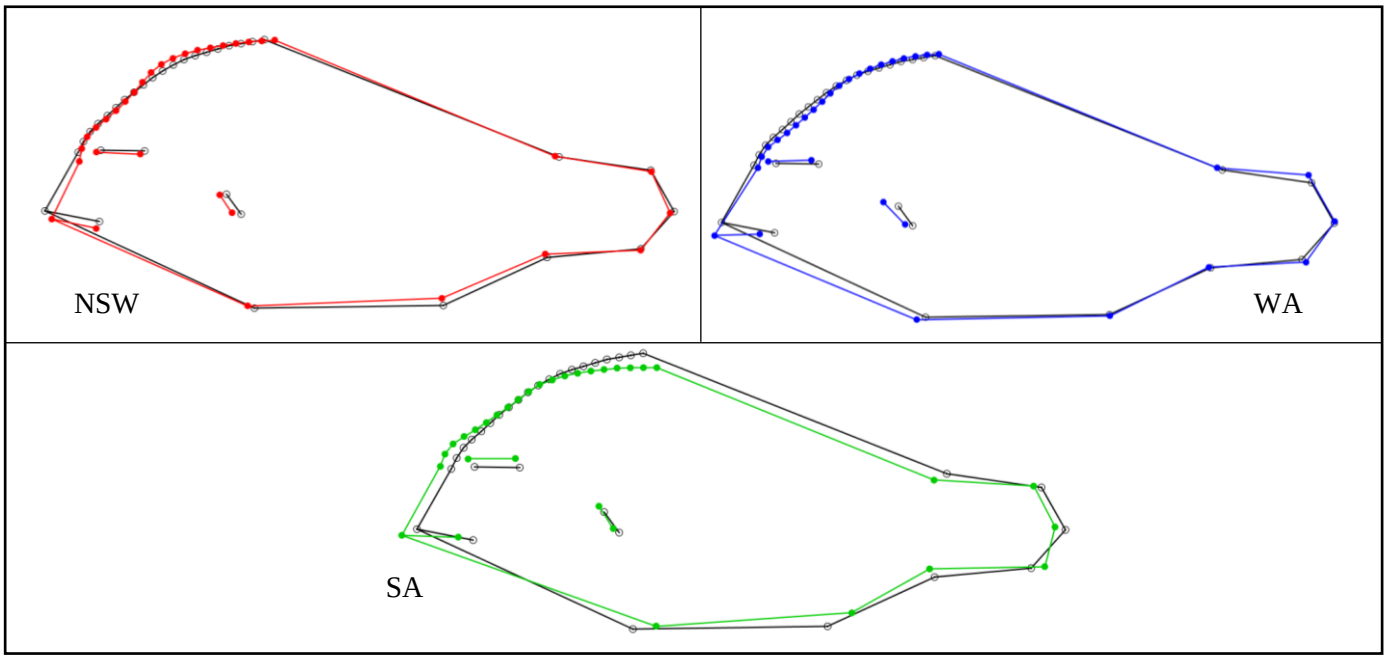

Figure 2.7 Average body profiles for each Australian *C. auratus* population in colour, overlayed on the average Australian *C. auratus* profile, in black as calculated using landmarks in MorphoJ. Differences are displayed with a scale factor of 2 for ease of interpretation.

2.3.1.3 Australia and New Zealand

Comparisons between Australian and New Zealand *C. auratus* morphology was done at the stock rather than population level for simplicity and ease of understanding. A Procrustes ANOVA tested for differences in morphology between Australian and New Zealand *C. auratus* and determined a high level of significance with a *p*-value of <0.0001. The CVA ordination also revealed differences between stocks, with New Zealand and Australian *C. auratus* being separated along canonical variate axis one (Figure 2.8). Within countries, the stocks were separated along canonical variate axis two (Figure 2.8).

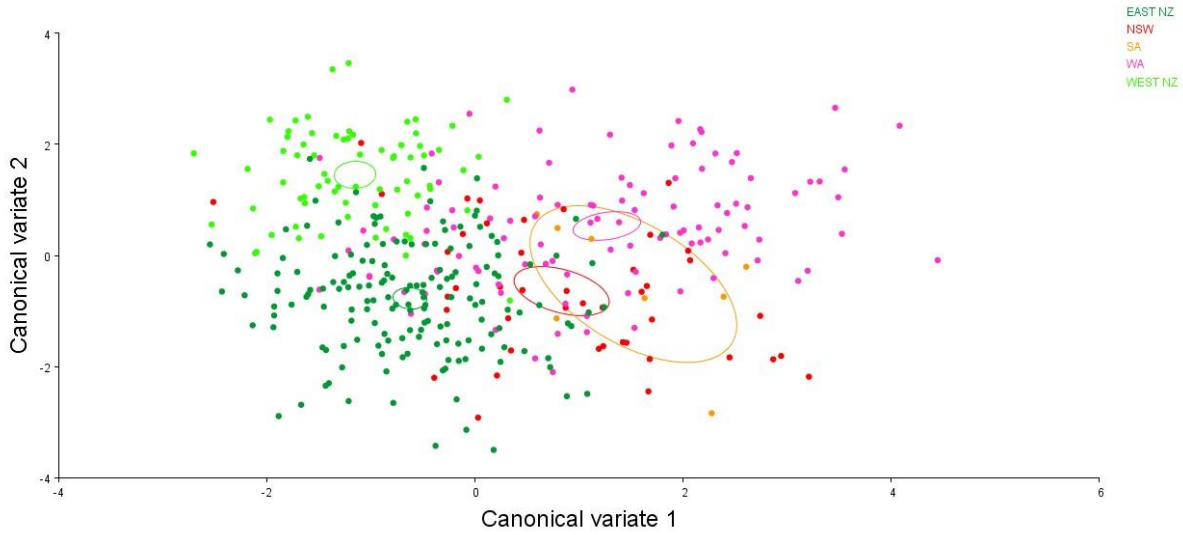

Figure 2.8 Ordination of Canonical Variate Analysis on the body morphology of *C. auratus* from three Australian populations and both of the New Zealand genetic stocks

Permutation tests were used to analyse the differences between each stock, and the results were highly significant for all pairwise differences (Table 2.7). The least significant difference was between the NSW and SA stocks, with a *p*-value of 0.0209 (Table 2.7).

Table 2.7: *p*-values from pairwise permutation tests (10,000 permutation rounds) for Procrustes distances for each *C. auratus* Australian population and New Zealand genetic stock.

	EAST NZ	NSW	SA	WA
NSW	<.0001			
SA	<.0001	0.0209		
WA	<.0001	<.0001	<.0001	
WEST NZ	<.0001	<.0001	<.0001	<.0001

Overall allocation success was high, but some stocks had lower accuracy than others. *C. auratus* in the SA stock had the poorest allocation success, with only 41% being correctly assigned (Table 2.8). 28% were incorrectly assigned into the East NZ stock (Table 2.8). The most accurately discriminated stock was East NZ, with 85% correctly assigned (Table 2.8).

Table 2.8: Allocation success of the leave-one-out cross-validation analysis expressed as a percentage based on morphological landmarks for each *C. auratus* Australian and New Zealand stock.

Original Group	East NZ	West NZ	NSW	SA	WA
East NZ	**85**	4	4	2	5
West NZ	7	**83**	4	5	2
NSW	9	7	**64**	8	12
SA	28	0	13	**41**	19
WA	8	5	6	2	**78**

2.3.2 Otolith morphology

Visual inspection of regression plots confirmed that each otolith morphology variable was strongly correlated with FL, so allometric size adjustment was conducted using the *GroupStruct* R package (Chan & Grismer, 2021; Figure 2.9). All populations had similar relationships between the four otolith morphology variables measured and FL (i.e. similar slopes for fish regardless of area) but varied in intersect (Figure 2.9). Hauraki Gulf fish had consistently larger and heavier otoliths than West Coast/Southern fish of the same size. The otolith thickness measurement provided the greatest separation between populations (Figure 2.9c).

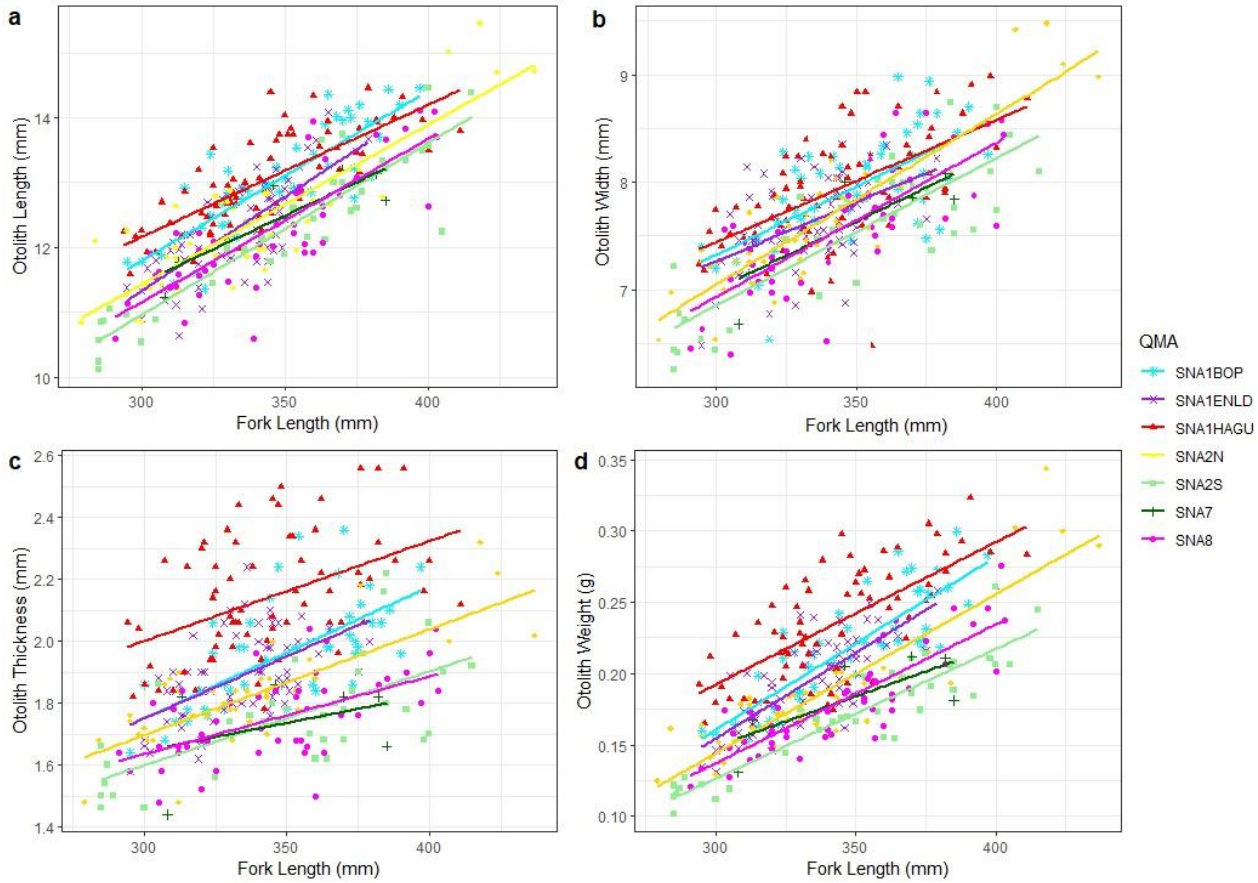

Figure 2.9: Regression of *C. auratus* Fork Length against otolith morphological measurements for each *C. auratus* population (a) Otolith Length (b) Otolith Width (c) Otolith Thickness (d) Otolith Weight.

LDA ordination of otolith variables demonstrated a gradient from SNA2N to SNA1HAGU with considerable overlap between populations (Figure 2.10). The separation of the SNA1HAGU population using otolith morphology aligned with the separation observed in the regression plots (Figure 2.9; 2.11). The first axis explained a much higher proportion of the variance than the second, as the separation between populations mainly occurred on the horizontal plane (Figure 2.10).

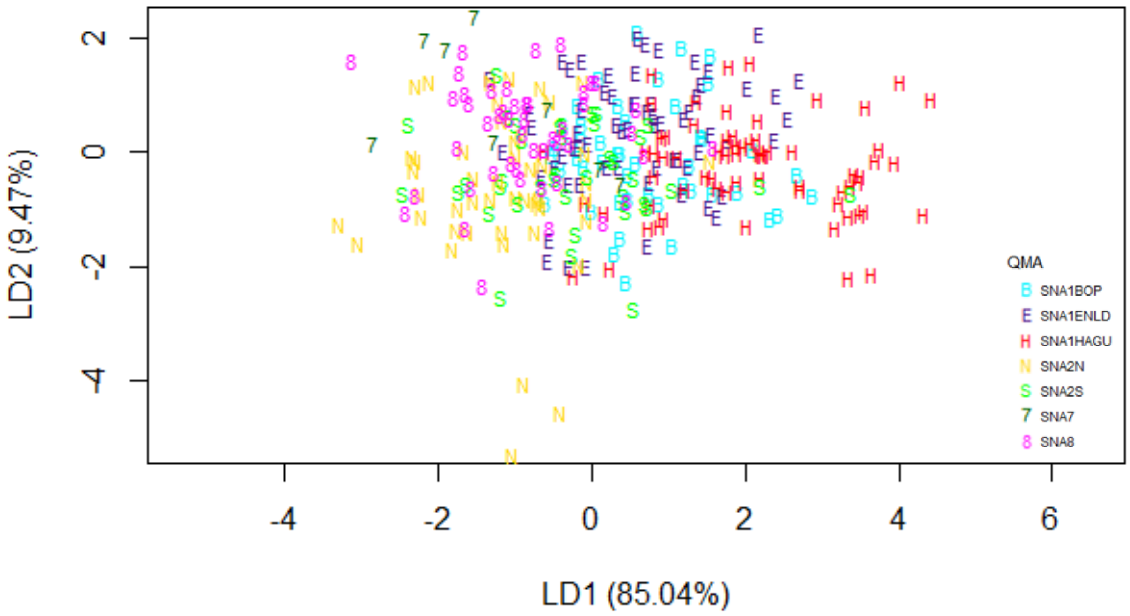

Figure 2.10: Linear Discriminant Analysis ordination using allometrically adjusted otolith measurements to distinguish *C. auratus* populations. LDA axis one explains 85% of the proportion of the variance while axis two explains 9%.

LDA successfully allocated 49% of snapper into their correct population by their otolith morphology (Table 2.9). When taking adjacent populations into account, allocation success rose to 74%. Due to random allocation, all of the SNA7 observations were in the training group and not the testing group, so allocation success wasn't measured for SNA7. SNA2S had the lowest allocation success, with predicted populations spread across all other areas.

Table 2.9 Allocation success of LDA on *C. auratus* populations using otolith morphology. % correct is the percentage of individuals allocated into the correct population and % adjacent is the percent of fish allocated into the correct population and the geographically adjacent populations.

Original group	SNA1ENLD	SNA1HAGU	SNA1BOP	SNA2N	SNA2S	SNA7	SNA8	% Correct	% Adjacent
SNA1ENLD	22	9	9	1	4	0	5	**44**	**72**
SNA1HAGU	9	29	9	0	1	0	1	**59**	**96**
SNA1BOP	4	5	9	0	4	0	4	**35**	**54**
SNA2N	2	1	0	18	4	0	1	**69**	**85**
SNA2S	3	0	3	2	2	0	1	**18**	**36**
SNA7	0	0	0	0	0	0	0	**0**	**0**
SNA8	4	1	0	6	3	1	12	**44**	**63**

2.3.3 Other morphology & meristics

Visual inspection of gill raker counts by *C. auratus* population showed no obvious differences (Figure 2.11) but was tested with a two-way ANOVA of gill raker count by population with an interaction of sex. Assumptions of normality and equal variances were checked visually, but the ANOVA was non-significant for both inner and outer gill rakers (*p*-value >0.05), meaning there were no significant differences in gill raker counts between *C. auratus* populations, sex, or combination of population and sex.

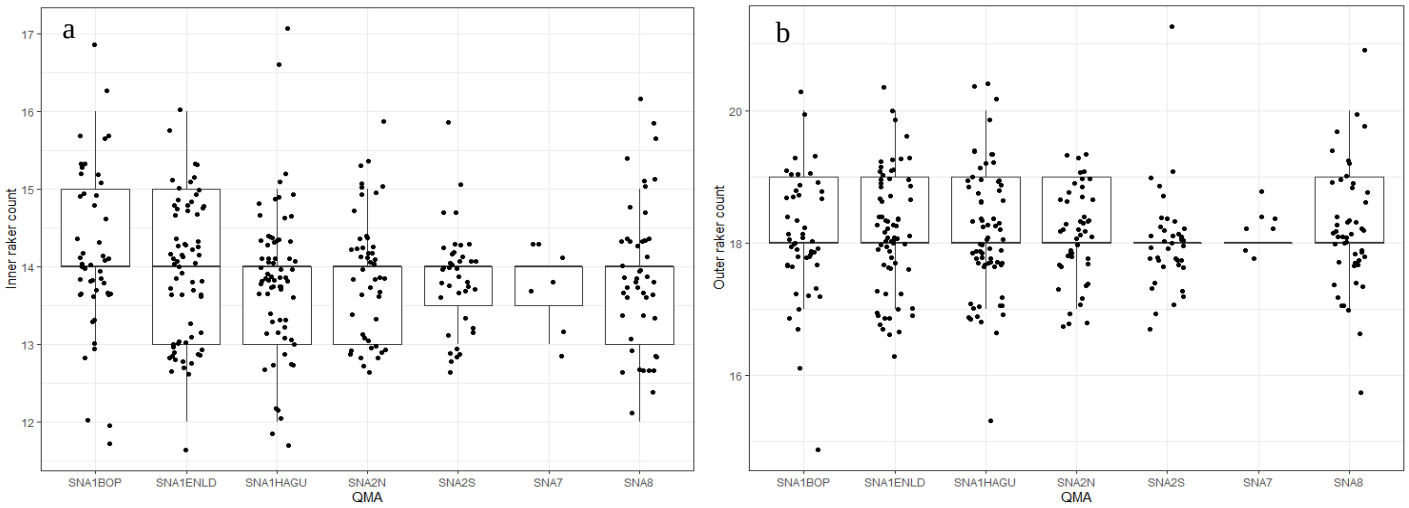

Figure 2.11: Box and whisker graph of (a) inner gill raker count (b) outer raker count across *C. auratus* populations displayed with jitter. The box represents the interquartile range between 25th and 75th percentile. The line in the middle of the box represents the median or 50th percentile and the whiskers extending from the box are 1.5* the interquartile range beyond the 25th and 75th percentile respectively.

The linear regression between weight and FL with an interaction by sex suggested a difference between sexes, where smaller FL females appeared to have a lower mean weight than males, whereas larger FL females were comparatively heavier (Figure 2.12). To account for unequal variance, the weight variable was logged and determined that the relationship between weight and FL did not significantly differ between sexes (*p*-value >0.05).

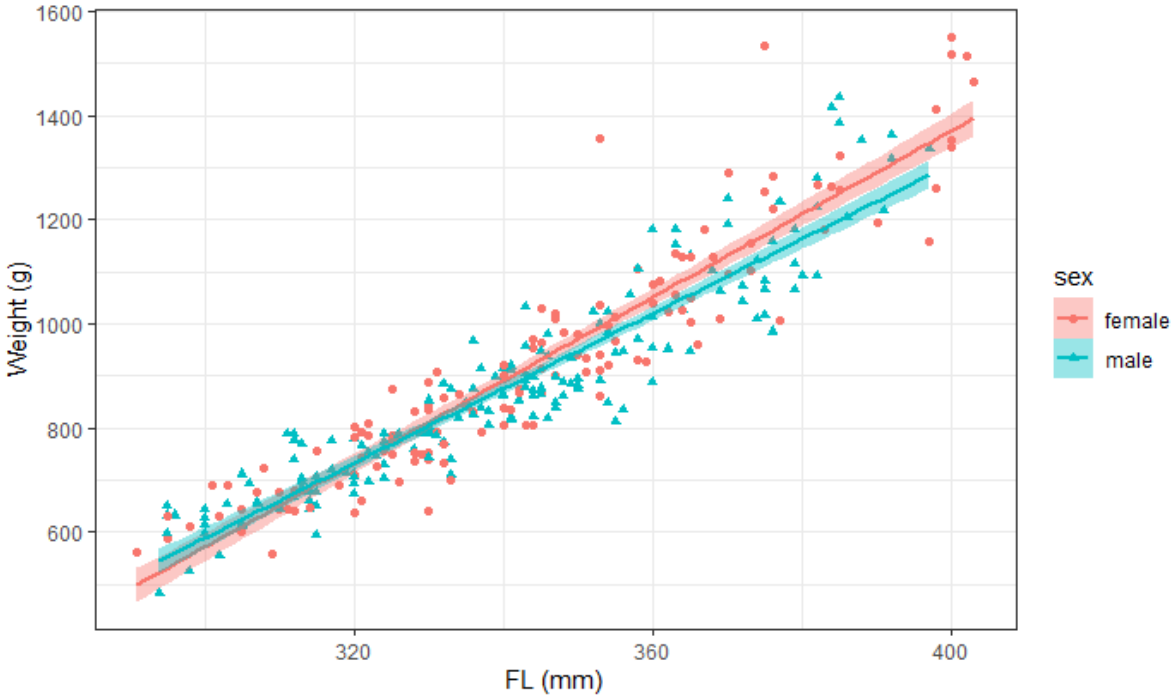

Figure 2.12: Linear regression of *C. auratus* fork length (mm) against total body weight for each sex

Inter orbit width was allometrically adjusted to account for significant correlation with FL however, box and whisker plots alongside a one-way ANOVA provided no evidence to suggest significant variation in inter orbit width between *C. auratus* populations (*p*-value > 0.05, data not presented).

