Supplementary Material S1 – Coastal Fish Life Histories

This is an overview of the life history characteristics that likely affected the geographic range, abundances, and mean body sizes of 38 archaeologically common marine fish species from northern Aotearoa as sea surface temperatures (SSTs) cooled during the Little Ice Age (LIA) from 1500–1900 CE. This review indicates there are numerous knowledge gaps, but some predictions are possible for a species that are closely studied, or that have clear relationships between water temperature and demography. For a summary of these predictions, see Chapter 3: Socioenvironmental Contexts of Aotearoa Fisheries.

CLASS CHONDRICHTHYES
SUBCLASS ELASMOBRANCHII

Note: All elasmobranchs considered here (excepting the great white shark) are ectotherms, and their growth rates are directly affected by temperature. However, they are all highly mobile and many of them migrate to follow particular ranges of water temperature. It is therefore unlikely that elasmobranch growth rates or body size distributions would have been substantially affected during the LIA.

Order Lamniformes

Family Lamnidae

<u>Great White Shark (*Carcharodon carcharias*)</u>

Great white sharks have a circumglobal distribution in temperate to tropical seas. They are found from the Kermadec Islands to Campbell Island in Aotearoa, but they are most abundant around the southern South Island and the fur seal rookeries on Rakiura. Great whites occupy open ocean from the surface to 1200 m depth, shallow coastal waters, and tidal river mouths as shallow as 3 m deep. They aggregate around seal colonies, rocky and coral reefs, and they are relatively common in large harbours of the northern North Island (Duffy 2015a; Francis 2012).

Reproduction is ovoviviparous with oophagy – embryos hatch in utero and consume other embryos – and gestation lasts for 18 months. Females give birth in relatively shallow water along the inner continental shelf around the upper North Island in spring and early summer, and then rest for around 18 more months before the next pregnancy (Duffy 2015a). Pups come in litters of 2 to 17 and measure 120 cm to 150 cm TL at birth. Juveniles smaller than 180 cm are found mainly in coastal shallows of the northern North Island and the large harbours of the Auckland Region. The young grow rapidly and can reach 3 m length in 4 years, and 5 m length in 15 years (Duffy 2015a; Francis 2012).

Male great white sharks mature at 3.6 m to 3.8 m and between 7 to 9 years old, while females mature at 4.5 m to 5.2 m in 12 to 17 years. Adults can live for as long as 72 years, but males only grow to 5.5 m TL while females have been observed at 6.4 m TL and are estimated to reach 7 m (Duffy 2015a). Great white sharks are highly mobile predators and their range increases with size. Sharks tagged in the Chatham Islands and Rakiura in autumn remained in shallow water for several months before dispersing throughout the southwest Pacific on 2500 km to 3000 km migrations between Tonga and the Great Barrier Reef for winter and spring, returning to their Aotearoa tagging locations by summer (Duffy et al. 2012).

Implications for Little Ice Age Populations

Considering the wide latitudinal range inhabited by great white sharks today, I do not expect the LIA would have directly impacted northern Aotearoa populations. O'Brien et al. (2013) similarly expected that the Last Glacial Maximum only had slight effects on Pacific great white populations, but they observed surprisingly low genetic diversity that could indicate either that colder temperatures had moderate to severe impacts or that great whites only colonized the North Pacific Ocean in the last 10,000 years.

Regardless of whether the species is vulnerable to direct climate impacts, great white shark abundances along coastal North Island may have varied substantially over the period of Māori occupation due to changes in pinniped availability in northern Aotearoa waters. I expect great whites would have been more abundant initially given the presence of Aotearoa sea lions rookeries along the Coromandel Peninsula and the strong tendency for great white sharks to congregate around pinniped rookeries. After these rookeries collapsed in the fifteenth century, the sharks would have dispersed to the south as well.

Order Carcharhiniformes

Family Scyliorhinidae

<u>Carpet Shark (*Cephaloscyllium isabellum*)</u>

Carpet sharks are endemic to coastal Aotearoa with greater abundances along the South Island and Rakiura, and they were the first shark to be scientifically described by early European visitors. They are benthic sharks that roam reefs and open, sandy to shelly cobble bottoms at night and resting in caves and overhangs during the day. These sharks may also be capable of swimming off the sea floor for sustained periods to cross deeper basins. If captured, they will inflate their stomachs with water and curl into a stiff ball for defence (Francis 2012; Nakaya et al. 2015).

Eggs are fertilized internally and females lay them in pairs of leather cases that attach to seaweed, sea fans, and corals with long spiralling tendrils. Juveniles hatch at around 16 cm TL. Females mature at 80 cm TL and grow larger than males, which mature at 60 cm TL. Carpet sharks grow to a maximum size of about 90 cm TL, but at least one has been reported at 150 cm length (Francis 2012; Nakaya et al. 2015).

Implications for Little Ice Age Populations

As carpet sharks inhabit a wide range of latitudes and habitats, it is unlikely that they would have been negatively impacted by environmental changes associated with the LIA. If the higher abundances of carpet sharks at higher latitudes are associated with lower temperatures, it's possible their abundances would have increased in the north as water temperature declined. However, there is very little information available about their life histories that could be used to support these predictions.

Family Triakidae

<u>School Shark (*Galeorhinus galeus*)</u>

School shark is a widely distributed coastal species that can be found across the northeast and southern Atlantic Ocean, South Africa, the northeast Pacific Ocean, Peru and Chile, Australia, and Aotearoa, where it is found from the Three Kings Islands to 54°S latitude (Duffy 2015b). Though they were once considered part of a large species complex, school sharks show very low genetic diversity across the Southern Hemisphere despite the absence of gene flow between populations on separated by large ocean basins (Bester-van der Merwe et al. 2017; Duffy 2015b). There is some gene flow between Aotearoa and Australia (Duffy 2015b).

Their habitat ranges from shallow coastal waters to pelagic environments up to 1100 m depth, and they are usually found in sex-segregated schools. School sharks appear sensitive to temperature fluctuations, with a strong preference for water between 10°C and 22°C. Southern Australian populations were found to stay within a 5°C range, and Argentinian stocks move offshore between January and March in response to warming water temperatures (Duffy 2015b; Lucifora et al. 2004; Olson 1984).

Mating takes place from May to June in congregations at the deep edges of continental shelves. Reproduction is ovoviviparous with a 12-month gestation period and takes place every three years. The concentration of gravid and pregnant females in nearshore waters in early summer makes this species very vulnerable to overfishing. Females give birth to litters of six to 54 pups off of shallow sandy beaches, in large harbours, and in estuaries in November and December, though females will not come inshore if bottom temperatures are below 14°C. Pups measure about 30 cm TL at birth and move to increasingly deep water as they grow (Duffy 2015b; Olson 1984). In southeast Australia juveniles up to 3 years old can be found in marine bays and estuaries during summer, and in deeper coastal bays and inshore waters from July to September, but 0+ year old Aotearoa pups born in Kaipara harbour don't return to nursery areas. Juveniles school by size and sex. They are rarely found in water temperatures below 8°C, though in some areas where they may have been cold-conditioned juveniles have been found in water as cold as 7.4°C (Olson 1984).

Males mature around 120 cm to 130 cm TL and 8+ years, and females mature between 135 cm to 144 cm TL and after 10+ years. School sharks can probably live for more than 53 years (Duffy 2015b). In Australia, both sexes migrate offshore or northwards at the start of winter with falling water temperatures, and migrate back inshore in spring with rising temperatures on the continental shelf (Olson 1984).

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Implications for Little Ice Age Populations

While Australian populations of school sharks show clear sensitivities to temperature change, it is not clear that water temperature decreases associated with the LIA would have impacted school shark populations in Aotearoa, which occupy a very wide latitudinal range.

Rig (*Mustelus lenticulatus*)

Previously considered con-specific with *M. antarcticus*, rig are now recognized as an endemic species that is common throughout Aotearoa and to 49°S latitude. Rig are benthic and mainly occur over sand and mud from the intertidal zone to 1000 m depth, though they are uncommon below 250 m depth (Duffy 2015b).

Reproduction is ovoviviparous, and during early pregnancy females move into shallow waters during the summer. They give birth to litters of two to 24 pups – with a mean of 11 pups – in large harbours in estuaries in September and October after 11 months of gestation, and then join males at inner continental shelf feeding grounds. The females rest for one month before ovulation and copulation takes place again (Duffy 2015b; King 1984). Francis (2013) observed a slightly different pattern in Porirua, where rig are born between October and December.

Pups measure 30 cm to 32 cm TL at birth, and they segregate by size and sex (Duffy 2015b). Small juveniles remain abundant at specific locations in the North Island for up to seven months after birth, with a clear preference for shallow, sheltered areas of large estuaries and harbours. Movement out of these nurseries into deeper channels coincides with spikes in river flow, causing changes in nearshore salinity (Francis 2013). Adult females grow to a maximum size of 150 cm TL, and males grow to only 110 cm. Males and females disperse offshore in the autumn between reproductive events (Duffy 2015b).