2.4 Discussion

Defining appropriate population units of a fished species is a crucial component of the sustainability of that fishery (Kerr et al., 2014). Unrecognised population structure within a management unit can lead to overexploitation of the more vulnerable populations and reduced intraspecific variation (Cadrin, 2020). This study aimed to understand more about *C. auratus* population structure using morphology as a separation indicator. External body shape is becoming a widely used technique to achieve this goal for many species, as it is a physical display of a fish's habitat, life history, ecological interactions and genetics (Moran et al., 1998; Sequeira et al., 2011; Thambithurai et al., 2022). Significant morphological differences were observed between populations of *C. auratus* aligned with the hypothesised population structure. Similarly, with otolith morphology, different populations had different relationships between otolith dimensions and their body length. Understanding these relationships meant fish could be allocated into the correct populations solely based on otolith morphology. Incorporating the findings of this study into the management of *C. auratus* populations may

contribute to biologically optimised stock sustainability and contribute to the body of literature on population delineation using GM.

2.4.1. Population variation in external morphology

There was clear evidence of morphological differences between *C. auratus* populations with all but two pairwise comparisons being significant. SNA2S and SNA27 are neighbouring populations, and *C. auratus* from these populations didn't have significantly different external morphology from each other. The other non-significant difference was between SNA1BOP and SNA1ENLD populations which geographically are separated by SNA1HAGU. The non-significance of non-adjacent populations contrasts the expected hypothesis that neighbouring populations would look most morphologically similar due to the increased likelihood of gene flow. In the SNA 1 stock, the most connected populations are SNA1HAGU and SNA1BOP, where some *C. auratus* from the SNA1BOP population migrate and mix with SNA1HAGU fish (Gilbert & McKenzie, 1999; Ministry for Primary Industries, 2013). All three SNA 1 populations are linked together in one large stock but are documented as separate populations with unique year class strengths, growth rates, and age structures (Fisheries NZ, 2020). Despite the clear evidence that the SNA 1 populations are separate, the present study demonstrates that their morphologies are still similar. Similarities in environmental conditions have resulted in lower levels of intraspecific variation between populations for other species, including riverine cyprinids, and may be contributing to non-significant differences in morphology between *C. auratus* in SNA1BOP and SNA1ENLD (Bravi et al., 2013). The reason *C. auratus* in the SNA1HAGU population was different to the other two SNA1 populations could be due to the unique subpopulations within the SNA1HAGU population. Parsons et al. (2015) found evidence of a subpopulation within SNA1HAGU with distinct morphology and a more pelagic life history. One of the morphological measurements unique to this pelagic subpopulation was an orbit related measurement, and in the present study, the eye diameter was the largest in SNA1HAGU *C. auratus* (Parsons et al., 2015). The *C. auratus* in the SNA1HAGU were caught in summer, at a time when this migratory pelagic group are known to aggregate (Parsons et al., 2015). In a review of morphology within the sparidae family, narrower bodies and caudal peduncles, like what was observed in the SNA1HAGU *C. auratus* are associated with a more pelagic life-history and suggest that pelagic associated *C. auratus* in the SNA1HAGU population might be driving the differences between other populations (Antonucci et al., 2009). If the fish in

this study were sampled at a time when the pelagic subpopulation were not present in the population, we might have seen more similarity on average with the other SNA1 populations.

This study has provided significant evidence supporting the hypothesis that the SNA2 stock is split into two populations, north and south of the Mahia Peninsula (Fisheries NZ, 2020). Genetic evidence suggests that the Mahia Peninsula serves as a physical barrier to gene flow and the statistically significant differences in external and otolith morphology for *C. auratus* north and south of this barrier in the present study strengthens this hypothesis (Oosting, 2021; Papa et al., 2021). It has not yet been determined whether the northern population, SNA2N is linked to the SNA1BOP population, but the present study provides evidence of separation between the two with highly significant differences in both external morphology and otolith morphology between SNA1BOP and SNA2N populations. Phenotypically, *C. auratus* from SNA2N appear to be at a convergence point between southwestern and eastern populations, with a body morphology very close to the overall average for the New Zealand *C. auratus*. This phenomenon of "intermediate morphs" aligned with physical geography can be observed across many different species, including the cichlid *Haplochromis nyererei* (Seehausen et al., 1996). The combination of the geographical gradient and corresponding change in environmental conditions resulted in distinct morphs at each end of the range, with an intermediate phenotype in between (Seehausen et al., 1996). For *C. auratus* in the SNA2N population, small numbers of individuals moving between neighbouring populations and similar ecologies likely contribute to this population being a distinct but intermediate morph.

Highly significant morphological differences were observed between the three Australian stocks. NSW and WA stocks were most different from each other with SA residing in between. There is evidence of further population structure within each of these stocks, similar to that observed in the New Zealand SNA1HAGU population (Parsons et al., 2015). South Australia has highly complex, fine-scale population structure, with six management units originally identified, now refined to three (Fowler et al., 2013; Fowler et al., 2017). West Australia has six recognised management units, three of which are within the Shark bay region (Nahas et al., 2003). The stocks within Shark Bay exhibit clear polymorphism of the head as well as prominent sexual dimorphism of the snout in fish larger than 45cm (Moran et al., 1998). In New South Wales, *C. auratus* population structure is on a much larger geographic scale with a northern stock that joins with the state of Queensland and a southern stock that spans over the states Victoria and Tasmania (Morgan et al., 2018). Stock discrimination of East Coast Australian stocks has been analysed genetically but uncertainty

on precise structure remains (Morgan et al., 2019). Within stocks, this study had little to no geographic replication so comparisons between stocks were done on only one stock within the wider region's stocks. Future analysis comparing all of the stocks within these and neighbouring regions may reveal interesting ecomorphological equivalences and help derive any functionality or environmental drivers of variation. Analysis of external and otolith morphology in the East Australian region, in particular, is likely to provide more insight into population structure like it has done for other *C. auratus* stocks in Australia and New Zealand (Parsons et al., 2015; Rogers et al., 2014; Moran et al., 1998).

Morphological comparisons between New Zealand and Australian *C. auratus* align with the literature that determines despite the same species, they are genetically and now proven to be morphologically different (Papa et al., 2021). Clear morphological differences between countries were observed, particularly in the head region, and it was apparent that there was further polymorphism within each country. The New Zealand stocks were better separated than Australian stocks, but this may have been overemphasised due to the better sampling coverage in New Zealand. Of the Australian stocks sampled, the NSW stock was geographically closest and most connected to New Zealand stocks and was also the most morphologically similar. Incorrect allocation of *C. auratus* in the NSW stock was roughly equally split between the WA, SA and East New Zealand stocks. Geographically, New South Wales is closer to the West Coast of New Zealand, but the East Australian and East Auckland current provide better connectivity with the East Coast (Tilburg et al., 2001). The Tasman sea limits genetic connectivity between the two countries but the East Australian and East Auckland current have intermittently enabled gene flow throughout the past 400,000 years (Briggs & Bowen, 2013). For the seahorse *Hippocampus abdominalis*, intermittent genetic connectivity has resulted in intraspecific similarities between countries, with further intraspecific complexity evolving independently within each country (Ashe & Wilson, 2018). It is possible that the same currents and gene flow events across the Tasman have shaped similarities and later polymorphism within Australian and New Zealand *C. auratus.*

Collaborative work provides the opportunity to expand the scope of a study but does introduce additional assumptions to be aware of. In this study, various cameras and settings were used to photograph *C. auratus* across Australian stocks and weren't identical to the apparatus used for New Zealand *C. auratus.* This non-consistency may slightly increase morphological variation but only decreases the chance of detecting a difference, strengthening the validity of the present study's findings.

Investigating polymorphism in *C. auratus* was limited by uneven sample sizes, particularly for SNA7, SA and NSW. Pandemic interruptions prevented complete sampling of these and additional Australian populations, which had to be removed from the study. There are hypothesised fine-scale populations structure within the SNA8 stock, North and South of the Taranaki Bight (Walsh et al., 2006). The Kaipara Harbour is a known nursery ground for the entire coast, but variation in growth rates and age composition structure suggests a divide (Morrison et al., 2014; Walsh et al., 2006). In the present study, SNA8 wasn't split into northern and southern regions due to inadequate sample sizes, but the ordinations of morphology by region didn't demonstrate any clear morphological partitioning within SNA8. Further research into morphological variation in the SNA8 region would help establish whether this population should be split into two management units. Additionally, SNA7 and SA had poor allocation success in leave-one-out cross-validation analyses, and thus additional future research with a more balanced survey design in these populations would allow for better analysis of potential polymorphism.

2.4.2 Population variation in otolith and meristic morphology

Otolith morphology has been used widely in fisheries science to discriminate populations and stocks of fish (Sadighzadeh et al., 2014; Hüssy et al., 2016; Jemaa et al., 2015) and was successfully used in the present study to distinguish between New Zealand *C. auratus* populations. The *C. auratus* from the SNA1HAGU population were the most distinct group, with much greater otolith thickness for a given fork length, followed by the other SNA1 populations, with the thinnest otoliths coming from SNA7 and SNA8 populations. In a study comparing otolith morphologies in wrasse species, thickness was the least useful trait, and several other otolith studies only analyse the two-dimensional structure of otoliths, so there is a lack of data on otolith thickness (Škeljo & Ferri, 2011). Otolith morphology is correlated with growth in several fish species, such as Atlantic mackerel (*Scomber scombrus*), king mackerel (*Scomberomorus cavalla*) and blue whiting (*Micromesistius poutassou*) (Zischke et al., 2016). Otolith thickness was studied explicitly in Pacific Hake (*Merluccius productus*), where thickness continued to increase as the fish aged while the other otolith morphological variables remained relatively constant (Beamish, 1979). The varying growth rates of New Zealand *C. auratus* populations align with the variation in the thickness of the otoliths by population. SNA1HAGU *C. auratus* were the slowest growing and had the thickest otoliths, and *C. auratus* from SNA7 and SNA8 populations were the fastest growing and had the thinnest otoliths (Walsh et al., 2019; Fisheries NZ, 2020). This variation in thickness suggests

that *C. auratus* otoliths follow a similar growth pattern to Pacific Hake. As otolith thickness isn't always an important morphological feature to discriminate between stocks but is known to be related to growth, it suggests that the significant differences in otolith morphology between *C. auratus* populations may be driven by differences in growth rates. Otolith increment analysis measures the distance between annual growth rings deposited as the otolith grows and can be used to calculate body growth year by year (Jones, 1992). In the future, pairing otolith increment analysis with otolith and body morphology would provide a complete picture of *C. auratus* variation by population and give insight into whether variation in growth rates is driving any polymorphism. Furthermore, this study used callipers to measure otolith morphology as a more cost and time-effective option than GM, but it is likely that using more advanced shape analysis methods such as GM or Fourier Analysis would yield even better results and allocation success (Ponton et al., 2006).

Sexual dimorphism of the head region has been documented across the Sparidae family and even within the *C. auratus* species itself (Minos et al., 2008; Moran et al., 1998). The variation in the head region occurs due to the enlargement of the supraoccipital and frontal bones of the skull, known as hyperostosis (Minos et al., 2008). It is not known why some teleost species or populations display ontogenetic hyperostosis as there are not any strong functional links (Smith-Vaniz et al., 1995). In some cichlid species, a prominent hump on the forehead is favourable for sexual selection, but this is not thought to be a driver of head morphology across all teleosts (Barlow & Siri, 1997; Smith-Vaniz et al., 1995). It has been suggested that due to the site-specificity and intraspecific predictability of hyperostosis, that it is a purely genetically driven trait (Smith-Vaniz et al., 1995). Neither the present study or a previous study that investigated morphological sexual dimorphism in New Zealand *C. auratus* has shown any evidence of occurrence, however, both of these studies only investigated fish between 30 and 40cm (Parsons et al., 2015). An investigation into the relationship between weight and fork length by sex of *C. auratus* in the present study did show some small differences, with longer females weighing comparatively heavier than their male counterparts but these differences were not significant. There is a possibility that like other ontogenetic sexually dimorphic differences in sparids (Minos et al., 2008), differences in New Zealand *C. auratus* head morphology by sex are only apparent in fish larger than 40cm. Further investigation into morphological differences in *C. auratus* could answer this question and potentially reveal more pronounced differences between populations.

2.5 Conclusion

Using morphology to investigate the population structure of a fish species is becoming an increasingly used technique in fisheries science (Bower & Piller, 2015). Understanding population structure helps ensure fisheries sustainability and preserves intraspecific biodiversity (Des Roches et al., 2021). This study has been the first to utilise the GM technique on New Zealand *C. auratus* and make comparisons to Australian *C. auratus.* Within New Zealand, there were significant differences in otolith and body morphology between most populations, and there was evidence to suggest that the current SNA2 stock comprises two populations north and south of the Mahia peninsula. For the three Australian stocks sampled, there was evidence of significant differences between each of them, as well as significant differences with the New Zealand stocks. The most pronounced morphological differences were in the head curvature, body depth, eye size and caudal peduncle width. Future analyses on areas of interest such as *C. auratus* stocks SNA8 and NSW with larger sample sizes would provide valuable insight into population structure. This study has demonstrated that *C. auratus* exhibits regional polymorphism and fine-scale population structure that should be considered at a management level in order to prevent localised depletions.

Chapter Three. Variation in diet and functional morphology between *C. auratus* populations

3.1 Introduction

The last decade has seen increasing recognition and quantification of the effects functional diversity within species has on community assemblages and ecosystem functioning (de Bello et al., 2011). Animals can widely be assigned into two dietary groups, either generalists or specialists (Grinnel, 1917). Generalists consume a diverse diet, while specialists have a narrow dietary niche (Smith et al., 2011). Across the animal kingdom, generalist predators are advantaged as they can exploit a wide variety of prey depending on what resources are available (Potter et al., 2018). On the other hand, specialists can avoid interspecific competition by utilising a specific niche (Balme et al., 2020). Diet preferences can change spatiotemporally within a species, and this complexity is not captured by the specialist and generalist label (Pagani-Nunez et al., 2016). For example, *Cyanistes caeruleus* (Blue tit) is considered to be a caterpillar specialist, but populations develop alternate foraging strategies depending on whether they live in evergreen or deciduous forests (Blondel et al., 1991). Individuals can exhibit varying niche preferences within a singular environment, known as individual diet specialisation (Pagani-Nunez et al., 2016). For *C. caeruleus*, within a single Mediterranean Forest it is possible to find individuals that show generalist strategies and others that display specialist strategies, despite being labelled as a specialist species overall (Pagani-Nunez et al., 2016).

Understanding the dietary niche of an aquatic predator is an essential component of understanding the wider ecosystem, and there are an abundance of different methods to quantify the diet of a fish, each with their own strengths and weaknesses. Molecular and stable isotope analyses are becoming increasingly popular but have increased costs and often poorer taxonomic resolution than other methods, so may not be suitable for fine-scale comparisons at the species level (Nielsen et al., 2018). Gut content analysis is typically a more cost-effective option where it is possible to identify prey to the genus or species level, but results can be biased towards hard-bodied prey (Buckland et al., 2017). Soft-bodied prey is more quickly digested than hard-bodied prey, so is less likely to be observed and identified in diet studies. There are many methods to chose from for gut content analysis. The presence-absence method is the most basic, providing a quick and easily interpretable method of diet

composition; however, its simplicity overestimates the importance of incidentally consumed prey, hard-bodied prey and prey types that are eaten in low abundances but high frequencies by a generalist consumer (Amundsen & Sánchez-Hernández, 2019). Numerical, gravimetric, volumetric and reconstructive methods are all highly laborious techniques that quantify the contribution of each prey type and, in addition to being costly methods, encounter problems when there are large size differences in prey or when the diet is highly fragmented (Amundsen & Sánchez-Hernández, 2019). Baker et al. (2013) determined the most robust measure of diet composition is the relative-fullness method, where the contribution of each prey type is quantified as a percentage, allowing a rapid and interpretable diet summary.

In terms of the methods that fish use to capture prey items, various methods are employed, which fall along a continuum of feeding modes (Liem, 1980). The spectrum runs from ram feeding to suction feeding, with manipulation falling between. Ram feeders rapidly move through the water column with their mouth open, engulfing any prey. Suction feeding is the most common technique employed by aquatic vertebrates where rapidly expanding the mouth cavity causes a suction, pulling prey into their mouths (Liem, 1980). Manipulative feeding covers a variety of techniques where the fish uses the oral jaws to bite, scrape, shred, rip or crush prey. Fish may also use a combination of these three techniques depending on the position and behaviour of the prey they are targeting (Wainwright, 1995). Varying morphologies are also associated with each of these techniques. Ram feeders are characterised by large gapes, weak jaws and low mechanical musculature force for mouth closing (Sonnefeld et al., 2014). Suction feeders have strong mechanical force for jaw opening but less reliance on strong closing forces or large gapes (Sonnefeld et al., 2014). Manipulator feeders have robust jaws and generate strong closing forces using large adductor mandibulae muscles (Sonnefeld et al., 2014). The bones and muscles utilised in each of these feeding modes can vary widely among individuals

The resource use of an animal is often reflected in its biological characteristics as individual diet specialisation is often linked to morphology and vice versa (Wainwright, 1994). Differences are often particularly noticeable in the jaw region and structures associated with feeding (Grubich, 2003). A study conducted on 31 species of Heroine cichlids (Genus *Cichlasoma*) revealed functional morphological specialisation according to the evasiveness of the prey each fish was targeting (Hulsey, Hendrickson & De León, 2005). In fish that fed almost exclusively on evasive teleosts, the structures related to jaw protrusion, particularly the maxilla and premaxilla were evolved and specialised for maximum protrusion (Hulsey et

al., 2005). The Heroine cichlids that targeted algae or sessile invertebrates had alternate jaw modifications to improve capture for the corresponding prey, typically at the expense of protrusion (Hulsey et al., 2005). In some instances, ecomorphological variation is observed beyond the structures directly involved in feeding and becomes apparent in the wider body form. For example, alternate forms of the threespine stickleback, *Gasterosteus spp,* are morphologically adapted to consume distinctly different prey (McPhail, 1984). The dietary specialisation is apparent in the fish profile, the benthic morph being larger and deep-bodied while the limnetic morph is small and slender (Day et al., 1994). Therefore, you can make ecomorphological inferences about some fish by simply observing their external form (Wainwright & Richard, 1995).

The ecomorphology of *C. auratus* in New Zealand is largely unknown. There is some evidence that within a specific region, *C. auratus* demonstrate trophic ecomorphology where fish with a more pelagic life-history had corresponding morphological adaptations (Parsons et al., 2015), but how functional morphology varies between populations and across environments is yet to be understood. This chapter aims to fill this research gap, identifying and linking diet patterns and morphological variation in *C. auratus.* This knowledge can then be compared and contrasted across the hypothesised populations identified in chapter 2 to strengthen understanding of population structure and ecosystem interactions in this highly valued species, particularly in the face of fishing pressure and climate change.

3.2 Methods and materials

The New Zealand *C. auratus* used for morphometric analysis in chapter two of this study were subsequently used in this chapter for diet analysis. As the data for Australian *C. auratus* came solely from photographs, it was impossible to collect diet samples, thus excluding those samples.

3.2.1 Diet methods

An incision from the anus to the ventral fin opened the gut cavity of each fish, allowing access to the alimentary tract. The alimentary tract was removed fully intact by cutting at the oesophaghageal opening and the anus. The liver, kidney and gonads were carefully removed allowing just the digestive tract to be weighed to the nearest gram. If the interstitial tissue was extremely fatty, this was noted. *C. auratus* have a distinctive foregut and hindgut, which were separated with dissecting scissors. The separated foregut was opened, and fullness was

estimated on a scale from 0-10, zero being empty, ten being completely full. The process was repeated for the hindgut.

As diet material moves through the digestive system, it gets progressively more digested. Estimating the digestive state using only the foregut would have meant all the samples that came entirely from the foregut would have no measure of digestion. Conversely, including the highly digested material in the rear of the hindgut in the estimate would impact the overall score, even if the foregut was completely undigested. To combat this, the digestive state of gut contents was estimated from any available material in the foregut and the first third of the hindgut. Digestive state was estimated on a scale of 0-5, zero being not at all digested and five being fully digested. For later identification, any potentially identifiable gut contents were scraped from the alimentary tract and preserved in 70% isopropanol (IPA). The empty alimentary tract was then weighed to the nearest gram, allowing the gut content weight to be calculated mathematically by subtracting the empty alimentary tract weight from the full alimentary tract weight.

Later, preserved contents were sieved to remove the IPA and rinsed with water onto a 100 square grid. Prey items were sorted into groups on the grid with forceps and identified to the smallest practical taxonomic level. If necessary, a dissecting microscope was used to help find identifiable structures. The relative contribution of each prey item was quantified as a percentage, known as the relative-fullness method and is considered one of the most robust yet least-time consuming diet analysis methods (Amundsen & Sánchez-Hernández, 2019; Baker et al., 2014).

3.2.2 Jaw morphology methods

Each snapper head was decapitated using a hacksaw and baked for 10 minutes at 220°C. Flesh was carefully removed from the jaw bones while retaining articulation. Twelve measurements were made on the jaws that provided a good picture of the overall morphology and function (Table 3.1, Figure 3.1). Each measurement was recorded to the nearest 0.2mm.

Table 3.1: Description of each jaw measurement taken on *C. auratus* samples

Bone	Name (Abbreviation)	Description
Mandible	Distal Tips (DT)	Inner distance between the distal tips of the mandible
	Opening in-lever (OIL)	Distance from quadratomandibular joint to the attachments of the interopercular ligament
	Closing in-lever (CIL)	Distance from quadratomandibular joint to the insertion of the A3 section of the adductor mandibular on the articular
	Outlever (OL)	Distance from Quadratomandibular joint to the base of the most anterior tooth on the dentary
	Jaw width (LJ.Width)	The maximum width of the tooth bearing region on the dentary
	Width biggest tooth (LJ.WBT)	The maximum width of the biggest tooth as occluded from the jaw
	Height biggest tooth (LJ.MTH)	The maximum height of the biggest tooth as occluded from the jaw
Premaxilla	Ascending process (AP)	Distance from the tip of the ascending process to the base of the more anterior tooth on the premaxilla
	Horizontal process (HP)	Distance between the most anterior tooth on the premaxilla to the tip of the horizontal process
	Jaw width (UJ.Width)	Maximum width of the tooth bearing region on the premaxilla
	Width biggest tooth (UJ.WBT)	The maximum width of the biggest tooth as occluded from the jaw
	Height biggest tooth (UJ.MTH)	The maximum height of the biggest tooth as occluded from the jaw

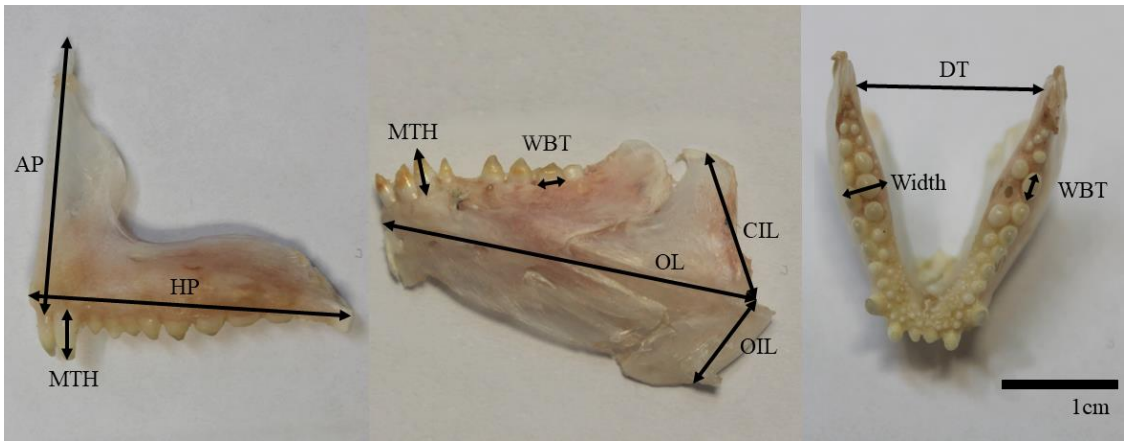

Figure 3.1: Visual description of *C. auratus* jaw measurement variables on the premaxilla (left) and mandible (centre and right). For description of the abbreviations refer to Table 3.1

3.2.4 Linking diet and morphology

To compare diet between individuals and groups of *C. auratus*, prey items were reclassified into fourteen broad prey groups (Table 3.2).

Table 3.2 Prey groups categorising the diet of *C. auratus* and each corresponding hardness rating

Prey group	Hardness rating
Crustacea- Brachyura	3
Crustacea- Caridea	2
Crustacea- Paguroidea	4
Crustacea- unidentifiable/other	3
Mollusca- Bivalve	4
Mollusca- Chitonidae	4
Mollusca- Gastropoda	4
Echinodermata- Hard echinoderm	3
Echinodermata- Soft echinoderm	1
Annelida- Polychaeta	1
Pelagic soft tissue	1
Sessile soft tissue	1
Cephalopoda	1
Teleostei	2

These 14 prey groups encompassed all identifiable prey material, grouped by phylogeny and ecology. Where a phylogenetic group contained two distinct subgroups (that different *C. auratus* morphologies may be differentially suited to catching or consuming), that group was split. For example, Echinodermata was split into hard and soft subgroups. Instead of having an "other" prey group containing very functionally different prey items, the small quantities

of prey that didn't fall into a clear phylogenetic group were split between sessile and pelagic soft tissue categories.

To quantify any relationship between jaw morphology and dietary hardness for *C. auratus*, each of the 14 diet groups was given a hardness rating, determined visually, from one to four (Table 3.2)

For each individual *C. auratus*, the proportion of each prey group was multiplied by the given hardness rating and then summed together to give an overall hardness score between one and four. For example, the hardness factor for a fish with 30% Caridea and 70% Bivalve would be calculated as follows

$$0.3 \times 2 + 0.7 \times 4$$
$$= 0.6 + 2.8$$
$$= 3.4$$
$$= \text{Hardness factor of } 3.$$

As each fish had varying degrees of fullness and thus volume of prey, the relative fullness method was adapted according to Binning & Chapman (2010) to better summarise and compare diet composition. For each individual, the relative fullness percentage of each prey item was multiplied by the fullness (and divided by 100) to get a number of points between 0 and 10. This was repeated for each fish on the broader prey groups rather than each individual species. For example, a fish with 30% Caridea and 70% Bivalve with a gut fullness of 4 would be calculated as follows

$$0.3 \times 4 + 0.7 \times 4$$
$$= 1.2 + 2.8$$
$$= \text{Caridea score } 1.2 \text{ \& Bivalve score } 2.8$$

These points were then summed to show the contribution of each prey item, and how diet composition varies by population or hardness groups.

Jaw opening and closing ratios were calculated by dividing each in-lever by the out-lever (Wainwright & Richard, 1995). This method allows an easily interpretable comparison of jaw mechanics. An opening lever ratio of less than one would indicate a mechanics system that intensifies jaw opening velocity, with the tip of the jaw moving faster than the muscle shortening (Wainwright & Richard, 1995). An opening lever ratio of 0.1 would have a jaw opening speed 10 times the speed of muscle shortening, therefore the lever ratio is inversely

proportional to the velocity of the jaw. However, this speed comes at the consequence of force. If a fish had a closing ratio of 0.3, their closing velocity will be 3 times that of the muscle shortening while the force exerted at the jaw tip will be a third of the force the muscle is generating. To relate this information on jaw mechanics to diet, the jaw ratio was converted to a factor by creating breaks according to Table 3.

Table 3.3: Jaw lever ratio definition for each level of the jaw factor category.

Jaw lever factor	Jaw lever ratio
1	<0.3
2	0.3-0.35
3	0.36-0.4
4	0.41-0.45
5	0.46-0.5
6	>0.5

3.2.5 Statistical methods

A matrix consisting of the diet of each individual *C. auratus* with points (as described above) for each prey group was transformed into a zero-adjusted Bray-Curtis dissimilarity resemblance matrix so that non-metric multidimensional scaling (nMDS) could be performed using PRIMER v7 (Anderson et al., 2008). The Bray-Curtis dissimilarity matrix is robust to data with an abundance of zeros, so it is a good choice for diet studies (Clarke et al., 2006). nMDS is purely an ordination, so a test statistic was provided using an Analysis of Similarity (ANOSIM). Pairing these analyses together is common practice in multivariate statistics. The ANOSIM R statistic calculates the average rank dissimilarities within and between groups and computes the difference between the two to provide a value between 0 and 1. An R value of 1 demonstrates that all samples in a group are more similar to each other than samples in other groups, whereas an R value of 0 means there are no group differences (Clarke et al., 2006). As a follow-up investigation, the nMDS and ANOSIM procedure described above was repeated on a Bray-Curtis dissimilarity matrix with a dummy variable added. The dummy variable essentially adds a species that all samples will have in common. For individuals with low quantities of only one or two diet groups, this created a certain amount of similarity with other sparse individuals while not affecting the similarity of species with more abundant gut contents (Clarke et al., 2006).

Two separate Canonical Analyses of Principal coordinates (CAP) were conducted on jaw morphology measurements based on different *a priori* groupings in PRIMER (Anderson et al., 2008). The first was to test the relationship between populations and jaw morphology, while the second linked jaw morphology to diet using the hardness grouping. Each dataset was normalised and transformed into a resemblance matrix of Euclidian distances before the analysis. Following the analysis, a hypothesis test was calculated using 999 permutations to determine if the groups differed significantly. To analyse the importance of individual components of the jaw on diet, univariate ANOVA's on each jaw measurement against the levels of hardness were conducted. Post-Hoc Tukey's Honest Significant Difference (HSD) tests was then used to investigate which hardness groups had significantly different jaw morphologies.

Exploration of individual patterns in diet composition was conducted using k-means clustering with a maximum of 7 clusters. The eighth cluster of fish, which had no identifiable gut material, was added manually. These k-means groups were then used as *a priori* groups in two CAP analyses. The first links jaw morphology and external morphology using the Procrustes Coordinates from chapter 2, and the second solely uses jaw morphology.

3.3 Results

3.3.1 Diet composition

Of the 329 *C. auratus* in Chapter two, 278 had at least some identifiable gut material (Appendix). These fish could then be used in the ecomorphological analyses linking diet to morphology. Including those with empty guts, the average gut fullness was 2.7 out of 10 for the foregut and 3.9 out of 10 for the hindgut, with an average content weight of 15.9 g. The average digestive state was 3.2 out of 5, where five represents complete digestion.

C. auratus diet in this study was highly diverse, with 52 different prey items belonging to 11 different phyla and 34 unique species identified (Table 3.4). Crustaceans were overwhelmingly dominant, followed by molluscs, polychaetes and teleost. Brachyura contributed over half of all the crustacea group, followed by paguroidea and Caridea. *L. tridentatus* (frog crab), *B. cheesmani* (nut crab), *U. hirtifrons* (mud shrimp), *Aphrodita spp* (sea mouse) *and G. habernatus* (little conger eel) were all species with abundances greater than 20 points, thus accounting for a large proportion of snapper diet.

Table 3.4: Summary of all prey items consumed by *C. auratus*. The points are a measure of the relative contribution of each prey item, from the modified relative fullness method, calculation description in the methods and materials. Totals are indicated in bold.

Prey				Points
Crustacean				**604.14**
	Amphipod			**0.31**
	Decapod			**588.2**
		Unidentified		42.88
		Brachyura		**314.34**
			Unidentified	53.18
			Majidae	4.09
			Inachidae	2.16
			Portunidae	12
			Bellidilia cheesmani	69
			Helicarcinus spp	0.15
			Hemiplax hirtipes	3.38
			Hymensomatidae spp	4.64
			Liocarcinus corrugatus	1.12
			Lyreidus tridentatus	142.37
			Nectocarcinus spp	20.4
			Neommatocarcinus huttoni	1.85
		Caridea		**59.86**
			Unidentified	29.69
			Upogebia hirtifrons	30.17
		Meiura		**11.42**
		Paguroidea		**159.7**
			Unidentified	155.19
			Lophopagurus spp	4.51
	Isopod			**1.77**
	Stomatopod			**13.86**
			Unidentified	6.86
			Heterosquilla tricarinata	2.25
			Oratosquilla oratoria	2.82
			Pariliacantha georgeorum	1.93
Cephalopod				**11.48**
			Unidentified	0.3
			Octopoda	11.18
Echinoderm				**53.9**
		Asteroidea		**1.23**
			Unidentified	2.85
		Echinoidea		**7.08**
			Unidentified	2.88
			Evechinus chloroticus	0.3
			Fellaster zelandiae	3.9
		Holothuroidea		**12.66**
			Unidentified	2.17

			Heterothyone alba	0.1
			Stichopus mollis	10.39
		Ophiuroidea		**32.93**
Mollusc				**90.94**
	Bivalve			**35.43**
			Unidentified	9.31
			Atrina zelandica	5.6
		Mytilidae		**8.8**
			Unidentified	4
			Perna canaliculus	3.6
			Xenostrobus neozelanicus	1.2
		Heterodonta		**5.86**
			Unidentified	4.26
			Austrovenus stutchburyi	1.6
		Pedinae		**4.48**
			Unidentified	2.07
			Pecten novaezelandiae	0.45
			Talochlamys zelandiae	1.96
		Ostreidae		**1.38**
	Gastropod			**55.51**
			Unidentified	20.2
			Buccinidae	11.36
			Turritellinae	5.1
			Fasciolariidae spp	0.94
			Philine spp	11.11
		Patellogastropoda		**0.67**
			Unidentified	0.23
			Cellana radians	0.44
		Neograstropoda		**6.8**
			Unidentified	2.75
			Marginella spp	4.05
		Chitonidae		**4.32**
Polychaete				**85.32**
			Unidentified	32.17
			Sabellida	8.81
			Aphrodita spp	28.37
			Urechis novaezealandiae	3.35
		Onuphidae		**12.62**
			Unidentified	8.26
			Hyalinoecia spp	4.36
Porifera				**9.21**
			Unidentified	9.06
			Callyspongia stellata	0.15
Teleost				**75.27**
			Unidentified	28.47
			Moridae	5.48
			Trachurus spp	7.40
			Cepola haastii	9.04
			Gnathophis habenatus	23.85
Algae				

	Rhodophyta	0.06
Tunicata		**27.78**
	Ascidiacea	6.41
	Salpidae	21.37
Bryozoa		0.9
Grand Total		**959**

C. auratus diet composition varied quite widely by population (Figure 3.2) Brachyura made up more than half of the gut contents in SNA2N, but it was not in the top three most abundant prey groups for SNA1BOP (Figure 3.2). *C. auratus* from the SNA1BOP population ate proportionally more hard echinoderms than the other populations and consumed minimal bivalves (Figure 3.2). *C. auratus* in SNA8 had the highest proportion of polychaetes in their diet but fish in SNA7 and SNA1ENLD had hardly any (Figure 3.2). SNA2S *C. auratus* ate comparatively more cephalopod and chitonidae, but less Caridea than other populations (Figure 3.2).

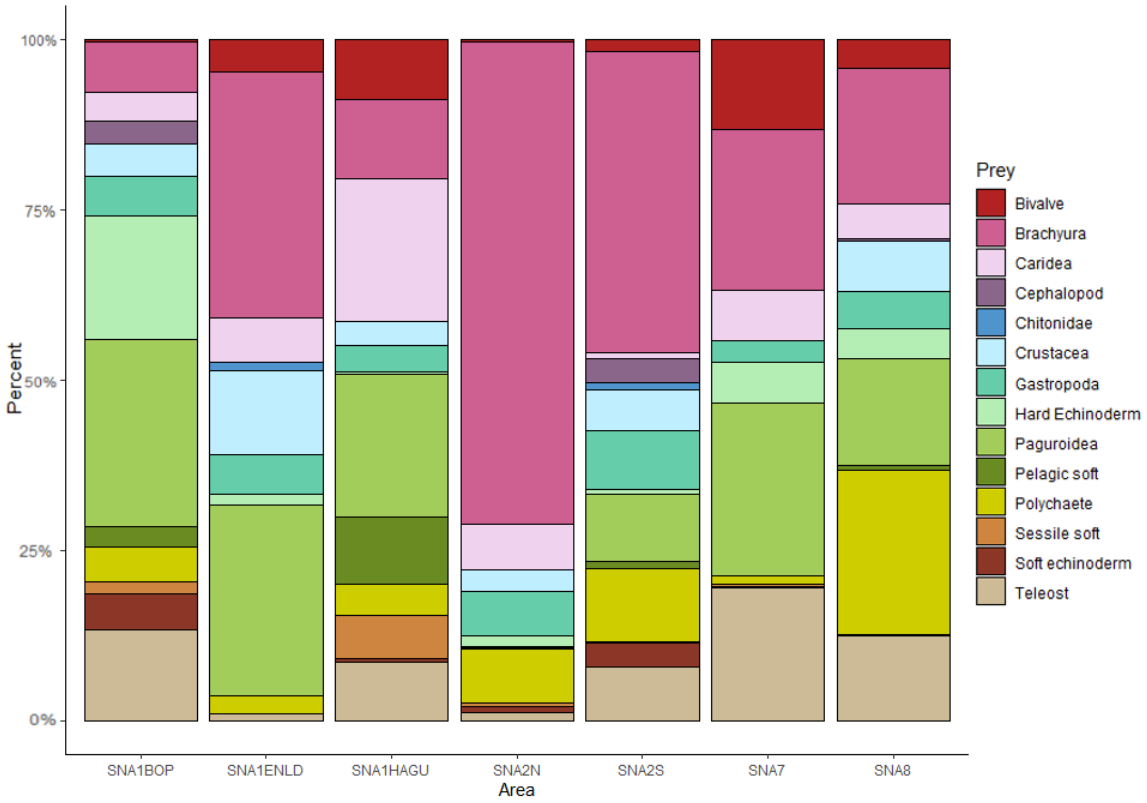

Figure 3.2: Comparison of diet composition using modified relative-fullness method, summing the points across *C. auratus* populations. Description of how the points were calculated is in the Methods and materials.

3.3.2 Dietary hardness

C. auratus within each hardness group primarily consumed diet items that had an identical hardness rating to the group rating, but there were some prey items consumed with a different rating (Figure 3.3). *C. auratus* in hardness group 1 overall ate more polychaetes than any other prey group, followed by pelagic soft prey, sessile soft prey and soft echinoderm. Fish in hardness group 2 ate roughly equal quantities of teleost and Caridea as well as polychaetes and Brachyura. More than half of the overall diet for *C. auratus* in hardness group 3 was Brachyura, and the remainder of the diet was mostly a mix of crustacea, gastropod, hard echinoderm, paguroidea, polychaete and teleost. Lastly, nearly 70% of the diet for *C. auratus* in the hardness group four was paguroidea, with the remaining 30% being mostly gastropods, bivalves and Brachyura.

Although the diet of most *C. auratus* within each hardness group was composed of prey with identical hardness ratings, some prey groups were found across all hardness groups, irrespective of their hardness rating. For example, Brachyura was observed in the diet of *C. auratus* assigned to each hardness group but made up the highest proportion of the diet in hardness group 3 (Figure 3.3). Similarly, Gastropods also made up a proportion of the diet of *C. auratus* in each hardness group, but most significantly in group 4. Sessile soft prey was even observed in the diet of some *C. auratus* with an overall hardness rating of 4 (the hardest group) (Figure 3.3). Contrastingly, Brachyura, crustacea and hard echinoderm, all harder prey items, were found in the least hard group (Figure 3.3). Group 2 was the most mixed group, with nearly even proportions of Caridea, polychaete and teleost in the diet (Figure 3.3).

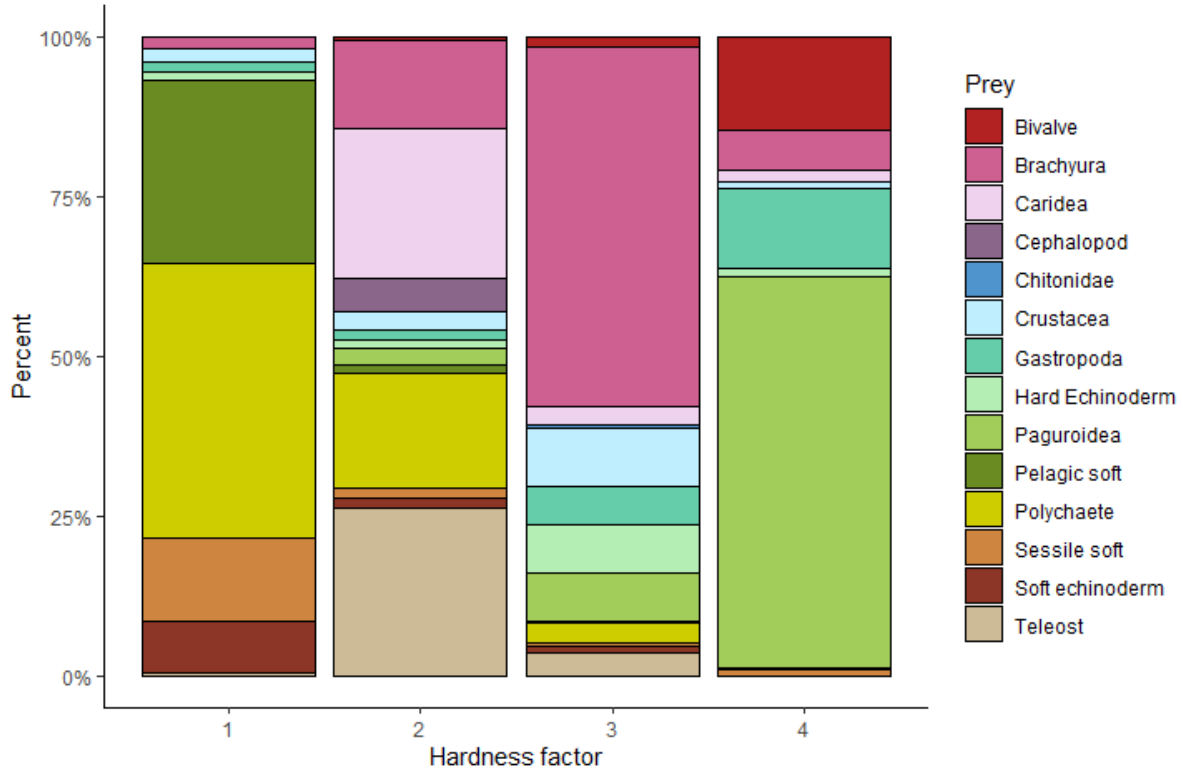

Figure 3.3: Composition of hardness groups by prey group. Abundance was calculated using the modified relative-fullness method and summing the points. An explanation of this process can be found in the Methods and materials.