Implications for Little Ice Age Populations

If differences in the timing of parturition observed at Porirua compared to other locations are related to the lower water temperatures at Porirua, the LIA could have affected the seasonality of rig life histories. However, given the wide latitudinal range inhabited by the species, it is unlikely that the LIA would have substantially impacted rig populations.

Family Carcharhinidae

Bronze Whaler (*Carcharhinus brachyurus*)

Bronze whaler is widely distributed in temperate regions of the Northern and Southern Hemispheres except for the northwest Atlantic Ocean and the northern Indian Ocean. It is common around the northern North Island, but it can also be found as far south at Cook Strait and Tasman Bay in the summer (Duffy 2015c).

Reproduction is viviparous with a yolk-sac placenta (Duffy 2015c). Bronze whalers in south Australia occupy gulfs from September to May for birthing and copulation, with birth probably taking place in the spring and summer (Drew et al. 2017; Izzo et al. 2016). There 7 to 24 pups in a litter, with an average litter size of 21 pups, and birth only occurs every other year (Drew et al. 2017; Duffy 2015c). Nurseries have not been directly observed in Australia (Izzo et al. 2016), but Lucifora et al. (2005) note that bronze whaler nurseries in Argentina are found at the highest latitudes of the shark's regional distribution. Pups measure 55 cm to 67 cm TL at birth and grow slowly to about 1500 cm TL by 8 years of age (Drew et al. 2017; Duffy 2015c).

Males mature at 2.0 m to 2.3 m TL after 13 to 19 years of age, and females mature at 2.2 m to 2.4 m TL between 19 and 20 years of age (Drew et al. 2017; Duffy 2015c), though a survey of biological literature by Lucifora et al. (2005) found moderate variation in length-at-maturity across its global range. Adults are highly mobile, with some individuals traveling tens to hundreds of kilometres over a few days (Izzo et al. 2016). Argentine females may sex segregate and move south or offshore during summer (Lucifora et al. 2005).

Implications for Little Ice Age Populations

If the Aotearoa population of bronze whalers shares life history traits with those from Australia and Argentina, the main nursery areas for the species may be located around Tasman Bay and Cook Strait where sharks are found during summer, the most likely season for parturition and mating. As this is the southern limit of their regional distribution, declining SST in the LIA could have caused a range shift with nurseries moving northwards. However, it's unlikely that either nurseries or adults would shift out of the northern North Island, and it's unlikely that there were any substantial changes in bronze whaler populations there.

Blue Shark (*Prionace glauca*)

Blue shark is one of the most abundant and widespread Chondrichthyan in the world, with a circumglobal distribution in temperate and tropical waters. Despite some distinctive morphological characters, genetic analysis suggests the species should be reclassified under genus *Carcharhinus* (Duffy 2015c). It is common throughout the Aotearoa exclusive economic zone, and the Aotearoa populations are part of a larger Indo-Pacific stock that exhibits little to no genetic variation (Manning and Francis 2005; Taguchi et al. 2015). Blue sharks are primarily oceanic inhabiting the surface waters to 1000 m depth in the tropics during fall and winter, but from spring to summer they migrate inshore and towards higher latitudes. They can apparently tolerate a wide range of temperatures from 5°C to 28°C, but they show very strong regional preferences for narrower temperature ranges; sharks from the Pacific Ocean are overwhelmingly found in water temperatures between 15°C and 20°C (Duffy 2015c; Nakano and Seki 2003; Vögler et al. 2012).

Reproduction is viviparous with a yolk-sac placenta (Duffy 2015c). Mating probably occurs in spring or early summer, and gestation lasts between 9 and 12 months. However, it's still unclear when or where pregnant females give birth as births have been reported over a wide seasonal range from spring to fall, which may reflect individual or regional variation (Duffy 2015c; Nakano and Seki 2003; Vögler et al. 2012). Litter size ranges from 4 to 135 pups measuring 35 cm to 50 cm TL at birth. Some sub-adult females are sexually active and store sperm in oviducal glands for up to a year before they fully mature and fertilize (Duffy 2015c).

Male sharks mature at a similar size (1.8 m to 2.8 m TL) and age (8 years) to female sharks (1.7 m to 2.6 m TL; 7 to 9 years). The oldest male shark in observed in Aotearoa was at least 22 years old, and the oldest female shark was 20 years old (Duffy 2015c; Manning and Francis 2005). Blue sharks undergo large scale movements that are strongly influenced by seasonal variations in water temperature, reproductive condition, and prey availability (Nakano and Seki 2003; Vögler et al. 2012).

Implications for Little Ice Age Populations

Taguchi et al. (2015) observed that blue shark is historically resilient to climate fluctuations. With their extremely wide latitudinal distribution and tolerance for water as cold as 5°C, I do not expect they were directly impacted by the LIA in Aotearoa.

Family Sphyrnidae

<u>Smooth Hammerhead Shark (*Sphyrna zygaena*)</u>

Smooth hammerhead sharks are globally distributed from tropical to temperate latitudes in the Atlantic Ocean, the Mediterranean Sea, the Indian Ocean, and the Pacific Ocean. In Aotearoa they can be found from Northland to Cook Strait and the outer Marlborough Sounds. Females give birth to 20 to 50 pups measuring 50 cm to 61 cm TL after a 10 to 11 month gestation period. Juveniles form loose inshore schools. Males mature at 2.5 m length, and females at 3.0 m. Adults grow to a maximum size of 3.9 m TL.

Implications for Little Ice Age Populations

As hammerheads appear to be at the edge of their regional distribution in Cook Strait, decreasing SST associated with the LIA could have prompted a northerly retreat in hammerhead populations. However, it is unlikely that they would have retreated past northern Aotearoa.

Order Hexanchiformes

Family Hexanchidae

<u>Broadsnout Sevengill (*Notorynchus cepedianus*)</u>

Broadsnout sevengill is globally distributed in cool-temperate coastal waters and common throughout Aotearoa (Stewart 2015a). They are benthic and range from 10 m to 226 m depth in shallow bays, muddy harbours and along the continental shelf, though they are also sometimes found in the lower reaches of rivers on Rakiura (Francis 2012; Stewart 2015a).

Reproduction is viviparous, with females giving birth to live young in the spring after a one-year gestation period. Parturition occurs in shallow bays and is followed by a one-year resting period. There can be up to 104 pups measuring 35 cm to 45 cm in each litter, but small sharks are rarely observed. Males mature at 1.5 m to 1.6 length after 4 to 5 years, and females mature at between 2.2 m and 2.5 m length and 11 to 21 years old. Adult males grow to a maximum size of only 2.3 m, while females grow much larger and may live for up to 50 years (Francis 2012; Stewart 2015a). Sevengills undertake long migrations between shallow, coastal bays in spring and summer and open coasts in winter, with some traveling over 1000 km, but they regularly return to the same locations in subsequent years (Francis 2012).

Implications for Little Ice Age Populations

There is no indication that broadsnout sevengills would be substantially affected by the onset of LIA conditions. Given their wide latitudinal distribution, it is unlikely that populations in northern North Island would be substantially impacted by decreases in SST.

Order Squaliformes

Family Squalidae

<u>Spiny Dogfish (*Squalus acanthias*)</u>

Spiny dogfish is circumglobally distributed in the temperate Northern and Southern Hemisphere excluding the North Pacific Ocean. It was previously thought to inhabit the North Pacific, but because of clear differences in the genetic and life history characteristics of dogfish populations there they have been reclassified as *Squalus suckleyi* (Duffy and Last 2015; Veríssimo et al. 2010). *S. acanthias* is present throughout Aotearoa over the continental shelf and upper continental slopes from surface waters to depths of 1446 m, and they are more common in surface waters at night. Two other species of *Squalus* are also present in coastal northern Aotearoa waters: northern spiny dogfish (*S. griffini*) and shortspine dogfish (*Squalus* sp.), which currently lacks a formally recognized taxonomic designation (Duffy and Last 2015). Spiny dogfish school in size-segregated groups of small fish, medium-sized mature males and immature females, and large mature females. Females are more common along nearshore continental shelf habitats with lower salinities and warmer temperatures, which may enhance embryo growth. Worldwide data show that dogfish have a strong preference for water temperatures between 7°C and 15°C, and their migrations may be driven in part by shifts in water temperature (Stehlik 2007).

Mating occurs after females give birth or right before birth at depths of 200 m to 300 m between March and September in Aotearoa (Duffy and Last 2015). Reproduction is ovoviviparous, with embryos developing in a transparent capsule called a 'candle' that breaks down and allows the pups to develop to term *in utero* without a placenta (Duffy and Last 2015; Stehlik 2007). Gestation lasts nearly two years, and in any given year there are two different groups of females carrying different size classes of embryos (Duffy and Last 2015). Litter sizes range from 1 to 16 pups measuring 18 cm to 33 cm TL at birth, but most measure 26 cm to 27 cm (Duffy and Last 2015; Stehlik 2007). In the northwest Atlantic juveniles are widespread across continental shelves in the boreal winter, and then concentrate offshore at 60 m to 200 m depth in spring and summer before moving northwards in autumn. Estimates of juvenile growth suggest they would reach a mean length of 56 cm after 5 years (Stehlik 2007).

Aotearoa dogfish males mature between 53 cm and 63 cm TL, and females mature between 61 cm and 81 cm TL; maturity in both sexes may occur after 10 years. Adult males grow to a maximum size of 90 cm TL, and females grow to 1.1 m, though individuals measuring 1.2 m have also been observed (Duffy and Last 2015). This long-lived, late maturing life history strategy is thought to protect dogfish populations from climate fluctuation, but it also makes them very vulnerable to overfishing (Yatsu et al. 2008). Dogfish make annual north-south migrations along coastal areas and between inshore and offshore regimes that coincide with changes in bottom water temperature. Long distance, trans-oceanic movements have also been observed (Veríssimo et al. 2010).

Implications for Little Ice Age Populations

As spiny dogfish migrations appear to be controlled by water temperature, the onset of LIA conditions may have affected the timing of their movements around Aotearoa. However, it is unlikely that they would have been directly impacted by changes in water temperature as they inhabit a wide latitudinal and thermal range.

Order Rajiformes

Family Rajidae

Smooth Skate (*Dipturus innominatus*)

Smooth skate is endemic to Aotearoa and can be found from the far north to the subantarctic islands (Forman and Dunn 2012; Francis et al. 2001; Last and Stewart 2015a). In the past the genus was synonymized with genus *Raja*, but it has recently been resurrected. Smooth skates are often confused with the rough skate (*Dipturus nasutus*) (Last and Stewart 2015a). *D. innominatus* is commonly found on sandy and muddy seafloors from shallow waters to 500 m depth, but it has also been captured at 1180 m and reported at 1300 m depth (Francis 2012; Francis et al. 2001; Last and Stewart 2015a).

Females lay egg cases in pairs on the seabed, though it is unknown how many an individual may lay annually (Forman and Dunn 2012; Francis 2012). Juveniles hatch after an unknown length of time and measure 10 cm to 15 cm in length. Growth rates are slow and similar in both sexes, with juveniles reaching 70 cm after 5 years (Francis 2012).

Males mature at lengths of 91 cm to 95 cm after 7 to 9 years, and females mature between lengths of 105 cm and 120 cm and 11 to 15 years (Forman and Dunn 2012; Francis 2012; Francis et al. 2001). Females live longer (24 years) and grow larger (1.6 m length) than males (15 years; 1.3 m length), but Last and Stewart (2015a) write that smooth skates can grow over 2.4 m TL with some individuals reportedly measuring 3 m long. Smooth skate diets have probably been anthropomorphically modified as many skates consume fisheries discards as a large portion of their diet (Forman and Dunn 2012).

Implications for Little Ice Age Populations

There is little information available about the climatic tolerances of smooth skates, but their wide distribution and their presence in subantarctic islands suggests they would be able to withstand decreases in water temperature associated with the LIA.

Rough Skate (*Dipturus nasutus*)

Rough skate is endemic to Aotearoa that is widely distributed (Francis et al. 2001; Last and Stewart 2015a). The species has previously been included in genera *Dipturus*, *Raja*, and *Zearaja*, but Roberts et al. (2020) recently returned it to *Dipturus*. Last and Stewart (2015a) caution that earlier species accounts may be unreliable as the distinctions between *D. nasutus* and *D. innominatus* were not appreciated. Rough skates are benthic, inhabiting sandy and muddy seafloors from shallow inshore waters to the continental slopes at up to 1500 m depth, but they are primarily found from 17 m to 600 m depth (Francis 2012; Last and Stewart 2015a).

Females deposit egg cases in pairs on the seafloor during spring and summer, but possibly also into fall. Juveniles measuring 10 cm to 15 cm TL hatch after an unknown period of time (Francis 2012; Last and Stewart 2015a). Growth rates are similar in both sexes, with males and females showing no differences in length-at-age between 4 and 6 years (Francis 2012; Francis et al. 2001).

Fifty-percent of males are mature between 51 cm and 53 cm when they are at least 3 years old, and 50% of females reach maturity by 58 cm to 60 cm when they are 4 to 5 years old. Females grow larger (80 cm length) and live longer (9 years) than males (72 cm; 7 years) (Francis 2012; Francis et al. 2001).

Implications for Little Ice Age Populations

There is little information available about the climatic tolerances of rough skates, but their wide latitudinal distribution suggests they would be able to withstand decreases in water temperature associated with the LIA.

Order Myliobatiformes

Family Dasyatidae

Short-Tail Stingray (*Bathytoshia brevicaudata*)

The global distribution of short-tail stingray is uncertain, but they are widespread in the Southern Hemisphere in three geographically distinct groups from South Africa, west Australia, and east Australia/Aotearoa, where they are uncommon south of Cook Strait (Francis 2012; Last and Stewart 2015b; Le Port et al. 2008; Le Port and Lavery 2012). Mitochondrial DNA analysis indicates each of these geographic centres are characterized by unique haplotypes, and that the east Australian and Aotearoa populations are genetically distinct from each other as well. A sample of 152 mtDNA sequences from Aotearoa show there are significant differences between populations from the east coast, Northland, Poor Knights Islands, and the west coast (Le Port and Lavery 2012). Short-tail stingrays occupy sandy or muddy areas at a mean depth of 30 m (range 5 m to 300 m) in harbours, estuaries, and bays, but they are also frequently seen at reefs and they congregate around archways (Francis 2012; Last and Stewart 2015b; Le Port et al. 2008). This species was previously included in genus *Dasyatis*, but Roberts et al. (2020) recently restored it to *Bathytoshia*.

Mating probably takes place in summer and autumn, as mating wounds are more frequent on females during this period and absent during winter, but they are also rarely observed in spring (Le Port et al. 2012). Reproduction is aplacental viviparous with litters of 6 to 10 pups measuring 36 cm disk width (DW) at birth (Last and Stewart 2015b; Le Port et al. 2012), though Francis (2012) writes that pups measure 50 cm at birth. Pups measuring 45 cm DW can be found in shallow, sheltered harbours over summer, and they may move to deeper offshore waters until they reach sexual maturity (Le Port et al. 2012).

Le Port et al. (2012) assigned short-tail stingrays to age classes based on comparison with size-at-maturity patterns in other species of *Bathytoshia*. According to their classification, juveniles measure less than 1 m DW, subadults between 1 m and 1.5 m DW, and adults over 1.5 m DW. However, female subadults from Poor Knights Islands were observed in courtship and with mating wounds, suggesting that short-tail stingrays mature closer to 1 m DW, or that warmer waters help stingrays mature at smaller sizes than in cooler conditions (Le Port et al. 2012). Adults grow to a maximum size of 4.3 m TL and 2.1 m DW, and are one of the largest marine stingrays in the world (Last and Stewart 2015b; Le Port et al. 2008).

Hundreds of short-tail stingrays congregate at the Poor Knights Islands each summer in the only documented gathering of this kind for the species across its global range. The migration is strongly sex-biased with subadult females arriving from spring through autumn, peaking at a 6x increase, compared with a 2x increase in the number of males. Changes in stingray abundance at this site are positively correlated with water temperature. It's likely that the Poor Knights Islands act as a mating ground, but there is no evidence they serve as a pupping ground or nursery. It's possible that similar congregations also occur elsewhere, but at deeper offshore locations where they would be very difficult to observe (Le Port et al. 2012). Overall, short-tail sting ray captures decrease dramatically from May through October, and tagging experiments suggest they spend more time at greater depths as winter approaches (Le Port et al. 2008).

Implications for Little Ice Age Populations

As short-tail stingrays appear to be at the edge of their regional distribution in Cook Strait, decreasing SST associated with the LIA could have prompted a northerly retreat. However, it is unlikely that they would have retreated past northern Aotearoa. If temperature plays a role in the speed of stingray maturation, decreases in SST could lead short-tail stingrays to mature at a later age. If there were no other changes in fecundity or growth rates, this change in maturation could cause short-tail stingray abundances to decrease (due to fewer productive years) and mean body size to increase (due to fewer pups annually).

Long-Tail Stingray (*Bathytoshia lata*)

Though the global distribution of long-tail stingrays is uncertain, they are widespread in the sub-tropic and temperate waters of South Africa, Reunion Island, Australia, and Aotearoa (Last and Stewart 2015b). In Aotearoa, they most abundant north of East Cape, and can be found between 5 m and 150 m depth in harbours, estuaries, and occasionally on reefs. *Bathytoshia lata* is generally found in muddier areas and in deeper water than *Bathytoshia brevicaudata*, though they may have very similar biological and behavioural characteristics (Francis 2012; Last and Stewart 2015b). According to Francis (2012) pups measure 60 cm at birth. Adults grow to a maximum size of 3.3 m TL and 1.8 m DW (Last and Stewart 2015b).

Implications for Little Ice Age Populations

There is little information available for assessing the possibility of LIA impacts on long-tail stingrays. However, as they are more abundant north of East Cape, decreases in SST could see their concentration shift northward, with local declines in abundance at Bay of Plenty and the west coast of Waikato.