The proportions of *C. auratus* with diet belonging to each hardness group varied by population. *C. auratus* from SNA2N and SNA2S both mainly had diets categorised into the hardness group 3 (Figure 3.4). SNA7 and SNA1HAGU were the populations with the highest proportion of *C. auratus* with diets categorised as hardness 4 despite SNA1HAGU also having the largest proportion of *C. auratus* with diets categorised as hardness 1 and many categorised as hardness 0 (Figure 3.4). SNA1ENLD had the most fish with no identifiable gut contents (Figure 3.4).

The variation in dietary hardness for *C. auratus* in each population was closely aligned with the prey group composition by population, as seen in Figure 3.2. For example, *C. auratus* from SNA2S and SNA2N were dominated by Brachyura, which is reflected by the high proportion of fish with a hardness group 3 categorisation in these populations (Figure 3.2, Figure 3.4). *C. auratus* from SNA8 had the most evenly split diet composition for each prey group and the evenest proportion of each hardness group (Figure 3.2, Figure 3.4).

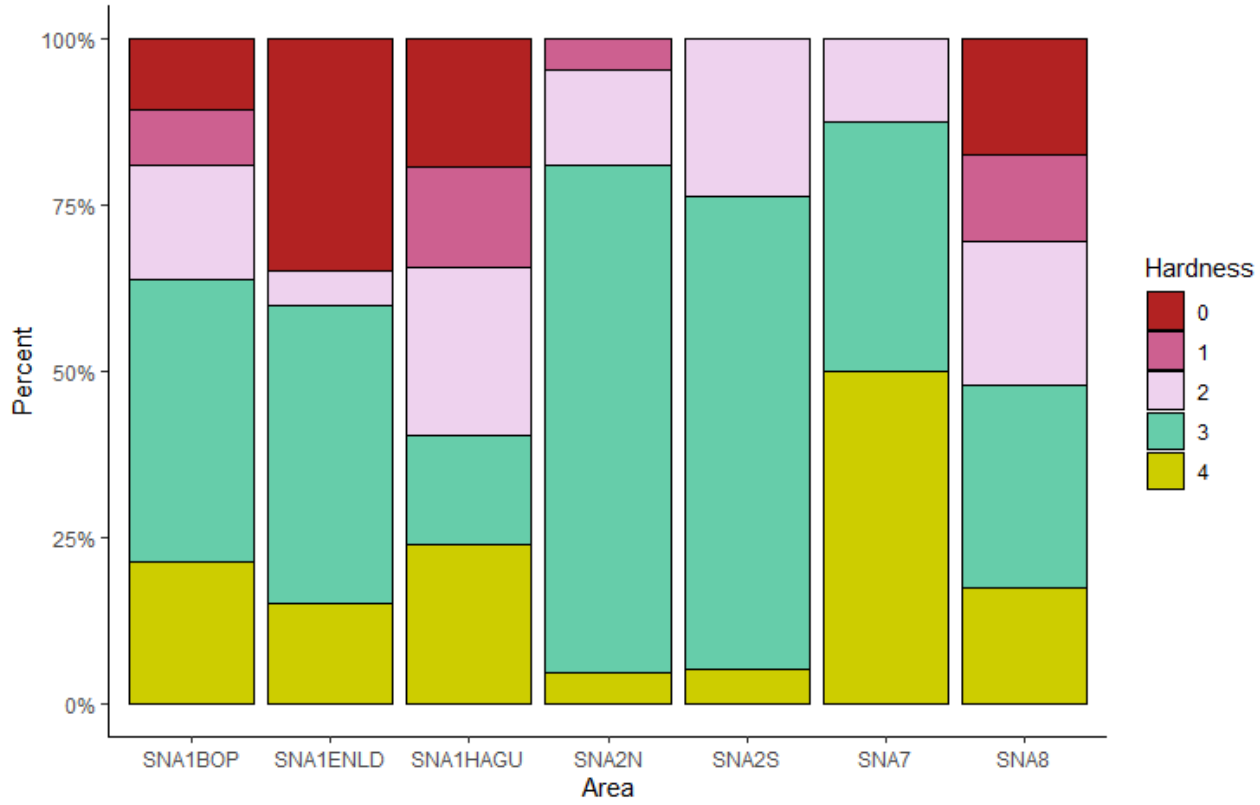

Figure 3.4: Proportion of *C. auratus* in each population belonging to each dietary hardness group. A hardness of zero means no gut contents were available to analyse, one being the softest diet composition and four being the hardest.

An nMDS ordination of prey groups by hardness showed one clearly separated group of *C. auratus*, all belonging to hardness group 1 (Figure 3.5). The diet of these fish primarily contained pelagic soft prey items, demonstrated by the strength of the pelagic soft vector overlay (0.72) (Figure 3.5). The other prey groups did not have strong correlations with the first canonical axis (maximum 0.16) and therefore had little influence on the separation of fish by hardness group (Figure 3.5). There was strong evidence of differences between hardness groups, with an ANOSIM R statistic of 0.407 (p-value < 0.001).

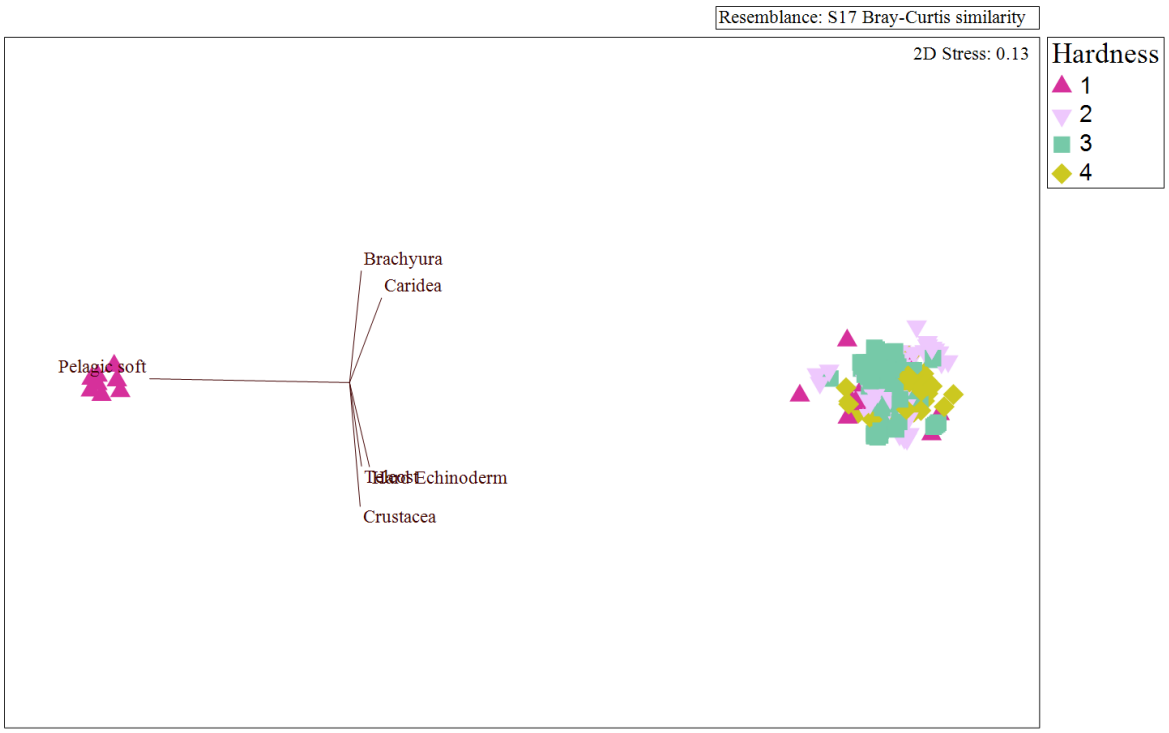

Figure 3.5: Non-Metric Multidimensional Scaling (nMDS) ordination of *C. auratus* diet categorised by hardness group. Analysis was completed on the zero-adjusted Bray-Curtis Dissimilarity matrix. Vector overlay displays prey groups with Pearson correlations greater than 0.3.

After a dummy variable was added to increase the similarity between samples with low quantities of one type of prey, the resulting nMDS no longer contained the separate group of *C. auratus* that were dominated by pelagic soft prey items (Figure 3.6). This new nMDS did not have obvious separation by hardness category, but there was a gradient aligned with the degree of dietary hardness, from hardness category 2 to 4 along canonical axis 2 (Figure 3.6). Individual fish with harder diets (Hardness 3 & 4's) were generally in the top right of the plot, while the softer groups were concentrated towards the bottom and the left (Figure 3.6). In this ordination, the strength of the Pearson correlations showed that Brachyura (0.8), paguroidea (0.69) and polychaete (0.48) prey groups were most responsible for driving separation (Figure 3.6). The Brachyura and paguroidea vectors are pointing towards the harder groups, while the polychaete vector is in the direction of the softer groups. The ANOSIM R statistic of 0.374 (p-value < 0.001) suggested significant differences existed between hardness groups; however, the ordination did have high stress. A stress value of 0.22 is deemed suspect and approaching arbitrary, so this result should be interpreted with caution (Buttigieg & Ramette, 2014).

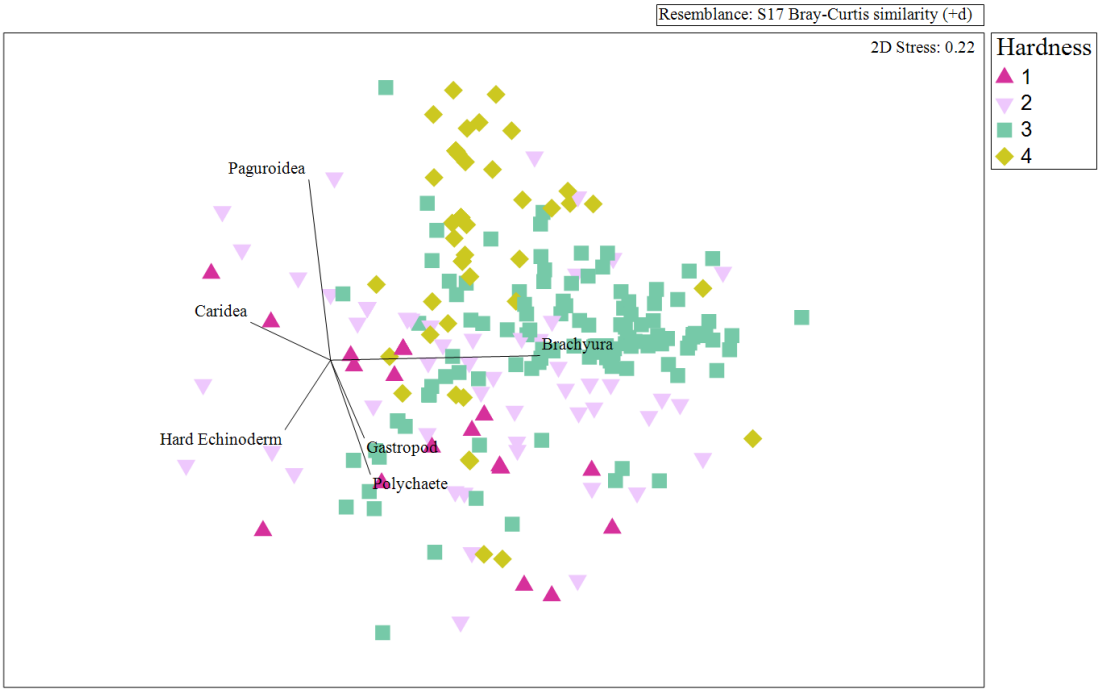

Figure 3.6: Non-Metric Multidimensional Scaling (nMDS) ordination of *C. auratus* diet for each hardness group. Analysis was completed on a Bray-Curtis dissimilarity matrix with a dummy variable of 1 added. Vector overlay of prey groups with Pearson correlations greater than 0.3.

3.3.3 Linking diet and morphology

K-means cluster analysis was successful in grouping *C. auratus* with similar diets together, with each k-means group dominated by a certain prey group. Subsequent analysis using these k-means groups as factors produced two CAPs which did not show any strong evidence of linkage between diet (i.e. k-means groups) and jaw morphology variables (plots not presented). As such, subsequent analysis focussed on assessing diet hardness as a factor in relation to jaw and tooth morphology.

The multivariate CAP ordination of jaw morphology measurements demonstrated no strong differences between *a priori* hardness groups (Figure 3.7). There was substantial overlap between all groups, the only slight variation being a concentration of a few hardness four individuals in the lower right corner (Figure 3.7). The variables with the highest Pearson correlations aligned with canonical axis 1 were the upper and lower jaw width (0.68, 0.70) and width of the biggest tooth (0.65, 0.67) (Figure 3.7). For canonical axis 2, the highly correlated variables were upper and lower jaw maximum tooth height (0.79, 0.74), distal tips (0.55) and opening in-lever ratio (0.59) (Figure 3.7). Despite the overlapping groupings, the trace test statistic from 999 permutations was significant at the 5% level, with a *p*-value of

0.001. However, the success of the leave-one-out cross-validation was low, with only a 34% success rate which indicates some minor differences between groups but not significant enough to be used to classify individuals.

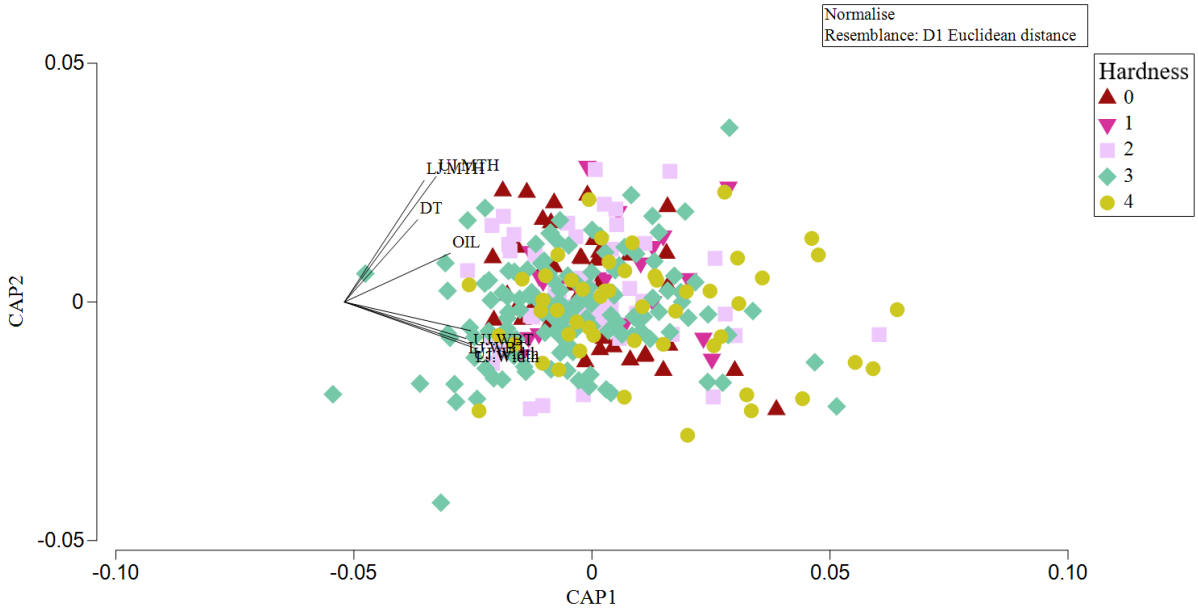

Figure 3.7: Canonical analysis of Principal Coordinates (CAP) ordination of *C. auratus* jaw morphology by dietary hardness group. Vector overlay of jaw morphology variables (abbreviations listed in table 3.1) with Pearson correlations greater than 0.55. Leave-one-out allocation success was 34%, and the squared canonical correlations for the first two canonical axes were 0.10 and 0.04, respectively.

Re-running the CAP ordination with the external Procrustes coordinates of body morphology as well as the jaw morphology measurements showed slightly better separation of dietary hardness groups (Figure 3.8). Individuals with diets classified as hardness group 4 were concentrated in the bottom right, group 3 in the bottom left, and the remainder of the groups spread across the top of the ordination (Figure 3.8). Again, the jaw and tooth width measurements (UJ.Width: 0.55, LJ.Width: 0.52, UJ.WBT: 0.54) were driving separation towards the bottom right and upper jaw maximum tooth height (0.50) in the top right (Figure 3.8). The upper jaw tooth height vector (0.5) had a similar correlation but was directly opposite to the vector for Procrustes Coordinate 45 (0.45), an x-axis forehead landmark (Figure 3.8). Vertical separation was mostly driven by two Procrustes coordinates, 40 (0.47) and 42 (0.46), which are both y-axis forehead landmarks (Figure 3.8). The vector for

Procrustes coordinate 2 (0.45), the y-axis landmark for the tip of the snout, was directly opposite the jaw width vectors (Figure 3.8).

The slightly better separation of hardness groups with the addition of external body measurements was reflected by the improvement in allocation success, up to 37% and a significant *p*-value following 999 permutations (*p*-value: 0.002). This significance demonstrated some indication that *C. auratus* morphology is linked to the hardness of their diet.

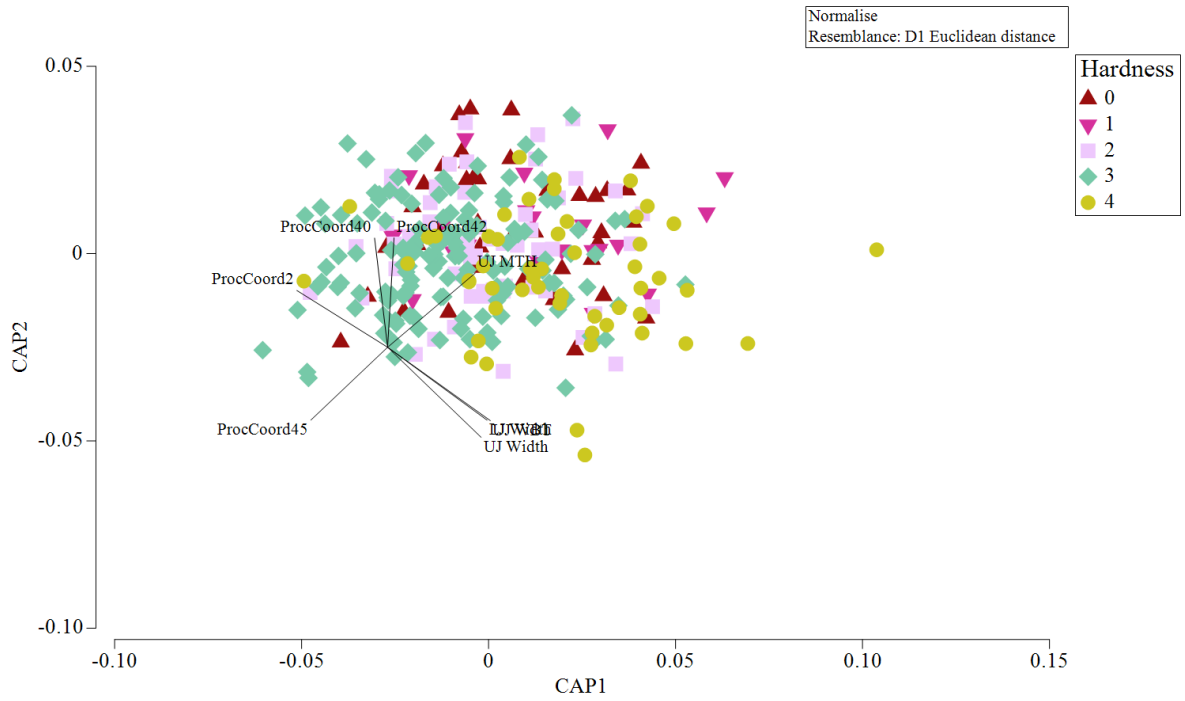

Figure 3.8: Canonical analysis of Principal Coordinates (CAP) ordination of *C. auratus* body and jaw morphology by dietary hardness group. Body morphology is represented by Procrustes coordinates. Vector overlay of variables with a Pearson correlation greater than 0.55. Leave-one-out allocation success was 37%, and the squared canonical correlations for the first two canonical axes were 0.19 and 0.08, respectively.

Box and whisker plots of fish length by each hardness group had very similar levels of spread, with medians for each hardness category just under 350mm (Figure 3.9). An ANOVA of fish length and hardness group confirmed this pattern, with no significant differences in fish length across hardness groups.