Family Myliobatidae

Eagle Ray (*Myliobatis tenuicaudatus*)

Eagle ray is distributed throughout South Australia, Norfolk Island, the Kermadec Islands, and in Aotearoa from northland to Foveaux Strait, though they are rare south of Cook Strait. They occupy soft sediments and rocky reefs from shallow waters to 422 m depth, but they are primarily found above 50 m depth (Duffy 2015d; Francis 2012). They are especially common in shallow estuaries and harbours in the summer where they excavate steep-sided holes 20 cm across by jetting water through the mouth or gills, disturbing up to 10 m^2 of sediment a day (Duffy 2015d; Francis 2012; Marcotte 2014; Thrush et al. 1994).

Reproduction is viviparous and probably occurs annually, with births taking place in bays and estuaries between late winter and early summer (Duffy 2015d; Francis 2012). Neonates are abundant in the same habitats from spring through early summer (Duffy 2015d). Females grow faster and larger than males (Francis 2012), but both sexes mature when their pelvic fins measure 40 cm to 41 cm length – at about 4 years old for males and 8 years for females (Duffy 2015d). Females grow to 105 cm DW and live for 26 years, while males only grow to 82 cm and live for 15 years.

Large numbers of adults and sub-adults congregate in shallow bays during summer, where they are sexually segregated (Duffy 2015d; Francis 2012; Marcotte 2014). Eagle rays inhabit deeper estuary channels during low tide and return to tidal flats during high tide. Semi-resident rays will leave estuaries during heavy rains while remaining close to the estuary mouth (Marcotte 2014). They move to deeper water over winter where they are solitary (Duffy 2015d; Francis 2012). Experimental displacements of eagle rays show they are capable of homing – returning to their preferred estuary (Marcotte 2014).

Implications for Little Ice Age Populations

There is little information available about the climatic tolerances of eagle rays. If their low abundances south of Cook Strait indicates they are sensitive to temperature, decreasing SST could have caused their abundances to decrease further north. However, I do not expect that northern North Island populations would have been substantially affected.

CLASS ACTINOPTERYGII

Order Mugiliformes

Family Mugilidae

Yellow Eye Mullet (*Aldrichetta forsteri*)

Yellow eye mullet are widely represented throughout Australian and Aotearoa coastal waters south of latitude 27°S, inhabiting estuaries, harbours, sheltered bays, and open coasts from the surface to a depth of 50 m, and entering rivers as well. They often form large schools in sheltered waters, and can also be found in smaller groups over coastal reefs at the surface (Chubb et al. 1981; Francis 2012; Kingsford and Tricklebank 1991; Trnski 2015).

Spawning takes place from late December to mid-March in east Australian and Aotearoa coastal waters close to shore (Chubb et al. 1981; Curtis and Shima 2005; Kingsford and Tricklebank 1991; Trnski 2015), though Francis (2012:146) suggests spawning occurs from late winter to summer. Larvae can be found in high abundances from November to March off of northeast Aotearoa up to 18 km from land, which supports Francis's observation. The larvae aggregate, respond as a group, and are competent swimmers at lengths of 4-6 mm, and migrate to estuaries at larger stages (Kingsford and Tricklebank 1991).

Yellow eye mullet juveniles settle in sheltered harbours, river mouths, and estuaries beginning in early summer (Francis 2012; Trnski 2015). They make extensive use of shallow banks as nursery areas, and storm surges sometimes push them over sand bars into estuaries that are closed off from the sea (Chubb et al. 1981). In the winter, juveniles move out from their nurseries into coastal waters (Francis 2012).

Aotearoa populations of yellow eye mullet display extremely heterogenous growth patterns, which are probably driven by temperature and by differences in the energy investment strategy of each sex (Curtis and Shima 2005). Females appear to have higher energetic costs associated with reproduction in colder water, leading to declines in their growth rates at increasing latitudes. Both sexes reach maturity between the ages of 2 and 3 years old, at lengths of 140 to 15 cm for males and about 17 cm for females. Adults have a maximum life span of 7 years, and grow up to a maximum size of 36 cm SL and 950 g (Curtis and Shima 2005; Francis 2012; Trnski 2015).

Implications for Little Ice Age Populations

Because yellow eye mullet are present at high latitudes today, it is unlikely that the LIA had any impact on northern Aotearoa population sizes or distributions. However, growth sizes probably would have been negatively impacted by decreases in mean SST, especially for females. There is no evidence that yellow eye mullet populations are sex-structured, so decreases in growth rates would manifest as a decrease in mean body size for the population.

<u>Grey Mullet (*Mugil cephalus*)</u>

Species identifications based on morphological classification present grey mullet as one of the most widespread inshore bony fishes in the world, with populations present in the tropical and temperate zones of all major oceans between latitudes 42°N and 42°S (Fortunato et al. 2017; Fraiola and Carlson 2017; Górski et al. 2015; Katselis et al. 2015; Lan et al. 2014; Trnski 2015). However, according to recent genetic analysis, *Mugil cephalus* may actually be a species complex that encompasses up to 14 separate lineages that possibly represent individual species (Durand et al. 2012; Trnski 2015; Whitfield et al. 2012). The southern limit of the worldwide *Mugil cephalus* distribution is in Aotearoa, where it is most abundant north of the Bay of Plenty (Górski et al. 2015; Trnski 2015). Aotearoa grey mullets inhabit harbours, estuaries, open ocean shorelines, and can extend over 150 km inland up rivers like the Waikato River (Francis 2012; Górski et al. 2015; Trnski 2015). Like Mediterranean populations (Fortunato et al. 2017), Aotearoa grey mullets can be separated into two groups: mullet that spend the majority of their lives in freshwater systems, and mullet that show permanent open sea residency (Górski et al. 2015).

Grey mullet spawn in large coastal schools over several months when water temperatures are close to 20°C (Ibáñez and Benítez 2004; Whitfield et al. 2012). Francis (2012:147) reports a spring to summer spawning period for Aotearoa, while Trnski (2015) indicates that spawning takes place from summer to autumn. Observations of grey mullet eggs in controlled lab conditions show they can tolerate temperatures of 20°C to 30°C, with optimal yields of hatched larvae occurring at 20°C and 25°C in separate experiments (Whitfield et al. 2012). The eggs and larvae may drift in the open ocean for several weeks or months before beginning a shoreward migration and entering estuaries in the postflexion stage (Fortunato et al. 2017; Francis 2012; Górski et al. 2015; Whitfield et al. 2012).

Schools of grey mullet fry temporarily occupy the surf zone, and then juveniles generally settle in estuaries, rivers, and coastal lagoons and lakes at lengths of 25-3 cm SL after a month at sea (Chubb et al. 1981; Francis 2012; Górski et al. 2015; Katselis et al. 2015; Trnski 2015; Whitfield et al. 2012). Movement into brackish and freshwater generally coincides with the end of the rainy season, reducing the chance that juveniles will be washed out to sea by heavy rains (Whitfield et al. 2012). However, some juveniles on the west coast of Aotearoa may develop entirely in marine environments (Górski et al. 2015).

Growth rates and size at maturity are highly variable on a global scale, but females generally grow faster than males with the former maturing between 270 and 35 cm SL, and the later at 250 to 30 cm SL, both at around 3 years old (Francis 2012; Whitfield et al. 2012). Adults commonly reach a maximum size of 40 cm TL by the age of 6 to 10 years old, but the largest recorded individuals measured approximately 90 cm TL (Francis 2012; Trnski 2015). However, growth and aging studies from around the world are not based on comparable methods, so we have a poor understanding of growth rates and the factors that control them (Whitfield et al. 2012). Grey mullets are generally able to withstand temperatures between 13°C and 33°C, but in some cases adults have survived lows of 6°C (Whitfield et al. 2012).

Implications for Little Ice Age Populations

While adult grey mullet are highly adaptable to temperature change, grey mullet eggs appear to be sensitive to SST. Declining SST could have reduced grey mullet populations in Aotearoa by reducing the length and number of spawning seasons with conditions that are favourable for the development and survival of eggs. It is likely that mullet ranges would have contracted northwards to lower latitudes, but it is unclear whether they would have retreated from the northern North Island. Given the poor understanding of grey mullet growth patterns, it is unclear how body size distributions might have changed, or whether they would have changed at all.

Order Scorpaeniformes

Triglidae

Red Gurnard (*Chelidonichthys kumu*)

Red gurnard are represented in south and east Australia, Lord Howe Island, Aotearoa, Rakiura, and the Chatham Islands (Elder 1976; Struthers and Gomon 2015). They were previously considered conspecific with *Chelidonichthys spinosus* from the northern Yellow Sea, the East China Sea, and Japan, but more recent determinations consider these to be separate species (Struthers and Gomon 2015). *C. kumu* inhabit coastal waters from 5 to 200 m depth. They are most commonly found above depths of 55 m on soft substrates like mud, sand, and sandy-shell, where they 'walk' across the bottom with specialized pectoral fin rays that probe the sediment and help startle concealed prey into the open for capture (Elder 1976; Francis 2012; Struthers and Gomon 2015).

There is an extended spawning period with spawning reportedly occurring year-round (Elder 1976), but it probably only lasts from September to May with peak activity in November and December (Clearwater and Pankhurst 1994). Gonads of both sexes appear to ripen when SST reaches its annual minimum and when day lengths begin to increase, and the peak spawning period ends when temperatures are peaking and day lengths begin decreasing. Clearwater and Pankhurst (1994) suggest that the photoperiod is a more important factor than temperature for controlling spawning activity. Inshore populations appear to move to deeper waters to spawn at depths between 51 and 99 m, with some males partially residing in offshore spawning areas (Clearwater and Pankhurst 1994; Elder 1976). Little information has been reported on red gurnard egg and larval development.

Juvenile red gurnard grow quickly and mature by the age of 4 years old (Elder 1976; Francis 2012; Struthers and Gomon 2015). Elder (1976) reports that males mature earlier than females, with 50% of males maturing earlier at 2 years old and 21 cm long and 50% of females maturing at 3 years old and 24 cm long, but Francis (2012:82) suggests that females actually grow faster. Adults reach a maximum size of 50 cm SL and live to 16 years old (Struthers and Gomon 2015), but a survey of red gurnard in the Hauraki Gulf showed that the population was dominated by 3+ year old females and 2+ year old males (Elder 1976). Lyon and Horn (2011) observed that size and age increases with depth, and that red gurnard on the west coast of South Island are consistently larger and older than individuals from Tasman Bay and Golden Bay, which may function as a red gurnard nursery area.

Implications for Little Ice Age Populations

Red gurnard are abundant over a wide latitudinal range, and there are no apparent vulnerabilities to decreasing temperatures at any stage of their life history. It does not seem likely that decreases in SST would have a measurable impact on their population size, body size distributions, or range.

Order Perciformes

Family Carangidae

<u>Trevally (*Pseudocaranx georgianus*)</u>

Trevally are present in coastal south Australia, Aotearoa, the Kermadec Islands, and Foveaux Strait, but they are most common north of Cook Strait (Francis 2012; French et al. 2012; Smith-Vaniz 2015; Smith-Vaniz and Jelks 2006). *Pseudocaranx georgianus* has previously been included with a complex of similar fishes under the designation *P. dentex*, but Smith-Vaniz and Jelks (2006) distinguish these as separate species based on differences in their morphological characteristics and numbers of caudal vertebrae. Francis (2012:103) notes that the ranges of *P. georgianus* and *P. dentex* may overlap in the Kermadec islands and possibly in Aotearoa. Trevally form large schools that range from the surface to depths of 250 m, and they are common at islands, pinnacles, reefs, and headlands where currents concentrate their planktonic prey (Francis 2012; Smith-Vaniz 2015; Stewart and Ferrell 2001).

Spawning takes place in the summer with a peak from January to February (Francis 2012). Little information has been reported on trevally reproduction, eggs, or larval development.

Juveniles settle in shallow coastal bays and harbours among reefs, where they school with small jack mackerels (*Trachurus* spp.), sweep (*Scorpis lineolata*), and blue maomao (*Scorpis violacea*). They grow to a length of 10 cm in their first year, and to 30 cm FL by 3 years old. Then growth slows after they reach maturity at lengths of 320 to

37 cm at about 5 years old (Francis 2012; Smith-Vaniz 2015). Stevens et al. (1984) observed that trevally size increases with depth over a range of 43 to 150 m. Trevally reach a maximum size of 82.7 cm FL and can live for up to 50 years (Francis 2012; Smith-Vaniz 2015).

Implications for Little Ice Age Populations

While trevally occur over a wide latitudinal range, their abundance may be partially limited by temperature, with higher abundances recorded in warmer waters north of Cook Strait. Decreases in SST could therefore may have caused reductions in northern Aotearoa trevally populations. While their range may have contracted northwards, it seems unlikely that any retreat would have moved very far to the north. There is not enough information about the factors that control growth to develop expectations about changes in trevally body size distributions.

<u>Jack Mackerel (*Trachurus declivis*)</u>

Jack mackerel are present throughout southern Australia, Tasmania, the Kermadec Islands, and Aotearoa north of the subtropical convergence in Otago and the Chatham Rise (Jones 1990; Smith-Vaniz 2015; Williams and Pullen 1993). They form large schools near the seabed from depths of 160 to 500 m, which move to feed on krill at the surface at dawn, throughout the day in overcast weather, and at dusk (Smith-Vaniz 2015; Williams and Pullen 1993). Krill concentrations appear to be driven by nitrate availability, which is related to water temperature. Thus, schools of jack mackerel closely follow the movements of SST gradients with a strong preference for 15°C to 17°C isotherms (Harris et al. 1992; Jordan et al. 1995). In Tasmania, the range of jack mackerel stocks have shifted southwards during years with unusually warm SST (Harris et al. 1992). However, Australian populations of jack mackerel are genetically distinct from the Aotearoa stock (Jones 1990; Jordan et al. 1995), so population characteristics in Tasmania might not apply in Aotearoa.

The spatiotemporal patterns of jack mackerel reproduction are poorly understood throughout its range (Jordan et al. 1995), but Aotearoa populations appear to spawn from November to January (Jones 1990; Smith-Vaniz 2015). Large spawning aggregations have been observed on the Taranaki coast from November to December, while eggs are found there in January. In Northland, eggs have been observed as early as

October, while relatively few eggs have been recorded in the Hauraki gulf (Jones 1990). In Tasmania, the highest densities of jack mackerel eggs appear in waters that are between 15°C to 17.5°C in February (Jordan et al. 1995).

There is little information available regarding the transition of larvae from the continental shelf to juveniles in inshore nursery habitats (Jordan et al. 1995). Aotearoa juvenile jack mackerels measuring 250 cm in length have been observed in shallows and offshore north of latitude 41°S on the west coast and approximately 480 km northeast from East Cape on the east coast (Jones 1990). Jones's (1990) personal observations suggest that year-class strength is inversely related to water temperature, but this may simply reflect changes in the distribution of surface schools rather than increases in population size (Jordan et al. 1995).

Jack mackerels grow faster in Aotearoa than in Australia, maturing at 30 cm FL and reaching a maximum size of 50 cm FL (Horn 1993; Jones 1990; Smith-Vaniz 2015). Schools are size-structured with larger fish schooling in deeper waters, and smaller fish occurring predominantly in shallower and surface waters (Jordan et al. 1995; Smith-Vaniz 2015). However, Horn (1993) notes that all age classes can be found between 75 and 150 m depth in Aotearoa waters.

Implications for Little Ice Age Populations

There is relatively little information available on the distribution and population characteristics of the jack mackerel stock in Aotearoa. If they are comparable to the better studied Tasmanian stock, they should be highly sensitive to changes in water temperature, which affects both prey abundance and distribution, and the distributions of eggs and larvae. Jack mackerels may have responded to decreases in mean SST associated with the LIA by shifting their range northwards. Decreasing temperatures could also increase the population size, or at least increase the apparent population size by creating conditions that are more favourable for surface schooling. Faster growth rates in Aotearoa compared to Australia could also be a product of mean SST, and further decreases could have resulted in even faster growth rates and higher mean body sizes.

Horse Mackerel (*Trachurus novaezelandiae*)

Horse mackerel have the most northerly range of any *Trachurus* species, with populations in Australia and in Aotearoa north of Otago (Jones 1990; Smith-Vaniz 2015). *Trachurus novaezelandiae* are found further inshore than either *T. declivis* or *T. murphyi*, with a large portion of the population occurring within 22 km of shore (Francis 2012; Horn 1993). Horse mackerel school in the midwater of shallow bays and harbours, off of islands, and near to reefs (Francis 2012). They also form dense concentrations on the seabed during the day (Smith-Vaniz 2015), and school at the surface inshore to the continental shelf edge from winter to early summer (Jones 1990). Stevens et al. (1984) observed that *T. novaezelandiae* are caught at depths up to 140 m, and that they often mixed with *T. declivis*, while Jones (1990) states they occur up to 200 m below the surface with kahawai (*Arripis trutta*), trevally, and blue mackerel (*Scomber australasicus*). Smith-Vaniz (2015) suggests a maximum depth of 550 m. According to Jones (1990), they are usually only found in water that is warmer than 13°C.

Spawning may take place from spring to summer, with eggs reported in east Northland and in the Hauraki Gulf, and high abundances of larvae appearing from December to February (Francis 2012; Jones 1990). Larvae have also been recorded in South Taranaki Bight (Jones 1990). Horse mackerel appear to grow faster in the Bay of Plenty than on the west coast of Aotearoa (Horn 1993). Little information has been reported on juveniles or the mechanisms of horse mackerel recruitment.

Maturity is reached by 25 cm FL or 3 years of age, and they grow to a maximum size of 45 cm (Francis 2012; Smith-Vaniz 2015). Body size appears to increase with depth (Stewart and Ferrell 2001).

Implications for Little Ice Age Populations

Decreases in SST would probably lead horse mackerel populations to shift northward, but it seems unlikely that they would retreat very far north from their current range limit. There is not enough information to develop expectations for changes in population size or body size distributions.