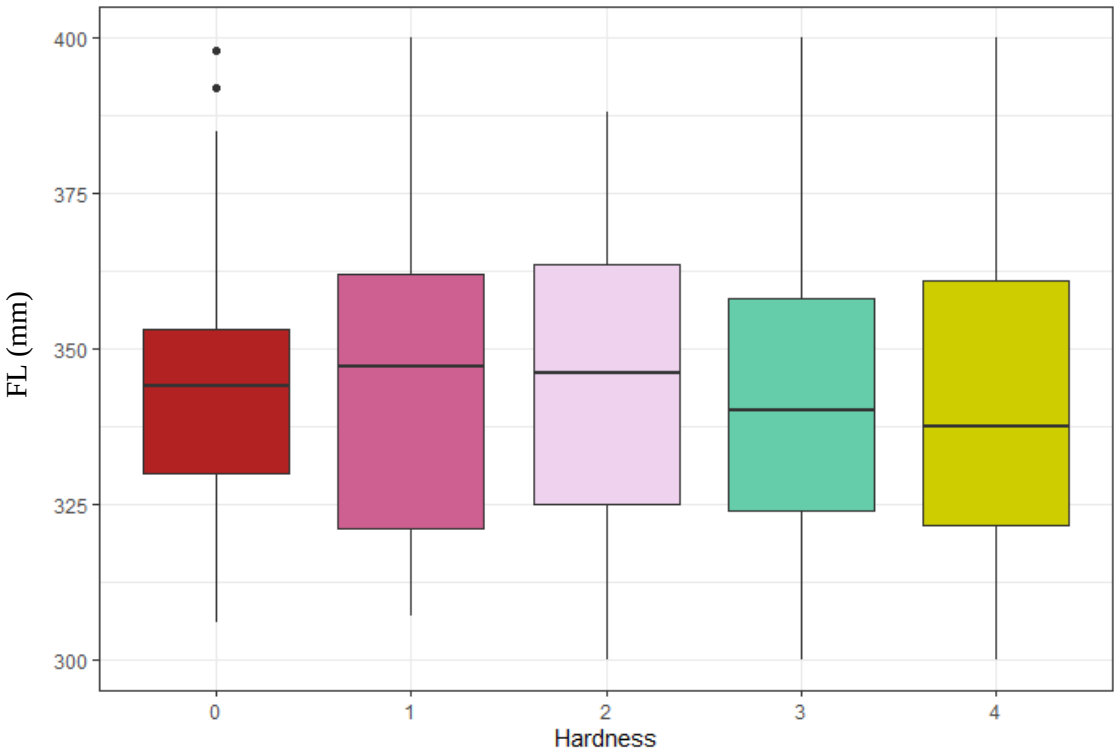

Figure 3.9: Box and whisker plots of the fork length (mm) of *C. auratus* in each hardness group. The box represents the interquartile range between 25th and 75th percentile. The line in the middle of the box represents the median and the whiskers extending from the box are 1.5* the interquartile range beyond the 25th and 75th percentile respectively

The relationship between each jaw morphology variable with hardness group was explored. *C. auratus* with a diet categorised as hardness group 4 appeared to have wider lower jaws and a wider biggest tooth from both the upper and lower jaws (Figureure 3.10). ANOVA's confirmed these differences were significant (*p*-values of 0.049, 0.013 and 0.048 for the width of the lower jaw and the width of the biggest tooth in both upper and lower jaws, respectively). The assumptions of the ANOVA were tested and met using Levene's test for homogeneity of variance and QQ-plot for normality. For each of the three jaw morphology variables assessed, Tukey's HSD tests confirmed that significant differences were associated with a difference in width between hardness groups 3 and 4.

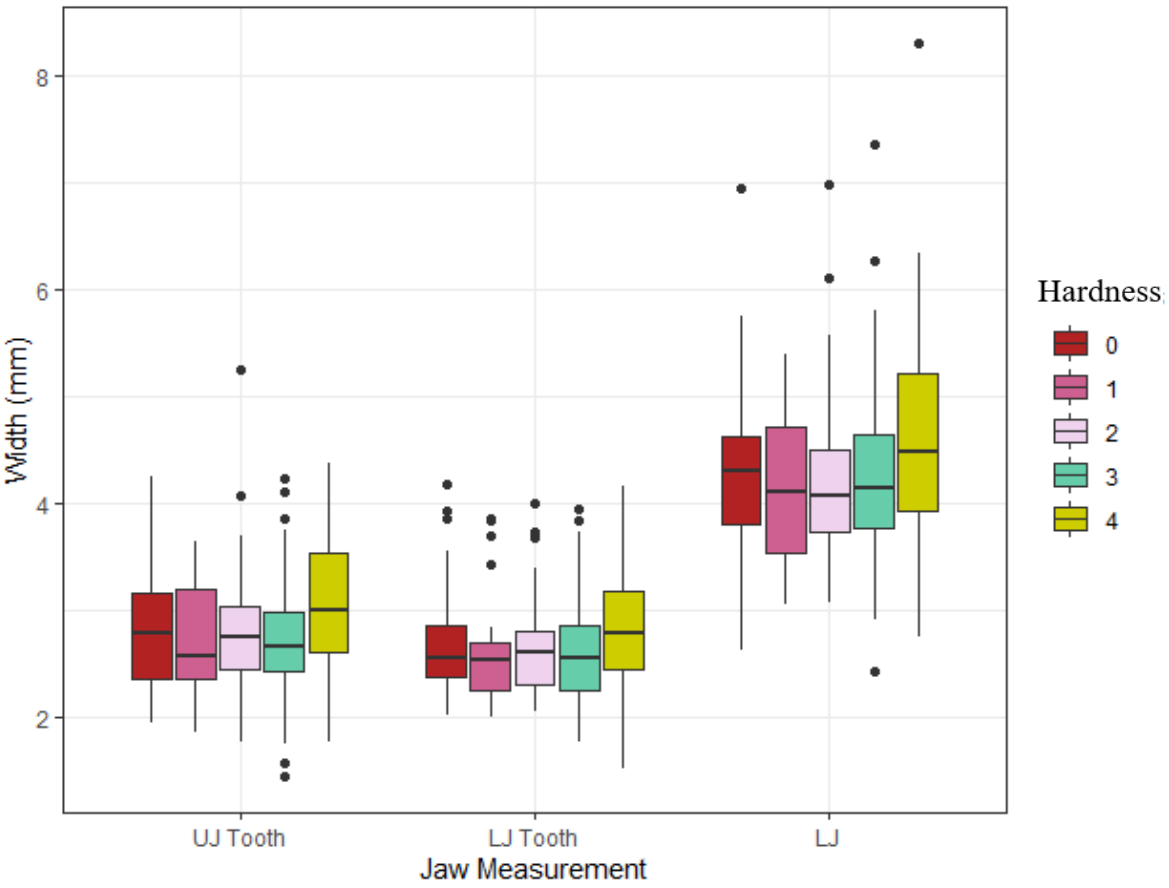

Figure 3.10: Box and whisker plots for *C. auratus* jaw measurements (Upper jaw width of the biggest tooth, lower jaw width of the biggest tooth and maximum width of the lower jaw) by diet hardness group. The box represents the interquartile range between 25th and 75th percentile. The line in the middle of the box represents the median and the whiskers extending from the box are 1.5* the interquartile range beyond the 25th and 75th percentile respectively. Only the jaw morphology variables with the most obvious differences across diet hardness groups are displayed.

3.3.4 Jaw morphology by population

The CAP ordination of jaw morphology variables by population showed some evidence of differing morphology by population, but these differences were not clear cut (Figure 3.11). The gradient between populations was primarily separated on canonical axis 1, with SNA1 populations on the right while SNA2 and SNA8 populations were further left (Figure 3.11). Along this axis, the four tooth measurements, maximum height and width of teeth on the upper and lower jaw are most responsible for driving this separation (Figure 3.11). The distal tips measurements was also a strong driver of separation, as seen by the length and direction of the vector (Figure 3.11). The opening in-lever measurement and the opening jaw lever ratio also contributed to separation, although these are separating along the y axis in a northeast direction (Figure 3.11). Because of the high overlap between groups, the success of

the leave-one-out cross-validation was poor, with a 31% classification rate. However, there was still some evidence that jaw morphology was linked to population, as the trace test statistic from 999 permutations was significant at the 5% level, with a *p*-value of 0.001.

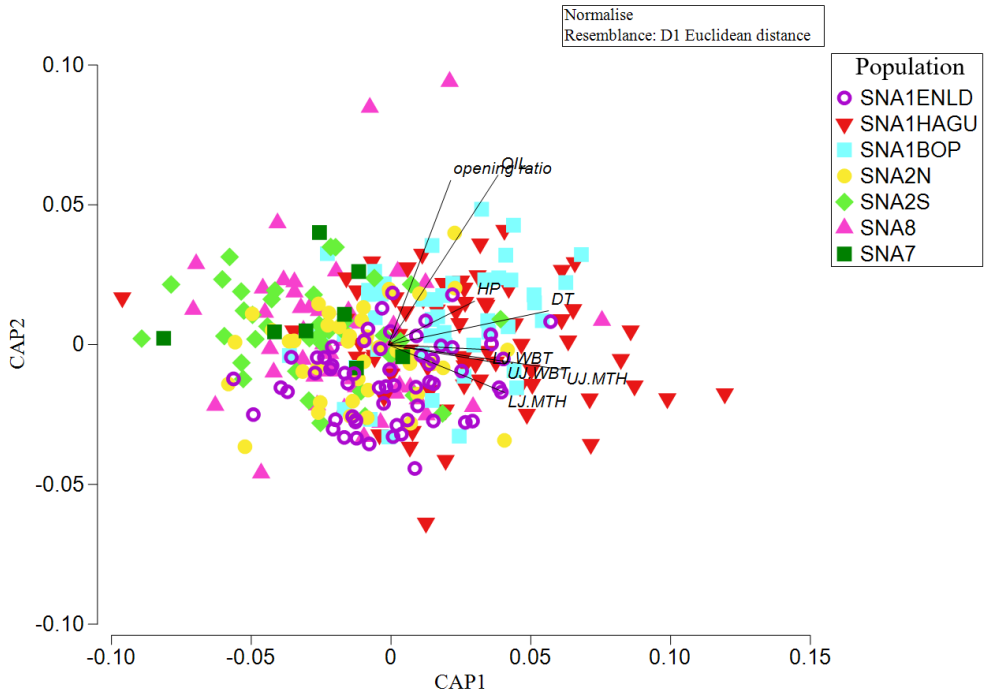

Figure 3.11: Canonical analysis of Principal Coordinates (CAP) ordination of *C. auratus* morphology by population. Vector overlay of jaw morphology variables (abbreviations listed in table 3.1) with Pearson correlations greater than 0.55. Leave-one-out allocation success was 31%, and the squared canonical correlations for the first two canonical axes were 0.34 and 0.13, respectively.

3.4 Discussion

Throughout the vertebrate subphylum, there are numerous examples of resource-based trophic polymorphisms (Skulason & Smith, 1995). Understanding links between diet and morphology within species has helped to advance knowledge of niche use, phenotypic plasticity, resource partitioning, speciation, natural selection and ecosystem interactions (Skulason & Smith, 1995). In a world faced with rapidly changing ecosystems, understanding species' ecomorphology and how they can adapt to evolving environments and resources is key to understanding their vulnerability to climate change and other anthropogenic interruptions (Oostra et al., 2018).

The present study is the first to quantify and compare *C. auratus* diet nationwide and the first comprehensive update of *C. auratus* diet in 50 years. As *C. auratus* are an important recreational and commercial species in New Zealand, understanding their ecological interactions is an important management consideration. Furthermore, in some regions, *C.*

auratus account for 90% of the fish biomass (Parsons et al., 2021), so the influence of predation exerted by *C. auratus* has the potential to be a significant structuring force on marine communities. *C. auratus* are typically labelled as generalists, as several previous studies within a set geographic range have documented a wide range of taxa in *C. auratus* diet (Usmar, 2012; Drummond, 2020; Godfriaux, 1969). The present study explored *C. auratus* diet and functional morphology with links to populations to attempt to understand whether observed dietary differences were purely down to access and opportunity or the result of optimised morphs targeting prey that they were more adept to capture and consume. Although there were some weak links between jaw morphology and the hardness of the diet, these were not substantial differences. The lack of distinct linkages between dietary hardness and morphology aligned with the variety of prey items found within individual fish. For example, 19 *C. auratus* contained seven or more different prey items in their alimentary tract at one time. One individual contained ten different items that spanned a variety of different taxonomic groupings, including teleost, soft echinoderm, paguroidea, Brachyura and polychaete. The dietary breadth not only varied across *C. auratus* as a species but also within individual *C. auratus* suggesting that they are opportunistic generalist feeders. Because of their lack of dietary specialisation, their morphology didn't appear to exhibit great plasticity to their choice in prey, nor were their morphological adaptations the sole driver of their prey choice.

3.4.1 *C. auratus* diet composition trends

The crustacean-dominant diet observed in this study is aligned with the previous literature on adult *C. auratus* diet (Usmar, 2012; Drummond, 2020; Godfriaux, 1969). Two brachyurans, in particular, appeared with surprising frequency; *Lyreidus tridentatus* (previously recorded as *L. fossor*) and *Bellidilia cheesmani* (previously reported as *Ebalia laevis*). *L. tridentatus* are a large burrowing crab belonging to a family sometimes known as "frog crabs". They have an unusual appearance for a brachyuran crab, with a carapace reaching up to 50mm in length, often more than double its width (Powell, 1949). *L. tridentatus* has club-like claws modified for digging burrows (Powell, 1949). *L. tridentatus* are frequently found with a much smaller burrowing crab *B. cheesmani* which rarely exceed 8mm in length and are sometimes referred to as "nut crabs" (Schembri, 1981; Bennett, 1964).

L. tridentatus and *B. cheesmani* made up 45% and 22% of all brachyura identified in *C. auratus* digestive tracts (Table 3.4; Ahyong, 2008). *L. tridentatus* was found in 19% of all

fish with identifiable gut contents and was found in 71% of all fish from SNA2N. *B. cheesmani* was also widely found, in 36% of all fish and 95% of *C. auratus* from SNA2S. These high occurrences meant the Brachyura prey group made up the highest proportion of *C. auratus* diet in SNA2N and SNA2S populations. *B. cheesmani* was observed in all populations, but *L. tridentatus* was only found in *C. auratus* from SNA1ENLD, SNA2S and SNA8. *L. tridentatus* is supposedly distributed around the entirety of the North Island (Ahyong, 2008) but has only once been recorded as a minor contribution to *C. auratus* diet in the Hauraki Gulf, less than 1% of overall prey (Godfriaux, 1969). In the Bay of Plenty region, Godfriaux (1974) found *L. tridentatus* was the second most abundant crab in *C. auratus* diet, following *B. cheesmani*. In the present study, it is surprising that L. tridentatus was not recorded in C. auratus diet in the SNA1HAGU and SNA1BOP populations when it was dominant in other populations and was recorded in *C. auratus* diet in these regions historically. Neither *B. cheesmani* or *L. tridentatus* have been recorded in guides of common crabs in New Zealand despite being such a large component of *C. auratus* diet (Naylor et al., 2005; Wilkins & Ahyong, 2015). This begs the question, in *C. auratus* populations where *L. tridentatus* wasn't recorded in the diet, are fish choosing other prey over *L. tridentatus* while *C. auratus* in the SNA2N population are preferentially targeting the crab, or is it a reflection of differing availability? It is possible that the distribution of *L. tridentatus* may have changed since snapper diet was assessed by Godfriaux (1974), but existing data on the distribution of benthic invertebrates, such as *L. tridentatus*, is not able to address such questions. Benthic surveys aligned with *C. auratus* sampling would help to address whether *C. auratus* in certain regions are preferentially targeting these crabs or any other specific prey.

Both *L. tridentatus* and *B. cheesmani* were benthic, sediment-dwelling species, as were many other species eaten by *C. auratus. Upogebia hirtifrons* is a small shrimp that forms complex burrows in the muddy benthos and was the third most consumed species by *C. auratus* in the present study (Sakai, 2006; Table 3.4). *Aphrodita spp* (sea mouse), the fourth most consumed species identified is a large polychaete worm, up to 12cm long (Hutchings & McRae, 1993). This worm, like many other polychaetes observed in this study, lives in sandy or muddy sediments (Tracey et al., 2011). All of the stomatopods found in *C. auratus* diet were burrowing species and many of the bivalves were also infaunal (Tracey et al., 2011). Summing the relative contribution of each of these infauna species shows that approximately 40% of *C. auratus* diet is benthic infauna. This percentage would be much higher if epibenthic species were included. Passive video documentation of *C. auratus* demonstrates a

feeding mechanism resembling ram suction feeding where they accelerate forwards, digging their snout into the benthos, presumably targeting benthic fauna (Underwood, 2022). Where *L. tridentatus* and *B. cheesmani* (or other benthic infauna) occurred in burrows in close proximity to each other, this feeding method could result in a variety of benthic associated species cooccurring in individual *C. auratus* diets, which is what was observed in the present and previous studies (Bennett, 1964). However, the gut contents of some individuals are completely dominated by one species which could be due to preferential feeding, patchiness in the distribution of species, or differences in digestibility (Binning & Chapman, 2010). Most of the time, when the dominant prey item was a benthic infauna species, the rest of the diet was also benthic associated species, but not always. The occurrence of both benthic and pelagic diet items within individual *C. auratus* suggests that they feed opportunistically, with somewhat plastic dietary choices.

3.4.2. Explanations for variation in diet by population

There are many explanations for dietary differences between populations, with differences in prey abundance and distribution at the top of the list. There is an approximate 3.5 °C difference in mean coastal sea surface temperature between the most northern and southern sites where *C. auratus* were caught in this study (Chiswell & Grant, 2018). This temperature variation may exceed the critical thermal maximum of those with low tolerances, and therefore it is expected across this large latitudinal range, prey abundance may vary and thus *C. auratus* diet due to climatic differences.

Compounding on the temperature differences, coastal New Zealand has a variety of different marine habitats *C. auratus* are associated with. Adult *C. auratus* can be found in rocky reefs, sandy or muddy, soft sediments, in harbours and estuarine habitats (Shaffer & Rovellini, 2020). In this study, 85% of fish were caught using benthic trawl, which is largely fished over soft-sediment habitats to prevent fouling of the net (Baird et al., 2015). The gear limitations, therefore, minimised the variation in habitats the fish were caught from, which was a limitation in the study, but there are still differences in soft-sediment habitat types between the region's samples. The habitats around SNA1ENLD and SNA1HAGU populations contain more reef and rocky areas compared with the regions of the SNA1BOP, SNA2S, SNA8 populations which have a sandier, muddier benthos (Jones et al., 2016; Parsons., 2021). It is also important to note that *C. auratus* from SNA1ENLD were caught by bottom longline, a method able to be fished over soft-sediment or rocky reef. While the habitat type for these

bottom longline caught fish from SNA1ENLD is unknown, it does raise a possibility that these fish could have been feeding on different prey than fish exclusively living in soft-sediment areas. *C. auratus* from SNA1ENLD had the highest dietary proportion of chitons, a rock-dwelling species, and the second-lowest proportion of polychaetes, which are typically soft-sediment associated (Figure 3.2). This diet composition indicates that some of the *C. auratus* in the SNA1ENLD population could have been feeding in a rocky reef area.

A limitation of the present study was that depth was not a standardised factor when collecting *C. auratus,* and there was considerable variation in the depth of the fishing gear. *C. auratus* can be found as deep as 200m but most typically less than 50m (Crossland, 1981). The shallowest depth *C. auratus* were caught from was in the SNA1HAGU population, in 11m of water. The deepest trawl caught *C. auratus* in 120m of water from the SNA8 population. Some of the fauna found in *C. auratus* diet have wide depth ranges, such as *Neommatocarcinus huttoni* (policeman crab) which can be found as deep as 600m. Alternatively, other prey items have a restricted range. Several of the bivalves observed in *C. auratus* diet are constrained to shallow waters, such as *Austrovenus stutchburyi* (New Zealand cockle), which can only survive down to 20m (Fisheries NZ, 2020). Community composition is likely to vary within a 100m depth gradient, and thus, some variation in individual *C. auratus* diet could be explained by variation in prey availability due to depth.

Seasonal dietary patterns in *C. auratus* have been observed, particularly over spring and summer (Drummond, 2020; Godfriaux, 1974). The primary change in *C. auratus* diet over the warmest months was an increase in the abundance of pelagic prey, particularly salps, a barrel-shaped tunicate that can join together to form large chains (Aguayo et al., 2020). Increased light and nutrient availability in spring leads to an abundance of phytoplankton, thus an abundance of food for salp (Aguayo et al., 2020), which creates the perfect environment for salp to thrive and reproduce, leading to blooms (Zeldis et al., 1995). It is unclear whether *C. auratus* feed intentionally or incidentally on salp, as salp have very little nutritional value but are repeatedly recorded as a component of *C. auratus* diet (Drummond, 2020; Godfriaux, 1969; Colman, 1972). Seven of ten of the *C. auratus* that contained salp contained no other prey groups, and six of these individuals were from the SNA1HAGU population. An additional three individuals had salp as a non-primary prey item, having also consumed benthic prey items. The combination of finding pelagic prey items as well as benthic prey in a single individual aligns with other *C. auratus* diet studies. Drummond (2020) observed an increase in salp in *C. auratus* diet in spring and summer, but this was

paired with an increase in benthic teleost prey and didn't find evidence that *C. auratus* were feeding exclusively pelagically. In the present study, one individual that ate salp also consumed polychaete, while another individual that consumed salp also ate the benthic crabs *L. tridentatus, B. cheesmani*. Historic documentation of *C. auratus* diet varying seasonally is reiterated in this study, with a higher proportion of individuals caught in the warmer seasons containing pelagic prey (Powell, 1937; Godfriaux, 1974).