Family Sparidae

Snapper (*Chrysophrys auratus* = *Pagrus auratus*)

Snapper are widely distributed throughout the Indo-Pacific region south of latitude 18°S. In Aotearoa, they are one of the most abundant coastal fish species in the northern North Island, and they are found throughout the North Island and the northern South Island (Francis 1993, 2012; French et al. 2012; Parsons et al. 2014; Trnski and Roberts 2015a). The taxonomic history of snapper is convoluted, and snapper have been described with over 20 scientific names. Genetic studies united Australian and Aotearoa snappers under one species name, *Pagrus auratus*, and determined that they are separate from Japanese snapper, *P. major*. More recently, fisheries biologists have recommended reinstating the genus *Chrysophrys* for Australian and Aotearoa snapper, with mixed acceptance (Parsons et al. 2014; Roberts et al. 2020; Trnski and Roberts 2015a).

Adult snapper are associated with a wide range of habitats, including estuaries, harbours, reefs, mud, and sand, largely between 20 and 60 m depth but also up to 300 m (Curley et al. 2013; Francis 2012; Jackson et al. 2014; Parsons et al. 2014; Trnski and Roberts 2015a). Some observations suggest there is a discrete population of semi-pelagic 'school snapper' that move together across long distances between inshore and open ocean environments (Curley et al. 2013; Parsons et al. 2014). Large spawning aggregations form in open water during summer, with 'resident' snapper migrating between 10 and 50 km from their home range and putative 'school' snapper migrating hundreds of kilometres to participate (Curley et al. 2013; Francis 2012; Parsons et al. 2014). The home ranges of adults overlap with one another and are about 650 m in diameter, but they are not fixed (Curley et al. 2013). For example, large adult fish may remain in protected marine reserves after seasonal onshore migrations if there is no harvest pressure, creating rapid changes in the abundance and mean body size of snapper in protected areas that could be mistaken for recovery of local populations (Denny et al. 2003).

Spawning activity across snapper's entire range is concentrated in months where mean water temperature is between 19°C and 21°C (Jackson et al. 2014; Wakefield et al. 2015). Aotearoa snapper spawn on a daily basis over an extended period beginning around September when SST increases to 15°C and ending around March when SST is approximately 20°C. Spawning success is only possible for a portion of that time – as low as 3.5 months in the Hauraki Gulf and 1 or 2 months in Kaipara Harbour – leading some to describe the long spawning season as bet-hedging behaviour (Francis 2012; Parsons et al. 2014; Scott and Pankhurst 1992; Sim-Smith et al. 2013). However, snapper may not spawn if temperatures do not reach a minimum threshold, as southern Australian stocks failed to spawn in 2005 during a 40 year low in SST (Wakefield et al. 2015).

Snapper are highly fecund, with individual females producing approximately 60,000 eggs per day per kilogram of body weight. A fish measuring 25 cm FL may produce 80,000 to 300,000 eggs per season, and a 50 cm fish might produce 4.5 to 6 million eggs per season (Parsons et al. 2014). Eggs hatch 20 to 30 hours after fertilisation (Jackson et al. 2014), but 83% of eggs die before hatching (Parsons et al. 2014). Experiments with laboratory hatched eggs indicate that mortality is probably related to SST, as less than 5% of eggs successfully hatched when held at temperatures between 15°C and 18.5°C, while eggs held at above 19°C had greater than 80% successful hatching rates (Sim-Smith et al. 2013).

Mortality is also high for larvae, with up to 98% of larvae dying within 8 days of hatching. Most deaths are probably caused by predation, but temperature and food availability also play important roles (Parsons et al. 2014; Zeldis et al. 2005). Larval growth rates increase with SST between 15°C and 24°C. Faster growth decreases the duration of the pelagic larval stage and helps to increase survival and recruitment rates, possibly because small, slow-growing individuals that have few lipid stores are vulnerable to starvation during winter in the early period of their lives (Francis 1993; Hamer and Jenkins 2004; Parsons et al. 2014). Overall, larval survival appears to be closely associated with SST greater than 18°C (Hamer and Jenkins 2004; Parsons et al. 2014). However, snapper larvae do survive abnormally cold temperatures if there is a high availability of their planktonic prey (Hirst and Hamer 2013; Parsons et al. 2014; Zeldis et al. 2005). For example, unusually low summer SSTs of 16.6°C to 17.3°C in 1987 coincided with unusually high prey abundances, enabling Hauraki Gulf snapper larvae to survive at normal rates. Even when summer SSTs are high and constant across successive years, fluctuations in planktonic productivity lead to high variability in snapper year-class strengths (Zeldis et al. 2005).

Juvenile snapper measuring 1 to 6 cm FL are common in shallow Aotearoa estuaries, harbours, and bays from December to April. The highest densities of newly settled juveniles 1 to 2 cm SL are particularly concentrated in sheltered estuaries with structured habitats like seagrass, horse mussel beds, and sponge gardens (Jackson et al. 2014; Parsons et al. 2014; Sim-Smith et al. 2013; Trnski and Roberts 2015a). However, some areas inhabited by snapper stocks lack estuaries, so larvae may also settle in coastal or deep-water inshore environments. Some sites with consistently high abundances of small juvenile snapper may have high larval supply or high food availability (Parsons et al. 2014). Snapper larvae and juveniles also appear to follow odour cues to preferred settlement areas (Sim-Smith et al. 2013). Juveniles may spend up to two years in nurseries, but they usually undergo an ontogenetic shift between 5 and 10 cm FL and migrate out into coastal environments and deeper harbour waters between 5 and 20 m deep (Curley et al. 2013; Hamer and Jenkins 2004; Parsons et al. 2014).

Snapper are probably protogynous hermaphrodites, where all fish are born as females and then about half change sex when they reach maturity (Francis 2012; Parsons et al. 2014). However, Curley et al. (2013) and Wakefield et al. (2015) write that juveniles possess both male and female reproductive tissue and then mature into sexually mature males or females. Growth rates, size at maturity, and age at maturity highly variable. Snapper may mature at anywhere between 20 and 30 cm FL, or between 2 and 5 years of age (Francis 2012; Hamer and Jenkins 2004; Jackson et al. 2014; Parsons et al. 2014; Trnski and Roberts 2015a). While growth rates in the first 6 months are largely correlated with SST, growth over the remaining life span is probably controlled by population density, where increasing density increases competition for food, decreasing growth rates (Parsons et al. 2014). Snapper live to a maximum age of 65 in Aotearoa (Francis 2012), while Australian snapper living in warmer waters only live to 41 years (Hamer and Jenkins 2004; Jackson et al. 2014).

Implications for Little Ice Age Populations

SST has several important effects on snapper recruitment during the early stages of its life history. Decreasing mean SST in the LIA would have almost certainly limited the survival and development of eggs, and the growth and survival of larvae, assuming that plankton productivity did not compensate for temperature effects. Because snapper is such a long-lived species, short-term fluctuations in annual recruitment rates probably don't have a large effect on the total biomass of the fishery, but it's likely that long-term shifts in SST could lead to cumulative effects that are visible at the population level, especially at the geographic extremes of snapper distributions (Francis 1993). In short, I expect that snapper population sizes would have decreased throughout Aotearoa in the LIA, and that they would have retreated northwards, potentially limiting their range to the North Island. I also expect that these decreases in population size caused the mean body size of snapper to increase for three reasons. First, decreasing recruitment rates in such a long-lived species would, by definition, decrease the proportion of small-bodied, young fish relative to large, older fish. Second, if juvenile and adult growth rates are limited by competition for food, decreases in population size should have increased the availability of food, leading to increased growth rates and shifting the body size distribution towards larger individuals. Finally, the maximum age of snapper may be influenced by temperature, with colder-water Aotearoa snapper living longer than populations in Australia. It is possible that decreasing SST in the LIA lead to even longer-life spans, increasing the number of very old, very large snapper in the population.

Family Arripidae

Kahawai (*Arripis trutta*)

Kahawai are found in southeast Australia and Aotearoa, where they are common in the North Island and the Chatham Islands, and present in all but the southernmost South Island (Francis 2012; Hughes et al. 2013; Moore and Chaplin 2013; Trnski and Roberts 2015b). They were previously described as a subspecies (*Arripis trutta marginata*) that was conspecific with the western Australian salmon (formerly *A. trutta esper*, now *A. truttaceus*) (e.g. Stanley and Malcolm 1977). These are now considered to be separate species that diverged 700 kya under Late Quaternary glacial conditions which isolated eastern and western populations on opposite sides of the Bassian Isthmus, a land bridge that appears in southeast Australia during glacial periods (Moore and Chaplin 2014). A third *Arripis* species, northern Kahawai (*A. xylabion*) can also be found in the Kermadec Islands and the northernmost North Island, but it is scarce in mainland waters. Kahawai (*A. trutta*) inhabit estuaries, bays, harbours, reefs, and open coasts, and can also be found in rivers. It is a pelagic species that feeds throughout the water column from the surface to 223 m depth (Francis 2012; Hughes et al. 2013; Trnski and Roberts 2015b). They also form large inshore schools, especially during spawning seasons (Stanley and Malcolm 1977).

Kahawai population demographics are widely influenced by latitudinal gradients in temperature, food quality and quantity, marine productivity, and habitat (Hughes et al. 2017). In northern Aotearoa, they spawn from January to March, but in the south spawning occurs in March and April (Francis 2012). Spawning in Australian stocks generally coincides with spring and summer periods that have the highest ocean current velocities, which helps transport and disperse eggs and larvae (Hughes et al. 2017; Moore and Chaplin 2013). Larvae grow into juveniles during their migration to estuaries and shallow coastal waters, which serve as nurseries (Francis 2012; Hirst and Hamer 2013; Robertson 1982).

Growth appears to be controlled by water temperature, as Aotearoa populations grow slower than Australian kahawai, and are on average 3 cm smaller at any given age. Within Aotearoa, South Island kahawai grow slower than North Island kahawai (Hughes et al. 2017). Maturity is reached in 3 to 5 years at lengths of 300 to 40 cm (Francis 2012; Trnski and Roberts 2015b), and females grow slightly faster and larger than males after 5 years (Hughes et al. 2017). Kahawai live for up to 26 years and grow to a maximum of 79 cm FL, though it is more common that they stop growing at 60 cm (Hughes et al. 2017; Trnski and Roberts 2015b).

Implications for Little Ice Age Populations

While Hirst and Hamer (2013) suggest that kahawai larvae are vulnerable to changes in water temperature, it is not clear how decreases in mean SST would affect kahawai population sizes. Growth rates appear to be correlated with SST, so it is likely that mean body size decreased during the LIA. Likewise, their range may have contracted northwards, but it seems unlikely that they would have retreated from the northern North Island.

Family Latridae

Tarakihi (*Nemadactylus macropterus*)

Tarakihi are distributed throughout south Australia, in Aotearoa from the Three Kings Islands in the north to the Snares Islands in the south, and the Chatham Islands

(Roberts 2015a). Some descriptions report that they also occur in the Indian Ocean and off the southern coast of South America (Annala 1987; Hanchet and Field 2001; Jordan 2001a), but these may be misidentifications or based on taxonomic designations that have since been revised; *Nemadactylus macropterus* was formerly assigned to genus *Cheilodactylus*. Roberts et al. (2020) also recently reassigned this species from family Cheilodactylidae to Latridae. Tarakihi are typically found over mud and sand, and occasionally in small groups near reef edges. They are caught at depths from 3 to 462 m, but they are most commonly above 100 m, and in southern Aotearoa they are typically in waters less than 25 m deep (Annala 1987; Francis 2012; Roberts 2015a). During the winter they move to slightly shallower waters (Annala 1987).

Spawning takes place in large schools that only form at a few known spawning grounds: Fiordland to south Westland, Bay of Plenty to East Cape, and in northeast South Island from Conway Ridge to Pegasus Bay (Francis 2012; Hanchet and Field 2001; Roberts 2015a). Ripe fish and eggs have also been found along the west South Island and the eastern North Island, which suggests there are spawning grounds in those areas, and it's likely that there is a separate spawning ground in the Chatham Islands (Hanchet and Field 2001). According to some surveys, eggs are not found from Dusky Sound, Fiordland to Banks Peninsula, Otago, nor in the Bay of Islands, nor off North Cape (Annala 1987), and there may not be any spawning grounds in these areas. Eggs are released in batches over several months, but the timing of the spawning period is highly variable across the various spawning grounds. Spawning largely takes place from summer to late autumn, but northern populations in the Bay of Plenty and East Cape spawn from March to June (Annala 1987; Francis 2012; Hanchet and Field 2001; Roberts 2015a).

After hatching, larvae spend an extended period of time drifting offshore. In this period, larvae develop a laterally compressed body and are referred to as 'paperfish.' These epi-pelagic larvae drift for 7 to 12 months before developing into juveniles and migrating to nursery grounds (Francis 2012; Jordan 2001a; Roberts 2015a). Juveniles predominantly settle over rocky grounds at lengths of 60 to 9 cm and shallow waters during the late spring and early summer in Tasman Bay and Golden Bay, east South Island, and the Chatham Islands (Francis 2012; Hanchet and Field 2001). Smaller nurseries have also been noted in the North Taranaki Bight, Hawke's Bay, east Bay of Plenty, Castlepoint, Manawatu, and Foveaux Strait (Hanchet and Field 2001). Overall, there is little understanding of the environmental factors that affect recruitment variability (Hanchet and Field 2001; Jordan 2001a).

Growth is rapid over the first three years, with females growing larger and faster than males (Francis 2012; Jordan 2001b). When maturity is reached after 4 or 5 years, females are between 280 and 34 cm in length, while males are only 250 to 30 cm long (Annala 1987; Francis 2012). Growth rates of Tasmanian tarakihi are also highly seasonal, with the fastest growth occurring during summer and autumn when water temperatures are at their maximum (Jordan 2001b). Adults move to deeper water as they grow larger (Jordan 2001a), reaching a maximum size of 50 cm SL and living for up to 50 years, though fish older than 15 years old are rare (Roberts 2015a; Stevenson and Horn 2004). Some tarakihi make long distance movements of up to 500 km, but they don't appear to be frequent, consistent, or directed and remain poorly understood (Francis 2012; Hanchet and Field 2001; Jordan 2001a).

Implications for Little Ice Age Populations

Because growing periods appear to be related to temperature in Aotearoa, decreasing mean SST may have caused decreases in the mean body size of tarakihi during the LIA by limiting the period and rate of growth. However, tarakihi also appear to respond to decreases in temperature by relocating to shallow water. Because body sizes are typically correlated with depth, this would have the effect of increasing the mean size of fish in shallow water where they are more vulnerable to human predation. I expect the former would have the greater effect of these two factors, especially along spawning grounds where the full body size distribution of schooling adult tarakihi could have been harvested; I expect that mean body size decreased over time. As tarakihi appear to be at the southern limit of their range in northern Southland and Otago regions, I expect their range would have contracted northward, but they probably would not have retreated from northern North Island. There is not enough information about the effect of temperature on tarakihi recruitment to develop expected responses to changes in SST.

Family Labridae

Labridae, the second largest family of marine fishes, was recently reorganized to integrate species that formerly belonged to Odacidae (butterfishes) and Scaridae (parrotfishes) based on genetic analysis. Today, there are eight recognized tribes of labrids, with four tribes and 31 species represented in Aotearoa (Gomon et al. 2015a). Only four species from two tribes have been identified archaeologically (Leach 2006). Virtually all labrid species are protogynous hermaphrodites, where all individuals develop into functionally reproductive females and then the largest adults transition sex to become functional "terminal phase" males when the dominant male dies or is removed (Denny and Schiel 2002; Gomon et al. 2015a).

Labridae: Tribe Hypsigenyini

Greenbone / Butterfish (*Odax pullus*)

Greenbone are endemic to Aotearoa, and are distributed from North Cape to the Antipodes Islands, the Chatham Islands, the Snares Islands, and the Bounty Islands. They are most common south of Cook Strait, and they grow larger at increasing latitudes (Francis 2012; Gomon et al. 2015b; Paul et al. 2000). At the Three Kings Islands, they are replaced by the bluefin greenbone (*Odax cyanoallix*), which is also present in Northland (Gomon et al. 2015b; Paul et al. 2000). Greenbone (*O. pullus*) inhabit reefs and rocky coastlines with dense macroalgae like large brown seaweeds (*Ecklonia* and *Carpophyllum*) up to 40 m deep (Francis 2012; Gomon et al. 2015b; Paul et al. 2000). However, the maximum depths they inhabit are related to latitude, as adults living in the north typically remain above 10 m depth, Cook Strait greenbone go down to 20 m, and further south they go as far as 40 m deep (Paul et al. 2000). Greenbone are also frequently found in turbid, turbulent waters in the subtidal zone (Paul et al. 2000; Trip et al. 2011a).

Territorial, terminal phase greenbone spawn between midwinter and midsummer, with peaks in reproductive activity in spring and longer spawning periods in Cook Strait (July to March) compared with Otago (August to January) (Francis 2012; Gomon et al. 2015b; Paul et al. 2000). The relative size of females' ovaries increase with size and age, so that older, larger females have disproportionately greater reproductive potential (Trip et al. 2011b). Planktonic greenbone larvae settle soon after hatching in turbulent water 1 to 2 m deep with dense seaweed (Francis 2012; Gomon et al. 2015b; Paul et al. 2000).

All greenbone are female at birth, and they mature at about 1-year old at lengths of 230 to 27 cm. When they are 2 to 3 years old and between 350 and 40 cm in length, some mature females transition into males immediately after their peak spawning period (Francis 2012; Paul et al. 2000; Trip et al. 2011a). Males are usually found at greater depth than females, with males predominantly below 15 m depth, and they are highly territorial during spawning season (Francis 2012; Paul et al. 2000). Adults grow to a maximum size of 70 cm SL (Gomon et al. 2015b), and there is no statistical difference in the growth of males or females (Trip et al. 2011a). However, life span, reproductive output, population size, and maximum size all increase with latitude and decreasing water temperature (Francis 2012; Gomon et al. 2015b; Trip et al. 2014, 2016). Greenbone living at the northern limits of their range are at the limit of the species' physiological capacity to withstand high water temperatures, and they are also limited by the patchiness of macroalgae stands, which is their primary food source (Trip et al. 2016).