As prey abundance varies seasonally, the season *C. auratus* in each population were caught needs to be considered and highlighted as a limitation of the present study. *C. auratus* in the SNA8 and SNA1HAGU population were caught in spring, *C. auratus* from SNA1BOP and SNA7 were caught in summer and *C. auratus* from SNA2N, SNA2S and SNA1ENLD were caught in autumn and winter. *C. auratus* from SNA1HAGU and SNA1BOP populations ate the highest proportion of pelagic soft prey in their diet, and SNA1BOP also had the second highest proportion of cephalod prey. This indicates that seasonality is likely a contributor of variation in *C. auratus* diet by population as individuals from certain populations had greater opportunity to feed pelagically at the time of capture which was reflected in the diet. The more pelagic, softer-bodied diet had consequences for the overall dietary hardness of *C. auratus* from the SNA1HAGU and SNA8 populations, which had the softest diets of all populations. These populations also had high proportions of individuals with no identifiable gut contents, which may be partially explained by seasonality. Softer prey items digest quicker than harder bodied prey, and if *C. auratus* were eating a more pelagic diet, it is more likely that the gut contents will be digested to an unidentifiable point than if they were eating a harder, more benthic diet (Buckland et al., 2017). Thus, there were likely more *C. auratus* individuals in this study that were feeding on salp or other soft-pelagic prey that could not be identified as such.

3.4.3 *C. auratus* dietary hardness

The dietary hardness factor successfully categorised types of diet, but there were some anomalies that arose within *C. auratus* individuals. In the hardness 4 group there was a small proportion of sessile soft prey consumed by *C. auratus* individuals and in the hardness 1 group there were small proportions of unidentified crustacea, Brachyura and gastropoda. *C. auratus* are both generalists and opportunistic in nature as a species and as individuals (Godfriaux, 1969). Even though most of an individual's diet might be composed of either harder or softer prey, they will feed on whatever is available. An opportunistic diet that spans across functional groups allows adaptability, making a species more resilient to changes in

prey availability. For example, temporal prey plasticity is demonstrated in *Coregonus lavaretus*, a generalist salmonid that predominantly eats harder benthic crustaceans but increases the proportion of pelagic soft-bodied prey consumed according to seasonal changes in resource availability (Hayden et al., 2014). Opportunistic generalist predators such as *C. lavaretus* and *C. auratus* are likely to adjust better to climate change than specialist species as the flexibility in a generalist's diet provides food security in the face of uncertainty (Sih, 2013). The adaptability in *C. auratus* diet may be a contributor to their success in coastal New Zealand, making up 90% of fish biomass in the Hauraki Gulf region (Parsons et al., 2021). Many *C. auratus* populations are increasing in biomass as stocks recover, which may have broader ecosystem effects due to the heightened predatory force (Ministry of Fisheries, 2020). Around the globe, changing abundances of predators have top-down consequences on the wider ecosystem (Baum & Worm, 2009). *C. auratus* are already understood to exert top-down control of sea urchin and algae abundance (Babcock et al., 1999) and with recovering *C. auratus* populations and potential adjustments in prey composition due to changing environmental conditions new trophic cascades may emerge.

3.4.4 Linking *C. auratus* diet and morphology

Diet patterns and specialised morphological adaptations linked to prey choices are observed in many species and certain features are recurringly important (Wainwright et al., 1991; Antonucci et al., 2009; Blasina et al., 2016). For some fish, gape is a stronger determinant of prey choice than body size, or morphology (Peterson & McIntyre, 1998), but gape wasn't ever a significant variable in this study's analyses on *C. auratus*. Parsons et al. (2015) didn't record any significant differences in *C. auratus* gape between subpopulations. The lack of difference in gape size may be a reflection of the dominance of small to moderate sized crustacea in *C. auratus* diet, as opposed to other fish which target larger teleost prey.

Another potential explanation for why distinct jaw morphologies weren't observed for each dietary hardness group could be due to the feeding mechanism *C. auratus* use to capture their prey. Some of the paguroidea and gastropoda observed in *C. auratus* stomachs, were devoid of their shell. Contrastingly, in many other *C. auratus* individuals, there were fully intact paguroidea and gastropoda shells, which were sometimes large and several centimetres long. One *C. auratus* contained 9 large, approximately 5cm long, fully intact whelks (buccinidae). The frequency of unbroken shells in the diet implies an intentional dietary choice. Unscathed shells show that the crushing capabilities of the jaw, or the size of the grinding surfaces of the

teeth weren't utilised in the capture and consumption of the hard prey. Many fish consume prey with minimal mastication but typically, fish with robust jaw bones and molariform teeth will crush prey such as gastropods and parguroidea (Norton, 1988). In several molluscivorous fish, the size of the molariform teeth can be used a predictor of the type of gastropods (and thus paguroidea) they are able to crush and consume (Hulsey et al., 2005). However, even fish with strong jaw in-levers and large molariform teeth have limits to the maximum hardness of prey they can consume (Hulsey et al., 2005). In this instance, the fish can either swallow the gastropod whole or adjust their feeding behaviour to adapt to the morphological constraints. Some cichlid fish which are limited by their jaw morphology, can suck the soft flesh from the gastropod shell (Hulsey et al., 2005). Some *C. auratus* may have learned this adaptive behaviour while others have not, potentially explaining why there were both whole gastropods and paguroidea as well as those devoid of shell. The variation in feeding mechanisms on the same prey groups within *C. auratus* would contribute to the lack of distinct jaw morphologies related to diet.

It could be expected that soft-bodied prey consumed by fish would be more masticated than hard-bodied prey due to the reduced crushing strength required. Polychaete predation by *C. auratus*, however, didn't appear to follow this logic. Many of the large onuphid polychaetes were fully intact, some of which were longer than the *C. auratus* that consumed it. In a study of feeding modes for each prey group consumed by a percoid fish, polychaetes were captured using suction ram-feeding (Luczkovich et al., 1995). Wainwright (1995) studied the feeding mode and corresponding morphologies of 34 species of Caribbean reef fishes. The study found that fish that were manipulating prey with their oral jaws had higher opening and closing jaw lever ratios than those that employed ram suctioning. The maximum opening jaw ratio observed for a fish that employs suction feeding was 0.28 and the maximum closing ratio was 0.25. In this study, the average *C. auratus* opening lever ratio was 0.35 and the closing jaw lever ratio was 0.47. These lever ratios indicate that as a species, *C. auratus* are more likely to feed using the manipulation mode, but the many fully in-tact polychaetes indicates that *C. auratus* may have also been employing the suction ram-feeding technique. The variation in *C. auratus* jaw morphology may mean individuals use different feeding modes when predating on polychaetes depending on their morphology. Additionally, if a prey item was bitten, this will likely accelerate the action of digestive enzymes, making identification of crushed polychaetes less likely. Furthermore, because there is an indication that biting apparatus were not employed in the capture of some of the hard and soft-bodied

prey groups of *C. auratus*, it explains why dietary hardness wasn't always closely related to jaw morphology. As generalist feeders, *C. auratus* are likely using a combination of feeding modes to capture prey depending on the prey they are targeting, which limits the degree of individual specialisation of the jaw.

The most important morphological variables explaining variation in dietary hardness in *C. auratus* were distal tips, opening in-lever, maximum tooth height and maximum jaw and tooth widths. The pairwise univariate analyses revealed the only significantly different variables between hardness groups were some of the width variables and only between hardness groups 3 and 4, not between the extremes of the hard to soft diet continuum. The similarity in jaw morphology between the fish consuming the hardest and softest prey indicates that the mechanisms for soft-prey predation may be different than expected. As previously discussed, the proportion of the soft pelagic prey in *C. auratus* diet was seasonally driven, and in the colder seasons, fish in the hardness 1 group might have switched to predating on harder prey, maintaining robust jaw morphology as a result. The other dominant prey in hardness groups 1 and 2 was polychaetes, which as discussed above, were often consumed whole without the use of jaws to masticate. The teleost prey group dominated hardness group 2. When capturing moderately sized teleosts, a reasonably robust jaw and leverage is needed to exert the stress necessary to incapacitate prey. The best adapted morphology for piscivorous fish is very similar to the morphological traits needed for crushing harder bodied organisms and potentially explains why there weren't significant differences in teeth and jaw width between the softest and hardest dietary groups. *C. auratus* are front-fanged macrodonts where the height of the front fangs and the width of the rear molariform teeth vary substantially. Front-fanged macrodonts can use the anterior teeth to emit high stress when capturing evasive prey (Mihalitsis & Bellwood). Following initial capture, the rounder anterior teeth are used to process and masticate prey (Mihalitsis & Bellwood). This morphology is ideal for a generalist like *C. auratus* as it enables a wide dietary breadth from soft evasive prey to hard sessile prey.

In addition to the jaw bones that provide the leverage for jaw opening and closing, the muscular and skeletal structure in the wider head region also contributes to the potential biting strength (Liem, 1967). In some fish, the profile of the head can be plastic to diet variation. The diets of two cichlid species (*Geophagus spp*) were experimentally controlled, and both developed two alternate morphs depending on diet and corresponding foraging behaviour (Wimberger, 1992). Polymorphism of the snout and head also occurs in the

mountain whitefish (*Prosopium williamsoni*), driven by dietary niche partitioning (Whiteley, 2007). The "Pinocchio" phenotype has a more upturned snout, adapted to upturn rocks to forage on benthic invertebrates, while the "normal" phenotype fed more pelagically (Whitely, 2007). Similar trophic polymorphism may be occurring in *C. auratus* as the snout landmark, Procrustes Coordinate 2, was significantly correlated with dietary hardness. The direction of the correlation shows the hardness group 3 had the most upturned snout (Figure 3.8). Variation in head profiles can also arise because of genetic variation. As *C. auratus* from different populations had both different head shapes and diet composition, the reproductive isolation between *C. auratus* populations could also be responsible for the disparity.

The length and angle of the horizontal process on the premaxilla affects the protrusion of the snout and base of the head profile (Lauder, 1982). The horizontal process was the only additional morphological variable correlated with the population groupings but not dietary hardness and indicates that reproductive isolation could contribute to snout profiles. Overall head morphology varied significantly by *C. auratus* population, and the horizontal process and associated musculature may be contributing to head shape. The driver behind variation in head shape in teleosts is largely unknown but, in some instances, has been linked to sexual selection and is a sexually dimorphic feature among several sparid species (Barlow & Siri, 1997; Minos et al., 2008; Rogers, 2014). Although the horizontal process wasn't strongly linked to dietary hardness, other head morphology variables were, suggesting that both diet and the population are compounding factors that combine to result in the observed morphological variation in *C. auratus.*

Ontogenetic diet shifts have been observed for *C. auratus,* and this study aimed to minimise some of that variation by only analysing individuals that were in the 30-40cm size range. As *C. auratus* diet diversifies with age, it is possible that the morphological response to prey choice is more pronounced in larger fish. The majority of *C. auratus* that primarily consumed teleost were above 36cm, although overall, there were no significant differences in fork length between hardness groups. If an individual *C. auratus* was categorised into the hardness 2 group, they tended to have wider and more robust jaws than the individuals that consumed Caridea or other soft prey. This indicates that jaw specialisation might only develop in larger *C. auratus.* This phenomenon of dietary niche specialisation leading to altered morphology has been observed in other fish species. The arctic charr (*Salvelinus alpinus*) is a polymorphic species where ontogenetic diet shifts cause unique jaw and external body morphologies adapted to their niche specialisation (Parsons et al., 2010; Snorrason et al., 1994). In this case,

the larger fish diversify into either a benthic or limnetic diet where the benthic group had larger heads and more robust jaws (Parsons et al., 2010; Snoorason et al., 1994). The present study showed that similar to *S. alpinus,* there were some linkages between diet and head, jaw and teeth morphology, but expanding this study to include larger individuals may show more marked differences.

3.5 Conclusions

Intraspecific functional diversity is an important component of biodiversity and ecosystem functioning (de Bello et al., 2011). Understanding how species and individuals utilise resources across a range of environments and populations will help predict responses to stressors such as climate change or fishing pressure (Beukhof et al., 2019). This study was the first to investigate and compare the diet and functional morphology of an exploited, ecologically important fish, *C. auratus,* across its range in New Zealand. *C. auratus,* as both individuals and as a species, consumed a wide and varied diet. They most frequently consumed crustaceans but also ate polychaetes, echinoderms, molluscs and teleosts. The diet of an individual *C. auratus* could be broadly classified into one of four hardness groups, which allowed links to be drawn between diet and morphology. There were some weak correlations between dietary hardness and certain jaw morphology variables such as jaw width, tooth width and lever ratios which were important determinants in the crushing strength of an individual's jaws. However, because of the diverse diet within a *C. auratus* individual, one fish may eat prey from both extremes of a dietary category- hard and soft prey or benthic and pelagic prey. The jaw mechanics involved in catching and consuming this prey is typically different, and there was evidence that even within a prey group, different *C. auratus* were processing the food in alternate ways. Additionally, for each population of *C. auratus,* there were differences in the abundance of different types of prey, such as the seasonal increase in soft pelagic prey for SNA1HAGU, SNA1BOP, SNA8 and SNA7. The variation in diet, proportions in the abundance of prey for each population and the mechanism of consuming prey all interact to minimise strong linkages between morphology and diet. The opportunistic, generalist nature of *C. auratus* means although their morphology may be most adapted to consume a certain type of prey, it doesn't restrict them from eating outside of their ideal niche and thus aren't an ecomorphological specialist.

This study has added to the body of research demonstrating linkages between the diet and morphology of fish to understand patterns in intraspecific variation and ecomorphology. The functional morphology of *C. auratus* showed similarities to many other species around the

globe, such as *C. lavaretus, Geophagus spp* & *Prosopium williamsoni* (Hayden et al., 2014; Wimberger, 1992; Whiteley, 2007). It was revealed that *C. auratus* are a polymorphic species, with polymorphism demonstrated between and within populations, likely driven by diet choices. The advanced knowledge of the dietary breadth and functional morphology of *C. auratus* has improved ecomorphological understanding, allowing improved management of this ecologically crucial and commercially, culturally and recreationally valuable species.

Chapter Four. General discussion

4.1 Thesis aims

This study aimed to understand the functional morphology of *C. auratus* to identify population structure and ecomorphological interactions of this highly valued species. There was evidence of morphological variation in body shape and otolith structure within identified populations. Nearly all populations were significantly different from one another. In general, the northeast populations, SNA1HAGU, SNA1BOP and SNA1ENLD, had narrower bodies, a more protruding snout, and a larger mouth and eyes than the southern and western populations SNA2S, SNA7 and SNA8. The morphology of *C. auratus* in the SNA2N population appeared to represent a convergence point, aligned with the previously identified genetic connectivity (Papa et al., 2021), where their body shape was in the middle of the spectrum between the average north eastern and south western morphology. New Zealand *C. auratus* morphology was significantly different to Australian *C. auratus* populations, although the NSW and Eastern NZ stocks were most similar, potentially as a result of periodic gene flow between the two over the last 400,000 years (Briggs & Bowen, 2013). In New Zealand, the otolith morphological variation was most pronounced in the thickness of the otoliths, which is likely reflective of differences in the somatic growth rates for each population. As such, the body and otolith morphological differences detailed here highlight the population structure of *C. auratus* and provide evidence of the management units that would be most appropriate to ensure sustainable exploitation and preserve intraspecific biodiversity.

Analysing dietary patterns showed how the resource use of *C. auratus* interacts with the environment. The diet of *C. auratus* was largely benthic associated, with the most frequent prey group being crustaceans, but molluscs, polychaetes and teleosts were also significant components of the diet. Individual niche partitioning and preferences were observed, for example, the many fish whose diet was dominated by the brachyuran crabs *L. tridentatus* and *B. cheesmani*. The hardness of the diet was linked with certain jaw and body shape features, particularly jaw and teeth widths and snout protrusibility, indicating in *C. auratus,* aspects of their morphology are functionally driven. The wide variation in functional morphology observed within and between populations highlights the generalist nature of *C. auratus* which results in significant intraspecific variation. Conserving the intraspecific variation for ecosystem functioning and the health of the *C. auratus* species should be a priority.

4.2 Environmental and ecological changes

At present, at least a third of all fish stocks globally are overfished, and a substantial proportion of ocean habitats are threatened by warming temperatures, acidification, pollution and eutrophication (Duarte et al., 2020). Marine management targets such as the United Nations Sustainability Goal 14, which aims to conserve the world oceans for sustainable use, is facilitating the recovery of marine ecosystems (Virto, 2018). For many marine species, recovery is possible once stressors are reduced or removed, and as there is a shift towards more sustainable fisheries and mitigating climate change effects, there is a potential for wide-scale restoration of marine ecosystems by 2050 (Duarte et al., 2020). Understanding the ecomorphology of key, recovering species will aid managers in predicting how ecosystems and communities might change throughout this process. For *C. auratus*, biomass in most areas is increasing, and population sizes are larger than they have been in several decades (Fisheries NZ, 2020). Larger *C. auratus* populations will invoke increased predation pressure, and as such, the wider ecosystem is likely to be affected. When *C. auratus* biomass is low, trophic cascades of rocky reefs have been observed (Babcock et al., 1999). With reduced *C. auratus* predation pressure on sea urchins, urchin biomass increases and overgraze the kelp forests, leaving urchin barrens devoid of macroalgae (Shears & Babcock, 2002). In areas where fishing pressure is removed using marine protected areas, *C. auratus* population sizes can increase, reversing the trophic cascade and restoring the macroalgal forest (Shears & Babcock). Similar ecosystem changes may occur outside of marine protected areas as *C. auratus* biomass increases.

This study has improved understanding of *C. auratus* diet choices and some of the mechanisms that contribute to prey choices across populations, such as jaw levers, teeth width and snout protrusion. *C. auratus* being generalist feeders by nature with non-specialist morphology means that the increased predation pressure due to population recovery is likely to be spread across the ecosystem, but species that appeared to be preferentially targeted by *C. auratus* may be especially impacted, such as *L. tridentatus* and *B. cheesmani*. For recovering species, ecomorphological studies may identify preferred prey, and if the preferred prey exerts strong pressure on community structure, managers should be aware of the flow-on effects recovery may have. Particularly if species are specialist and their narrow dietary niche could cause a resource to be depleted and have negative effects on the wider ecosystem, recovery and strengthening of prey populations would need to coincide with predator recovery.

In roughly the last half a century of heavy exploitation of many fish stocks, significant biodiversity loss has occurred across communities, populations and intraspecifically within populations (Des Roches et al., 2021). Ignoring intraspecific diversity in fisheries management can contribute to localised depletions of populations or morphs that are more vulnerable to stressors (Kerr et al., 2014). For fish such as *C. auratus* that are caught using nets, deeper bodied fish are disproportionately retained by the fishing gear. Stouter body profiles in fish are typically associated with a more benthic, lower-trophic level diet, and this was seen in *C. auratus.* Fish in the SNA2S population had a deeper body overall and, as a population, consumed a highly benthic, lower trophic level diet than *C. auratus* in the SNA1HAGU and SNA1BOP populations which were the slenderest fish overall and consumed a more pelagic, higher trophic level diet. If deep-bodied *C. auratus* that fill a unique dietary and functional niche continue to be disproportionately targeted, this may have consequences for the ecosystem. As populations recover, if more slender-bodied, high-trophic, pelagic fish are available to reproduce, there will be increased demands on the corresponding prey than before intraspecific biodiversity loss occurred. Ensuring management units account for such intraspecific biodiversity and variation is conserved should minimise adverse ecosystem effects and retain much-needed population complexity (Cadrin, 2020).

In many areas where fish population recovery is occurring, there is a corresponding increase in ocean temperatures (Johnson & Lyman, 2020). As most fish are ectotherms, their physiology is at the mercy of the external environment, and rising temperatures raise energetic demands, which results in increased feeding rates (Sokolova & Lannig, 2008). The combined effects of increased biomass and energetic demands increases intraspecific competition and fish are likely to be forced to exploit new food sources (Svanbäck & Bolnick, 2007). Increased competition for food is known to drive ecomorphological specialisation as the morphs most advantaged for selecting specific prey succeed over the more generalist morphs (Svanbäck & Bolnick, 2007). In *C. auratus,* increased competition may result in more pronounced dietary divergence and further resource-driven polymorphisms within and between populations. Warming temperatures and increased competition for resources is causing range expansion of species globally (Wernberg et al., 2011), and there is evidence of southward range expansion occurring in *C. auratus* (Fisheries NZ, 2020). As fish move into new ecosystems, new prey types will become available and new trophic cascades or morphological adaptations may emerge. Additionally, temperature

changes are facilitating the rise of marine invasive species as well as native prey availability, which impacts ecosystem composition (Havel et al., 2015). The present study documented *C. auratus* consumption of the invasive mantis shrimp *Oratosquilla oratoria,* and as the biomass of *O. oratoria* and other invasive species increases in New Zealand, it is likely they will become a more significant proportion in *C. auratus* diets. Predicting with certain how an ecosystem will respond to the increased abundance of a new aquatic predator is impossible but understanding the ecomorphology of a species prior to range expansion is likely to provide some insight (Winemiller, 1991). As this study required *C. auratus* collection from areas guaranteed to get a sufficient sample size, samples weren't concentrated near the limits of their range. Future studies on *C. auratus* diet and functional morphology at the southern extremities of the range would help scientists understand how *C. auratus* are responding to climate change and predict the effects on southern ecosystems with the arrival of *C. auratus*.

4.3 Future directions

This study investigated polymorphism over large geographic areas that incorporated many different fine-scale habitat differences. When focussing on specific areas, further fine-scale polymorphism and population structure of *C. auratus* is revealed, as was observed in the Hauraki Gulf, South Australia and Shark Bay (Parsons et al., 2015; Rogers, 2014; Moran et al., 1998). The present study aimed to identify populations of *C. auratus* using morphological and functional morphological markers, but there was no attempt to reveal smaller groups within these populations, only to identify the interpopulation biodiversity. The areas sampled were mostly offshore, coastal areas, but different diets and associated morphology may have been identified if inshore, inner harbour and/or estuarine habitats were sampled. These habitats expose fish to different environmental conditions such as increased habitat complexity, turbidity, eutrophication, and salinity variation (Borland et al., 2017). Additionally, prey assemblages are likely to differ from the further offshore communities, with inner-harbour habitats more dominated by polychaetes and estuaries typically having an abundance of bivalves. As observed in the present study, these diet choices can have corresponding changes in morphology as they require different feeding mechanisms. Turbidity reduces the predation success of fish that use visual cues to detect evasive prey (Higham et al., 2015), so fish can either adapt and, over generations, evolve larger eyes and alternate prey detection methods or, in the case of a generalist, switch to consuming less evasive prey. As described in this thesis, the morphology best adapted for consuming evasive prey is narrow caudal peduncles and streamlined body profiles, but a corresponding

morphology switch in inner harbour and estuarine environments may result in fish with smaller mouths and larger tooth-bearing surfaces to consume the benthic, sedentary prey (Antonucci et al., 2009). Both abiotic and biotic factors that change across environments interact, resulting in intraspecific ecomorphological differences and future measurements to quantify phenotypic variation in *C. auratus* would uncover how environmental factors shape morphology in the species.

Many fish continue to grow throughout their life, and in order to keep up with the energy demands that come with increased size, ontogenetic shifts in dietary niche can occur (Johansson et al., 2006). To increase foraging efficiency to fit the new niche, it's expected that corresponding changes in morphology will occur (Johansson et al., 2006). This phenomena is observed over many aquatic vertebrates, including the study species of this thesis (Searle et al., 2021; Davis et al., 2011; Rogers, 2014). Otolith discrimination and head morphology differences were more pronounced in South Australian *C. auratus* that were larger than 450mm (Rogers, 2014). To date, morphological studies of *C. auratus* in New Zealand have been limited to 400mm (Parsons et al., 2015). *C. auratus* fecundity is exponentially linked to body size, where a 50cm individual produces approximately five times more eggs than a 30cm fish (Crossland, 1977). These large fish play a vital role in the population sizes of *C. auratus,* so ensuring we understand how they interact and may be affected by environmental changes is crucial for the sustainability of the species. Thus, investigating ontogenetic shape changes and ecomorphology of large *C. auratus* should be addressed in future research.

4.4 Implications and conclusions

Being able to identify the area a fish came from using GM has the potential to affect fisheries compliance. "Trucking" is the process where fish are caught from one management area but declared as being from another area to get around quota limits (Broadmore, 2010). Compliance offers can use vessel tracking to help identify where a boat has been fishing in relation to where they declare their catch, but as fishing trips often span multiple areas, there is an opportunity to mix and match where the fish were caught. Additionally, more marine protected areas with fisheries restrictions are being established globally, and preventing illegal, unreported and unregulated (IUU) fishing is a priority area of fisheries management (Canty et al., 2018). Morphometrics is a cost-effective screening tool that can be used in conjunction with vessel tracking to identify the origin of the fish (Canty et al., 2018). As automated technologies increase, this process could become even quicker, instantaneously

screening a sample of fish as they are landed. If this tool was successfully enacted, it would revolutionise global fisheries compliance, making strides towards eliminating IUU fishing (Canty et al., 2018).

The results of this thesis have implications for *C. auratus* management in New Zealand. Analyses of productivity measures have indicated that there is a mismatch between population and management units (Fisheries NZ, 2020), and the present study has provided more evidence to suggest this is true. Ecomorphological differences were apparent in the three populations within the current SNA 1 stock. The ecomorphological disparity between *C. auratus* in the northern and southern region of the SNA2 stock supports the claim these are two separate management units and should be assessed and managed as such. Some of the morphological differences revealed have direct applications for fisheries, such as the population differences in body depth, which should be taken into consideration when setting minimum mesh sizes of trawl nets in each area. Advanced understanding of how *C. auratus* are adapted to utilise different resources and, in turn, interact with the ecosystem helps predict how the species might respond to future changes in resources and environments due to climate change. In summary, significant intraspecific ecomorphological variation is apparent in *C. auratus.* Different populations demonstrate unique ecomorphological functioning, and to conserve this precious biodiversity and wider ecosystem functioning, this variation should be protected using appropriately matched management units (Kerr et al., 2014; Ying et al., 2011).

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Appendix

Appendix: Gut contents of each individual New Zealand *C. auratus* identified to the lowest practical taxonomic level using the relative-fullness method. Information on the population retrieved from, digestive state from 0-5 (zero being completely undigested, five being fully digested) and average fullness of the gut are also listed.

Population	Digestive	Avg fullness	Prey 1	%	Prey 2	%	Prey 3	%	Prey 4	%	Prey 5	%	Prey 6	%	Prey 7	%	Prey 8	%	Prey 9	%	Prey 10	%
SNA8	5	1	Caridea	90	Shrimp	10																
SNA8	5	1.5	Decapod	100																		
SNA8	3	2.5	Paguroidea	100																		
SNA8	4	1.5	Paguroidea	80	*Bellidilia cheesmani*	10	Polychaete	10														
SNA1 HAGU	5	2	Meiura	100																		
SNA1 HAGU	3	7.5	Sessile soft tissue	90	*Evechinus chloroticus*	4	Meiura	3	Amphipod	3												
SNA1 HAGU	3	2	Sabellida	33	Decapod	33	Gastropod	34														
SNA1 HAGU	5	2	Brachyura	100																		
SNA1 HAGU	4	2	Paguroidea	100																		
SNA1 BOP	2	6	Ophiurida	60	Decapod	24	Polychaete	10	Sabellida	3	Paguroidea	3	Gastropod	4								
SNA1 BOP	4	2	Decapod	62	Paguroidea	23	Brachyura	15														
SNA1 BOP	5	2.5	Onuphidae	95	Decapod	5																
SNA1 BOP	4	4	Ophiurida	55	Isopod	33	Holothuroidea	12														
SNA1 BOP	5	4.5	Ophiurida	48	Decapod	48	Holothuroidea	4														
SNA8	0	8	Polychaete	41	Decapod	35	Ophiurida	23	Amphipod	1												

Population	Digestive	Avg fullness	Prey 1	%	Prey 2	%	Prey 3	%	Prey 4	%	Prey 5	%	Prey 6	%	Prey 7	%	Prey 8	%	Prey 9	%	Prey 10	%
SNA8	0	6.5	Onuphidae	88	Gastropod	12																
SNA8	0	6	Polychaete	80	Decapod	16	Gastropod	4														
SNA8	5	1.5	Decapod	79	Polychaete	9	Bivalve	7	Paguroidea shell	3	Ophiuroidea	2										
SNA8	0	6	*Trachurus spp*	40	Polychaete	40	*Atrina zelandica*	12	Paguroidea	4	Sabellida	4										
SNA1 HAGU	5	5	NA																			
SNA1 HAGU	4	1.5	Brachyura	100																		
SNA1 HAGU	4	4	Mytilidae	100																		
SNA1 HAGU	3	5	*Trachurus spp*	100																		
SNA1 HAGU	1	7	*Coelorinchus spp*	100																		
SNA1 HAGU	4	2.5	Ascidian	100																		
SNA8	5	2.5	Gastropod	100																		
SNA8	5	1	NA																			
SNA1 BOP	5	1.5	NA																			
SNA1 BOP	0	5.5	Octopoda	55	Paguroidea	34	Polychaete	5	Brachyura	5	Ascidian	1										
SNA1 BOP	3	4	Paguroidea	95	Gastropod	5																
SNA8	2	2	Paguroidea	100																		
SNA8	4	1.5	Paguroidea	80	*Turritellidae*	20																
SNA1 HAGU	3	4.5	Paguroidea	100																		
SNA1 HAGU	5	0.5	NA																			
SNA1 HAGU	2	4	*Upogebia hirtifrons*	100																		

Population	Digestive	Avg fullness	Prey 1	%	Prey 2	%	Prey 3	%	Prey 4	%	Prey 5	%	Prey 6	%	Prey 7	%	Prey 8	%	Prey 9	%	Prey 10	%
SNA1 HAGU	4	2	*Upogebia hirtifrons*	100																		
SNA1 HAGU	3	1.5	Salpidae	100																		
SNA1 HAGU	1	7	*Upogebia hirtifrons*	100																		
SNA1 BOP	4	2	Paguroidea	100																		
SNA1 BOP	2	4	Paguroidea	99	Caridea	1																
SNA1 BOP	1	2.5	Paguroidea	34	Brachyura	28	*Scolecenchelys australis*	27	Polychaete	8	Tunicate	3										
SNA1 BOP	3	2.5	*Nectocarcinus spp*	70	Paguroidea	20	Caridea	10														
SNA1 BOP	5	1.5	Meiura	66	Brachyura	34																
SNA1 BOP	0	6.5	*Cepola haastii*	54	Octopoda	27	*Aphrodita spp*	10	Paguroidea	9												
SNA1 BOP	5	1	Brachyura	50	Paguroidea	50																
SNA1 HAGU	0	3	*Upogebia hirtifrons*	60	Gastropod	20	Bryozoan	20														
SNA1 HAGU	3	2	Salpidae	100																		
SNA1 HAGU	1	5.5	Paguroidea	40	Bivalve	30	Ostreidae	25	Porifera	5												
SNA1 HAGU	5	0.5	Brachyura	100																		
SNA1 HAGU	5	1	Salpidae	100																		
SNA1 HAGU	5	1	Salpidae	100																		
SNA1 HAGU	5	2	Paguroidea	60	Bivalve	40																
SNA8	3	1	*Nectocarcinus spp*	100																		
SNA8	1	4	Brachyura	100																		

Population	Digestive	Avg fullness	Prey 1	%	Prey 2	%	Prey 3	%	Prey 4	%	Prey 5	%	Prey 6	%	Prey 7	%	Prey 8	%	Prey 9	%	Prey 10	%
SNA8	5	2	Brachyura	100																		
SNA8	3	1.5	Paguroidea	100																		
SNA8	5	1.5	NA																			
SNA8	2	5.5	*Atrina zelandica*	75	Paguroidea	20	Ophiurida	5														
SNA8	1	2	Teleost	100																		
SNA8	2	3.5	Polychaete	30	*Nectocarcinus spp*	20	*Bellidilia cheesmani*	15	*Aphrodita spp*	15	*Neommatocarcinus huttoni*	15	Paguroidea	8	Ophiurida	3	Gastropod	2				
SNA1 BOP	0	5.5	*Gnathophis habenatus*	95	Meiura	5																
SNA1 BOP	5	3	Paguroidea	50	Salpidae	47	Caridea	3														
SNA1 BOP	0	5.5	*Fellaster zelandiae*	40	Echinoidea	40	Gastropod	10	Paguroidea	5	Brachyura	5										
SNA1 BOP	4	4.5	Sessile soft tissue	45	Brachyura	25	Paguroidea	16	*Aphrodita spp*	14												
SNA1 BOP	3	6	Paguroidea	75	Ophiurida	25																
SNA1 BOP	5	2.5	NA																			
SNA1 BOP	5	2	Paguroidea	100																		
SNA1 BOP	5	3	Brachyura	100																		
SNA1 BOP	1	3.5	*Pariliacantha georgeorum*	55	Paguroidea	35	Brachyura	8	Sabellida	2												
SNA1 BOP	5	2.5	Crushed shell particles	100																		
SNA1 BOP	3	2.5	Gastropod	97	Decapod	3																
SNA1 BOP	4	2	Teleost	57	Caridea	28	Brachyura	15														
SNA1 BOP	0	7.5	Moridae	73	Paguroidea	25	Teleost	2														

Population	Digestive	Avg fullness	Prey 1	%	Prey 2	%	Prey 3	%	Prey 4	%	Prey 5	%	Prey 6	%	Prey 7	%	Prey 8	%	Prey 9	%	Prey 10	%
SNA1 BOP	1	3	Ophiurida	80	Sabellida	20																
SNA1 HAGU	5	1	NA																			
SNA1 HAGU	2	4	*Upogebia hirtifrons*	75	Brachyura	25																
SNA1 BOP	5	4.5	Paguroidea	100																		
SNA1 HAGU	4	2	Caridea	100																		
SNA1 HAGU	4	2	*Austrovenus stutchburyi*	80	*Philine spp*	20																
SNA1 HAGU	5	1	NA																			
SNA1 HAGU	5	1	NA																			
SNA1 HAGU	4	1.5	Brachyura	100																		
SNA1 HAGU	5	2.5	NA																			
SNA1 HAGU	3	4.5	Paguroidea	95	*Bellidilia cheesmani*	5																
SNA1 HAGU	4	6.5	Salpidae	100																		
SNA1 BOP	3	3	Soft echinoderm	95	Decapod	5																
SNA1 BOP	3	2.5	*Stichopus mollis*	25	Salpidae	25	Tunicate	18	Polychaete	12	Paguroidea	10	Brachyura	10								
SNA1 BOP	5	0.5	NA																			
SNA1 BOP	5	1.5	Caridea	55	Bivalve	45																
SNA1 BOP	4	2	Paguroidea	48	*Bellidilia cheesmani*	48	Holothuroidea	4														
SNA1 BOP	5	1.5	Paguroidea	60	*Gnathophis habenatus*	40																

Population	Digestive	Avg fullness	Prey 1	%	Prey 2	%	Prey 3	%	Prey 4	%	Prey 5	%	Prey 6	%	Prey 7	%	Prey 8	%	Prey 9	%	Prey 10	%
SNA1 BOP	5	1	NA																			
SNA1 BOP	5	4.5	Paguroidea	45	*Urechis novaezealandiae*	45	Ophiurida	6	Caridea	4												
SNA1 HAGU	4	2	*Xenostrobus neozelanicus*	60	Meiura	40																
SNA1 HAGU	1	4.5	Marginella	90	Ophiurida	10																
SNA1 HAGU	1	4.5	*Nectocarcinus spp*	90	Paguroidea	5	*Bellidilia cheesmani*	5														
SNA1 HAGU	5	1.5	NA																			
SNA1 HAGU	3	4	Paguroidea	77	Caridea	23																
SNA1 HAGU	1	3.5	*Aphrodita spp*	54	Meiura	20	Brachyura	10	*Scolecenchelys australis*	10	*Philine spp*	3	Paguroidea	3								
SNA1 HAGU	0	4	Paguroidea	65	Brachyura	14	Tunicate	14	*Bellidilia cheesmani*	4	Bivalve	3										
SNA1 HAGU	0	3	Brachyura	30	*Nectocarcinus spp*	20	*Bellidilia cheesmani*	20	*Aphrodita spp*	12	Paguroidea	10	Caridea	8								
SNA1 HAGU	0	3.5	Brachyura	60	*Aphrodita spp*	30	*Hymenosomatidae spp*	10														
SNA1 HAGU	0	2.5	*Bellidilia cheesmani*	45	Sabellida	38	Paguroidea	17														
SNA1 HAGU	3	2	Paguroidea	60	*Philine spp*	25	Caridea	15														
SNA1 HAGU	5	1	NA																			
SNA1 HAGU	5	4.5	NA																			
SNA1 HAGU	2	4.5	Paguroidea	100																		
SNA1 HAGU	1	7	Paguroidea	76	*Upogebia hirtifrons*	13	*Bellidilia cheesmani*	6	Caridea	2	Bivalve	2	Bryozoan	1								
SNA1 HAGU	2	2.5	Decapod	50	Paguroidea	17	*Bellidilia cheesmani*	17	Brachyura	8	*Hymenosomatidae spp*	4	Caridea	4								

Population	Digestive	Avg fullness	Prey 1	%	Prey 2	%	Prey 3	%	Prey 4	%	Prey 5	%	Prey 6	%	Prey 7	%	Prey 8	%	Prey 9	%	Prey 10	%
SNA1 HAGU	2	3	Heterodonta	66	Portunidae	22	*Upogebia hirtifrons*	12														
SNA1 BOP	1	4.5	Ophiurida	100																		
SNA1 BOP	4	3.5	Caridea	100																		
SNA1 BOP	5	2	Ophiurida	60	Paguroidea	40																
SNA1 BOP	2	2	Paguroidea	95	Gastropod	5																
SNA1 BOP	1	5	Teleost	60	Salpidae	30	Polychaete	7	Decapoda	3												
SNA1 BOP	4	3	Ophiurida	100																		
SNA1 BOP	4	3.5	Paguroidea	50	Ophiurida	40	*Gnathophis habenatus*	8	Sabellida	2												
SNA2S	0	6.5	Inachidae	28	Brachyura	20	*Nectocarcinus spp*	15	*Macrophthalmus hirtipes*	15	Paguroidea	14	*Bellidilia cheesmani*	5	*Philine spp*	3						
SNA2S	0	5.5	Brachyura	55	Portunidae	18	*Aphrodita spp*	17	*Hymenosomatidae spp*	6	*Bellidilia cheesmani*	2	Tunicate	2								
SNA2S	1	6	Meiura	36	*Hymensomatidae spp*	30	*Bellidilia cheesmani*	18	Paguroidea	8	*Philine spp*	4	Majidae	4								
SNA2S	3	5.5	Paguroidea	40	Meiura	17	Brachyura	12	*Hymenosomatidae spp*	12	Holothuroidea	8	*Bellidilia cheesmani*	6	Polychaete	5						
SNA2S	0	4.5	Brachyura	40	*Hymensomatidae spp*	15	Portunidae	14	*Talochlamys zelandiae*	13	*Bellidilia cheesmani*	7	Chitonidae	6	*Philine spp*	5						
SNA2S	1	4	Portunidae	55	Brachyura	25	*Bellidilia cheesmani*	7	*Hymenosomatidae spp*	7	*Philine spp*	4	Paguroidea	2								
SNA2S	1	4.5	Meiura	33	Paguroidea	25	Majidae	17	*Hymenosomatidae spp*	9	*Bellidilia cheesmani*	8	*Philine spp*	8								
SNA2S	1	3.5	*Stichopus mollis*	33	Paguroidea	32	*Bellidilia cheesmani*	16	Brachyura	12	Ophiuroidea	3	Sabellida	3	Hymenosomatidae spp	1						
SNA2S	1	4	*Nectocarcinus spp*	33	Talochlamys zelandiae	23	Chitonidae	23	*Cellana radians*	11	Brachyura	6	Majidae	2	Polychaete	2						
SNA2S	2	7.5	*Philine spp*	28	Teleost	26	Pedinae	18	Polychaete	8	*Bellidilia cheesmani*	7	Brachyura	7	*Upogebia hirtifrons*	5	Sabellida	1				

Population	Digestive	Avg fullness	Prey 1	%	Prey 2	%	Prey 3	%	Prey 4	%	Prey 5	%	Prey 6	%	Prey 7	%	Prey 8	%	Prey 9	%	Prey 10	%
SNA2S	3	4.5	Decapod	48	Paguroidea	30	Brachyura	10	*Bellidilia cheesmani*	10	Polychaete	2										
SNA2S	0	6.5	Teleost	40	Stichopus mollis	30	Portunidae	8	*Aphrodita spp*	6	Decapoda	5	*Bellidilia cheesmani*	5	*Philine spp*	3	Polychaete	1	Sabellida	1	Paguroidea	1
SNA2S	2	5	Decapod	47	*Bellidilia cheesmani*	37	Teleost	10	Paguroidea	6												
SNA2S	0	6	*Bellidilia cheesmani*	23	Decapod	20	*Nectocarcinus spp*	15	Polychaete	15	Paguroidea	13	Majidae	6	*Stichopus mollis*	6	Sabellida	2				
SNA2S	0	7	Octopoda	70	*Nectocarcinus spp*	20	*Bellidilia cheesmani*	8	Paguroidea	2												
SNA2S	3	5	*Bellidilia cheesmani*	40	Paguroidea	31	*Stichopus mollis*	10	*Philine spp*	8	Chitonidae	6	Sabellida	5								
SNA2S	3	3	Octopoda	50	Meiura	24	Portunidae	10	Polychaete	10	Pedinae	6										
SNA1 HAGU	4	1.5	Paguroidea	100																		
SNA1 HAGU	4	1.5	*Upogebia hirtifrons*	94	Bivalve	5	*Bellidilia cheesmani*	1														
SNA1 HAGU	5	1.5	NA																			
SNA1 HAGU	4	1.5	*Upogebia hirtifrons*	98	*Pecten novaezelandiae*	2																
SNA2S	2	5.5	*Nectocarcinus spp*	96	Chitonidae	3	*Bellidilia cheesmani*	1														
SNA2S	0	5.5	Neogastropoda	50	*Stichopus mollis*	12	*Aphrodita spp*	12	*Bellidilia cheesmani*	6	Meiura	6	*Philine spp*	6	Polychaete	4	Majidae	3	Paguroidea	1		
SNA2S	4	3	Brachyura	40	Pedinae	16	*Philine spp*	12	Chitonidae	12	*Nectocarcinus spp*	12	Majidae	4	*Bellidilia cheesmani*	3	Pebble	1				
SNA1 HAGU	5	0.5	NA																			
SNA1 HAGU	2	1	Bivalve	95	Paguroidea	5																
SNA1 HAGU	4	2	Sabellida	45	Holothuroidea	45	Paguroidea	10														
SNA1 HAGU	3	6	*Upogebia hirtifrons*	99	Pedinae	1																

Population	Digestive	Avg fullness	Prey 1	%	Prey 2	%	Prey 3	%	Prey 4	%	Prey 5	%	Prey 6	%	Prey 7	%	Prey 8	%	Prey 9	%	Prey 10	%
SNA1 HAGU	4	1.5	*Upogebia hirtifrons*	100																		
SNA1 HAGU	5	1	NA																			
SNA1 HAGU	3	1.5	Paguroidea	100																		
SNA8	1	5.5	Onuphidae	65	*Urechis nova ezealandiae*	20	Brachyura	9	Ophiuroidea	6												
SNA8	1	3.5	*Gnathophis habenatus*	75	Paguroidea	25																
SNA8	2	5	Teleost	45	Portunidae	30	*Bellidilia cheesmani*	12	Paguroidea	7	Cephalopod	6										
SNA8	3	3.5	Decapod	32	*Liocarcinus corrugatus*	32	*Talochlamys zelandiae*	13	*Pecten novaezelandiae*	12	*Stichopus mollis*	5	Teleost	5	Bryozoan	1						
SNA8	5	3.5	NA																			
SNA8	5	2	Polychaete	50	Sabellida	50																
SNA8	5	1.5	NA																			
SNA8	5	3.5	Caridea	100																		
SNA8	5	1	NA																			
SNA8	5	0.5	Salpidae	100																		
SNA1 BOP	2	2	Polychaete	60	*Upogebia hirtifrons*	20	*Bellidilia cheesmani*	18	Sabellida	2												
SNA8	3	3.5	*Gnathophis habenatus*	80	Polychaete	20																
SNA1 BOP	0	7.5	Turritellinae	64	*Stichopus mollis*	21	Teleost	15														
SNA2 N	5	1	Decapod	50	Gastropod	50																
SNA2 N	4	1	*Bellidilia cheesmani*	100																		
SNA2 N	3	2.5	*Lyreidus tridentatus*	70	Brachyura	29	Teleost	1														
SNA2 N	0	7.5	*Lyreidus tridentatus*	72	*Stichopus mollis*	18	*Bellidilia cheesmani*	10														

Population	Digestive	Avg fullness	Prey 1	%	Prey 2	%	Prey 3	%	Prey 4	%	Prey 5	%	Prey 6	%	Prey 7	%	Prey 8	%	Prey 9	%	Prey 10	%
SNA2 N	2	8.5	*Lyreidus tridentatus*	83	Fasciolariidae spp	11	Chitonidae	6														
SNA2 N	3	2.5	*Lyreidus tridentatus*	94	*Bellidilia cheesmani*	5	Sabellida	1														
SNA2 N	2	4	*Lyreidus tridentatus*	82	*Bellidilia cheesmani*	14	Polychaete	4														
SNA2 N	4	4	*Lyreidus tridentatus*	50	Caridea	38	*Bellidilia cheesmani*	12														
SNA2 N	5	0.5	Decapod	100																		
SNA2 N	2	3	*Lyreidus tridentatus*	76	*Philine spp*	19	Worm 3	5														
SNA7	1	5.5	Paguroidea	70	Brachyura	9	Gastropod	9	*Bellidilia cheesmani*	5	Sabellida	3	Polychaete	2	Sessile soft tissue	1	Holothuroidea	1				
SNA7	0	5	Paguroidea	76	Brachyura	13	*Bellidilia cheesmani*	4	Majidae	4	*Callyspongia stellata*	3										
SNA7	2	5	Ophiuroidea	46	*Philine spp*	18	Paguroidea	14	Brachyura	9	*Bellidilia cheesmani*	9	Sabellida	4								
SNA7	3	6	Perna canaliculus	60	Hemiplax hirtipes	40																
SNA7	5	2.5	Caridea	100																		
SNA7	1	4.5	Portunidae	61	Teleost	26	Paguroidea	9	Ophiuroidea	4												
SNA7	0	6.5	*Cepola haastii*	85	Stomatopoda	14	Polychaete	1														
SNA7	4	6.5	Paguroidea	40	Heterodonta	35	Brachyura	23	Caridea	2												
SNA1 HAGU	5	0.5	NA																			
SNA1 HAGU	5	1.5	*Bellidilia cheesmani*	55	*Gnathophis habenatus*	40	Sabellida	5														
SNA1 HAGU	5	1	Polychaete	57	Portunidae	20	Salpidae	20	Sabellida	3												
SNA1 HAGU	5	1.5	Sabellida	100																		
SNA1 HAGU	5	4	Salpidae	100																		

Population	Digestive	Avg fullness	Prey 1	%	Prey 2	%	Prey 3	%	Prey 4	%	Prey 5	%	Prey 6	%	Prey 7	%	Prey 8	%	Prey 9	%	Prey 10	%
SNA1 HAGU	5	1	Caridea	100																		
SNA8	5	1	NA																			
SNA1E NLD	5	0.5	NA																			
SNA1E NLD	3	2	*Lyreidus tridentatus*	80	*Bellidilia cheesmani*	20																
SNA1E NLD	2	3.5	*Lyreidus tridentatus*	100																		
SNA1E NLD	5	1.5	*Gnathophis habenatus*	95	Paguroidea	5																
SNA1E NLD	5	0.5	NA																			
SNA1E NLD	5	1.5	*Lyreidus tridentatus*	88	*Bellidilia cheesmani*	7	*Neommatocarcinus huttoni*	5														
SNA1E NLD	5	0.5	*Bellidilia cheesmani*	100																		
SNA1E NLD	5	0.5	NA																			
SNA1E NLD	5	0.5	Decapod	100																		
SNA1E NLD	3	3	*Fellaster zelandiae*	50	Decapod	50																
SNA2 N	2	3	*Lyreidus tridentatus*	61	Bivalvia	20	Gastropod	10	*Bellidilia cheesmani*	9												
SNA2 N	4	3.5	*Lyreidus tridentatus*	78	Gastropod	10	Brachyura	5	*Neommatocarcinus huttoni*	5	Philine spp	2										
SNA2 N	4	4	*Lyreidus tridentatus*	55	Gastropod	12	Caridea	8	Brachyura	8	*Bellidilia cheesmani*	6	Teleost	6	Sabellida	5						
SNA2 N	2	5	*Lyreidus tridentatus*	92	*Bellidilia cheesmani*	6	Sabellida	2														
SNA2 N	0	2.5	Caridea	60	*Bellidilia cheesmani*	35	Ophiurida	5														
SNA2 N	0	5.5	*Lyreidus tridentatus*	93	Polychaete	5	*Bellidilia cheesmani*	2														
SNA2 N	5	3	Caridea	62	Polychaete	25	Isopod	13														

Population	Digestive	Avg fullness	Prey 1	%	Prey 2	%	Prey 3	%	Prey 4	%	Prey 5	%	Prey 6	%	Prey 7	%	Prey 8	%	Prey 9	%	Prey 10	%
SNA2N	2	4.5	*Lyreidus tridentatus*	96	*Bellidilia cheesmani*	4																
SNA2N	5	2	*Aphrodita spp*	100																		
SNA2N	2	2	*Lyreidus tridentatus*	51	*Aphrodita spp*	43	Polychaete	4	*Bellidilia cheesmani*	2												
SNA1ENLD	5	0.5	NA																			
SNA1ENLD	5	0.5	NA																			
SNA1ENLD	4	1	Meiura	80	Paguroidea	20																
SNA8	3	4	Teleost	39	*Philine spp*	28	Polychaete	17	Decapoda	12	Paguroidea	2	Sabellida	2								
SNA8	2	2.5	Paguroidea	35	Caridea	30	Gastropod	30	*Philine spp*	5												
SNA8	3	4.5	Paguroidea	83	*Bellidilia cheesmani*	11	Gastropod	5	Ophiuroidea	1												
SNA8	5	4.5	NA																			
SNA8	3	4	*Hyalinoecia spp*	83	*Bellidilia cheesmani*	16	Polychaete	1														
SNA8	5	5	NA																			
SNA8	3	2.5	Ophiuridea	100																		
SNA1ENLD	5	2	Bivalve	100																		
SNA1ENLD	5	1.5	Decapod	80	Bivalve	12	Pebble	8														
SNA1ENLD	1	3	*Heterosquilla tricarinata*	75	Atrina zelandica	25																
SNA1ENLD	5	1.5	Paguroidea	100																		
SNA8	5	4.5	Decapod	62	Paguroidea	20		10	Sabellida	5	Hyalinoecia spp	3										
SNA8	4	1	Brachyura	65	Sabellida	30	Parguroidea	4	Teleost	1												
SNA8	4	5	*Lyreidus tridentatus*	58	Gastropod	37	*Bellidilia cheesmani*	5														

Population	Digestive	Avg fullness	Prey 1	%	Prey 2	%	Prey 3	%	Prey 4	%	Prey 5	%	Prey 6	%	Prey 7	%	Prey 8	%	Prey 9	%	Prey 10	%
SNA8	4	4.5	Brachyura	40	Paguroidea	38	Polychaete	12	*Bellidilia cheesmani*	10												
SNA8	3	4.5	Paguroidea	95	Byrozoan	5																
SNA8	2	5	Teleost	55	Portunidae	45																
SNA8	3	3.5	Brachyura	46	*Lyreidus tridentatus*	30	Brachyura	18	Paguroidea	6												
SNA8	4	2	Caridea	100																		
SNA1E NLD	5	0.5	NA																			
SNA1E NLD	3	1.5	*Lyreidus tridentatus*	77	*Fellaster zelandiae*	13	*Bellidilia cheesmani*	10														
SNA1E NLD	5	0.5	NA																			
SNA1E NLD	5	0.5	NA																			
SNA1E NLD	4	1.5	Decapod	60	*Bellidilia cheesmani*	24	Teleost	11	Gastropod	5												
SNA1E NLD	5	0.5	Decapod	100																		
SNA1E NLD	5	0	NA																			
SNA1E NLD	5	0.5	NA																			
SNA1E NLD	5	2.5	*Lyreidus tridentatus*	60	Brachyura	25	*Bellidilia cheesmani*	15														
SNA1E NLD	3	1.5	*Lyreidus tridentatus*	85	*Bellidilia cheesmani*	15																
SNA2 N	0	5	*Aphrodita spp*	56	*Lyreidus tridentatus*	28	Brachyura	7	Caridea	4	Paguroidea	3	Ophiurida	2								
SNA2 N	5	1.5	Stomatopoda	100																		
SNA2 N	4	4	*Lyreidus tridentatus*	38	*Neommatocarcinus huttoni*	23	*Bellidilia cheesmani*	20	Stomatopoda	19												
SNA2 N	2	7	*Lyreidus tridentatus*	88	*Bellidilia cheesmani*	8	Polychaete	4														

Population	Digestive	Avg fullness	Prey 1	%	Prey 2	%	Prey 3	%	Prey 4	%	Prey 5	%	Prey 6	%	Prey 7	%	Prey 8	%	Prey 9	%	Prey 10	%
SNA2N	4	3.5	*Lyreidus tridentatus*	85	*Bellidilia cheesmani*	10	Paguroidea	5														
SNA2N	5	2	Decapod	80	Teleost	15		5														
SNA2N	3	2.5	Stomatopoda	40	*Bellidilia cheesmani*	20	*Lyreidus tridentatus*	15	Caridea	13	*Neommatocarcinus huttoni*	6	Salpidae	5	Sabellida	1						
SNA2N	2	3.5	Ophiuridea	38	Asteroidea	35	*Lyreidus tridentatus*	17	Polychaete	8	Sabellida	2										
SNA2N	2	5.5	*Lyreidus tridentatus*	76	*Bellidilia cheesmani*	16	Gastropod	5	Brachyura	3												
SNA2N	1	6	Oratosquilla oratoria	47	*Lyreidus tridentatus*	47	*Bellidilia cheesmani*	5	Filamentous rhodophyte	1												
SNA2N	2	6.5	*Lyreidus tridentatus*	96	Sabellida	2	*Bellidilia cheesmani*	2														
SNA2N	0	1.5	*Aphrodita spp*	50	Polychaete	28	Gastropod	14	*Bellidilia cheesmani*	5	*Lyreidus tridentatus*	3										
SNA2N	5	0.5	NA																			
SNA2N	5	2.5	*Lyreidus tridentatus*	100																		
SNA2N	1	9.5	Buccinidae	70	*Lyreidus tridentatus*	19	Patellidae	6	Polychaete	3	Stomatopoda	2										
SNA2N	5	3	*Lyreidus tridentatus*	95	Helicarcinus spp	5																
SNA2N	4	1.5	Buccinidae	31	Brachyura	31	Ascidian	20	*Bellidilia cheesmani*	18												
SNA2N	0	10	*Lyreidus tridentatus*	98	Paguroidea	1	*Bellidilia cheesmani*	1														
SNA1BOP	5	1	Sessile Soft tissue	100																		
SNA2S	2	6.5	*Bellidilia cheesmani*	96	Polychaete	3	Paguroidea	1														
SNA2S	0	7	Gnathophis habenatus	65	*Bellidilia cheesmani*	13	Polychaete	10	*Aphrodita spp*	10	Paguroidea	1	*Philine spp*	1								
SNA2S	1	7	*Bellidilia cheesmani*	88	*Aphrodita spp*	7	Paguroidea	5														

Population	Digestive	Avg fullness	Prey 1	%	Prey 2	%	Prey 3	%	Prey 4	%	Prey 5	%	Prey 6	%	Prey 7	%	Prey 8	%	Prey 9	%	Prey 10	%
SNA2S	4	4	*Bellidilia cheesmani*	36	Caridea	27	Decapod	18	Paguroidea	10	Teleost	9										
SNA2S	3	2.5	*Bellidilia cheesmani*	30	Paguroidea	30	Ophiurida	15	Gastropod	15	Polychaete	5	Heterothyone alba	4	*Philine spp*	1						
SNA2S	5	2.5	Paguroidea	72	Brachyura	18	*Bellidilia cheesmani*	10														
SNA2S	5	2.5	*Bellidilia cheesmani*	51	*Stichopus mollis*	35	Decapod	12	Paguroidea	2												
SNA2S	0	8.5	Buccinidae	40	*Aphrodita spp*	22	Echinoderma ta	8	*Bellidilia cheesmani*	8	Majidae	8	Decapod	4	Caridea	4	Leucosi idae	4	*Philin e spp*	2		
SNA2S	4	1.5	Brachyura	50	Paguroidea	35	*Bellidilia cheesmani*	15														
SNA2S	4	6	*Aphrodita spp*	32	*Philine spp*	16	Paguroidea	16	*Stichopus mollis*	10	Gastropod	8	Polychaete	8	*Bellidilia cheesmani*	6	Ophiuri da	4				
SNA2S	2	8	*Bellidilia cheesmani*	85	*Stichopus mollis*	7	*Philine spp*	4	Brachyura	2	Polychaete	1	Paguroidea	1								
SNA2S	5	5	*Lophopagu rus spp*	79	*Nectocarcinu s spp*	13	*Bellidilia cheesmani*	5	Ascidian	3												
SNA2S	5	4.5	*Bellidilia cheesmani*	56	*Aphrodita spp*	12	*Nectocarcinu s spp*	8	Buccinidae	8	Paguroidea	8	Majidae	8								
SNA2S	3	3.5	*Aphrodita spp*	55	*Bellidilia cheesmani*	33	Majidae	12														
SNA2S	5	7	*Aphrodita spp*	74	*Bellidilia cheesmani*	12	Buccinidae	12	Paguroidea	2												
SNA2S	4	3.5	Sessile soft tissue	63	*Bellidilia cheesmani*	31	*Philine spp*	6														
SNA2S	5	2	*Bellidilia cheesmani*	70	Lophopaguru s spp	28	Sabellida	2														
SNA2S	0	7	*Gnathophis habenatus*	64	*Aphrodita spp*	32	*Bellidilia cheesmani*	4														
SNA2S	5	3.5	*Lyreidus tridentatus*	60	*Bellidilia cheesmani*	16	Majidae	20	Sabellida	3	Holothuroide a	1										
SNA1E NLD	5	1	Paguroidea	35	*Hyalinoecia spp*	33	Rhodophyte	32														
SNA1E NLD	5	1.5	*Nectocarci nus spp*	70	Paguoidea	18	Bivalve	12														

Population	Digestive	Avg fullness	Prey 1	%	Prey 2	%	Prey 3	%	Prey 4	%	Prey 5	%	Prey 6	%	Prey 7	%	Prey 8	%	Prey 9	%	Prey 10	%
SNA1E NLD	4	2	Paguroidea	100																		
SNA1E NLD	5	2.5	Bivalve	54	Decapod	27	Paguroidea	19														
SNA1E NLD	3	4.5	Paguroidea	100																		
SNA1E NLD	4	4	Paguroidea	100																		
SNA1E NLD	4	4	NA																			
SNA1E NLD	4	1.5	NA																			
SNA1E NLD	2	4.5	NA																			
SNA1E NLD	5	2	NA																			
SNA1E NLD	1	7.5	NA																			
SNA1E NLD	4	2.5	Stomatopoda	100																		
SNA1E NLD	3	2.5	Paguroidea	100																		
SNA1E NLD	4	2	Caridea	100																		
SNA1E NLD	2	1.5	Decapod	100																		
SNA1E NLD	5	2	Decapod	100																		
SNA1E NLD	2	4	Paguroidea	100																		
SNA1E NLD	4	2	Paguroidea	100																		
SNA1E NLD	3	6	Paguroidea	100																		
SNA1E NLD	5	2	Decapod	100																		

Population	Digestive	Avg fullness	Prey 1	%	Prey 2	%	Prey 3	%	Prey 4	%	Prey 5	%	Prey 6	%	Prey 7	%	Prey 8	%	Prey 9	%	Prey 10	%
SNA1ENLD	4	3.5	*Lyreidus tridentatus*	93	*Bellidilia cheesmani*	4	Paguroidea	2	Ophiuroidea	1												
SNA1ENLD	4	3.5	*Lyreidus tridentatus*	95	Sabellida	4	*Bellidilia cheesmani*	1														
SNA1ENLD	5	1	*Bellidilia cheesmani*	90	Brachyura	10																
SNA1ENLD	5	1.5	Decapod	40	Gastropod	35	*Bellidilia cheesmani*	25														
SNA2N	2	2.5	*Lyreidus tridentatus*	53	Brachyura	35	Urechis novaezealandiae	9	Sabellida	3												
SNA2N	5	2.5	*Lyreidus tridentatus*	83	*Bellidilia cheesmani*	9	*Philine spp*	8														
SNA2N	2	5.5	*Lyreidus tridentatus*	58	Onuphidae	40	Isopod	1	*Bellidilia cheesmani*	1												
SNA2N	1	7	*Lyreidus tridentatus*	60	Gnathophis habenatus	18	*Bellidilia cheesmani*	18	Gastropod	4												
SNA2N	4	1.5	*Lyreidus tridentatus*	62	Decapod	20	Brachyura	10	*Bellidilia cheesmani*	8												
SNA2N	3	2.5	*Lyreidus tridentatus*	85	Polychaete	8	*Bellidilia cheesmani*	7														
SNA2N	2	5	*Lyreidus tridentatus*	80	Decapod	18	*Bellidilia cheesmani*	2														
SNA2N	3	1.5	*Lyreidus tridentatus*	55	Decapod	15	Brachyura	15	*Bellidilia cheesmani*	15												
SNA2N	5	0.5	NA																			
SNA1ENLD	5	2	Chitonidae	30	Bivalve	24	Polychaete	21	Caridea	9	Paguroidea	9	Gastropod	7								
SNA1ENLD	5	0.5	*Philine spp*	100																		
SNA1ENLD	5	1	Polychaete	100																		
SNA1ENLD	5	1	NA																			
SNA1ENLD	4	2	Brachyura	85	Paguroidea	15																

Population	Digestive	Avg fullness	Prey 1	%	Prey 2	%	Prey 3	%	Prey 4	%	Prey 5	%	Prey 6	%	Prey 7	%	Prey 8	%	Prey 9	%	Prey 10	%
SNA1E NLD	2	4.5	NA																			
SNA1E NLD	2	4.5	Gastopod	100																		
SNA1E NLD	5	0.5	NA																			
SNA1E NLD	2	4.5	Brachyura	65	Chitonidae	15	Paguroidea	15	Limpet	5												
SNA1E NLD	1	6	NA																			
SNA1E NLD	2	2.5	NA																			
SNA1E NLD	5	0.5	NA																			
SNA1E NLD	5	1	NA																			
SNA1E NLD	5	2	Decapod	100																		
SNA1E NLD	1	5	*Lyreidus tridentatus*	100																		
SNA1E NLD	5	1	NA																			
SNA1E NLD	2	2.5	*Lyreidus tridentatus*	47	*Bellidilia cheesmani*	30	Hyalinoecia spp	23														
SNA1E NLD	2	2	*Lyreidus tridentatus*	100																		
SNA1E NLD	4	2	*Lyreidus tridentatus*	100																		
SNA1E NLD	5	1.5	*Lyreidus tridentatus*	90	*Bellidilia cheesmani*	10																