Implications for Little Ice Age Populations

Greenbone populations in northern Aotearoa would have greatly benefitted from decreases in mean SST during the LIA. I expect their population sizes would have increased, and that their range expanded northwards. Detecting a range expansion might be difficult though, as they are only absent from the very northern end of North Island at present. As southern populations grow larger than norther greenbone, temperature may have an effect on growth rates, and decreasing SST may have increased mean body sizes in northern Aotearoa.

Labridae: Tribe Pseudolabrini

<u>Spotty (*Notolabrus celidotus*)</u>

Spotty are endemic and widespread in Aotearoa, including Rakiura and the Chatham Islands, but it is absent from many of the smaller offshore islands like the Three Kings Islands and the Snares Islands (Francis 2012; Russell 2015). They are one of the most abundant fishes in shallow, inshore rocky reefs and estuaries up to 10 m deep, but they have also been found at up to 145 m depth (Davis and Wing 2012; Francis 2012; Russell 2015).

Spawning takes place from July to December, and both sexes spawn multiple times each season. Larvae remain planktonic for two months, and then they settle in algae as juveniles at 2 cm SL between December and February, and they reside there until they grow to 4 cm SL. Immature spotty clean other fish and feed in mid-water (Francis 2012; Russell 2015).

All spotty are female at birth, and they reach maturity at lengths of 100 to 15 cm SL by the end of their first year, though maturity may be delayed until the second year if water temperatures are low. Some fish change sex to males at about 20 cm SL when they are between 3 and 4 years old (Davis and Wing 2012; Francis 2012; Russell 2015). The ratio of females to males is reportedly 4.1:1 (Denny and Schiel 2002). Males are highly territorial during the spawning season, while females have larger home ranges and may form schools in the midwater of sheltered areas (Francis 2012:168–169). Adults grow to a maximum size of 24 cm SL (Russell 2015). Studies of heat induced cardiac failure in spotty suggest they are susceptible to heat stress, and that mitochondrial function in heart cells is impaired at 20°C (Iftikar et al. 2015).

Implications for Little Ice Age Populations

While spotty apparently experience heat stress in waters at 20°C, it is not clear that it limits their population size or distribution in northern Aotearoa, or that there are any differences in the demographics of spotty at the northern and southern extremes of their distribution. Changes in the SST may not have had measurable effects on spotty populations during the LIA. There is not enough information about spotty growth to determine if body size distributions would have changed over time.

<u>Banded Wrasse (*Notolabrus fucicola*)</u>

Banded wrasse are present in south Australia and in Aotearoa from the Three Kings Islands to the Snares Islands, and the Chatham Islands (Denny and Schiel 2002; Russell 2015). They inhabit rocky reefs with "luxuriant seaweed cover" (Francis 2012:171) and are usually above depths of 15 m, though large males have been found at up to 91 m depth (Cole et al. 2012; Russell 2015). In exposed areas, banded wrasse are usually more abundant than spotty (Francis 2012).

Spawning takes place from July to December (Denny and Schiel 2002; Francis 2012; Harwood and Lokman 2006; Russell 2015), but it may only last for a portion of this period in specific regions. For example, Harwood and Lokman (2006) found that spotty in Otago only spawned from September to December. They also observed that the timing of individual spawning events appeared to be related to tidal stimuli

(Harwood and Lokman 2006), but an earlier study in Kaikoura found that spawning coincided with increases in water temperature and primary productivity, possibly to enhance larval survival and growth (Denny and Schiel 2002). Denny and Schiel (2002) write that females of all body sizes have similar reproductive potential, while Harwood and Lokman (2006) found that females produced highly variable quantities of eggs and suggested that fecundity is related to habitat type and inversely related to latitude. Little information is available on the egg and larval period of spotty life cycles, but juveniles settle in seaweed at 30 to 4 cm from January to March, and grow to 120 cm length by the end of their first year (Francis 2012:171–172).

All banded wrasse are born female, but they can transition into males at any age. Some change sex to male before they reach maturity, and then juvenile males may mature into reproductive males or females. Juvenile females mature into reproductive females, but may change sex from female to male later in time (Denny and Schiel 2002; Russell 2015). Males are highly territorial (Russell 2015). The ratio of females to males is 1.6:1 (Denny and Schiel 2002). Maturity is reached at 20 cm, and the maximum adult size may range from 400 to 60 cm SL (Davis and Wing 2012; Denny and Schiel 2002; Russell 2015). Banded wrasse live for up to 25 years (Francis 2012; Russell 2015).

Implications for Little Ice Age Populations

If Harwood and Lokman's (2006) suggestion that banded wrasse fecundity increases with decreasing latitude is correct, temperature may have an important effect on reproductive potential, and decreasing mean SST in the LIA might have caused reductions in banded wrasse population sizes. On the other hand, there aren't any clear differences in banded wrasse populations at the northern and southern extremes of their distribution, so changes in fecundity may not actually affect population size. Given the wide latitudinal rage that banded wrasse inhabit, it is unlikely that the LIA caused appreciable range shifts. There is not enough information available on banded wrasse growth to determine whether body size distributions would have changed.

<u>Scarlet Wrasse (*Pseudolabrus miles*)</u>

Scarlet wrasse are endemic to Aotearoa and are found from the Three Kings Islands to the Shares Islands and in the Chatham Islands (Francis 2012; Russell 2015). They have also been reported in Japan and Australia but these are probably misidentifications (Russell 2015). They are most abundant in the Three Kings Islands and at the southernmost part of their range (Francis 2012). Scarlet wrasse inhabit deeper reefs, and can usually be found among boulders, broken rock, and in crevices below 10 m depth (Cole et al. 2012; Francis 2012; Russell 2015).

Breeding fish move to deeper water between late winter and spring for the spawning season (Russell 2015). Little information is available on the development of scarlet wrasse eggs and larvae. Juveniles 5 cm long arrive in shallow waters and rockpools between February and March, where they might act as cleaner symbionts (Francis 2012; Russell 2015). Adult females also clean larger fish (Francis 2012).

Different authors have various perspectives on scarlet wrasse maturation. Francis (2012) writes that scarlet wrasse mature at 1 year old into females that breed for two to three years before changing sex at 4 years old. Davis and Wing (2012) note that scarlet wrasse are hermaphroditic, and that they mature at 4 years old. Russell (2015) writes that females usually change sex to males during the non-breeding season when they are 3 years old and measure 20 cm SL. Adults reach a maximum size between 325 and 35 cm SL (Davis and Wing 2012; Russell 2015).

Implications for Little Ice Age Populations

There is very little information available on scarlet wrasse that helps to develop expectations about the effects of the LIA. The higher abundances in the southernmost part of their range may indicate that lower temperatures favour larger populations. However, they are also reportedly abundant in the Three Kings Islands at the northernmost limit of their range, so these differences in population size may actually be related to food availability, habitat availability, or other factors. Scarlet wrasse inhabit a wide latitudinal range, and it is unlikely that decreases in water temperature would affect their distribution, especially in northern Aotearoa.

Family Pinguipedidae

Blue Cod (*Parapercis colias*)

Blue cod are endemic to Aotearoa and are present from the Three Kings Islands south to the Snares Islands, though they are most abundant in cooler waters south of Cook Strait. They are often found resting on the seabed propped up on their pelvic and caudal fins over sand, gravel, and reef edges at depths of 5 to 150 m, but they are most abundant between 15 and 150 m depth (Beentjes and Carbines 2005; Beer 2011; Francis 2012; Johnson and Struthers 2015).

The reproductive biology of blue cod is poorly understood even though it has been studied since the 1950s (Beer 2011). Spawning occurs over a period of several months between June and January, where southern populations spawn earlier and longer (Beer 2011; Johnson and Struthers 2015). Female egg productivity is closely related to age and, to a lesser degree, body size. In Fiordland, a 24 year old female produces over 100 times more eggs than a 6 year old fish, and over 60 times more eggs than a 7 year old fish (Beer 2011). Blue cod eggs remain pelagic for five days after spawning, and larvae spend another 5 days before settling (Beer 2011; Gebbie 2014). According to one study, eggs can drift 74 km before hatching, and larvae have travelled to sites 111 km from spawning locations (Robertson, 1980 in Beer 2011). Despite the short pelagic larval duration, juveniles measuring 5 cm long only begin to appear in January and February near reef edges on pebble and shell substrates below 15 m depth. As they grow, they move into progressively shallower waters (Francis 2012).

From birth, blue cod populations have a mix of males and females (Beentjes and Carbines 2005). Males grow faster than females, and growth rates are comparable across their geographic distribution (Beer 2011). Males in Northland appear to mature at a smaller size (100 to 19 cm long, 2 to 3 years old) than Southland males (260 to 28 cm long, 4 to 6 years old) (Gebbie 2014). Females show a similar pattern, maturing at 11 cm TL by the age of 2 years old in Northland, at 28 cm TL and 6 years old in Foveaux Strait, and at 29 cm TL in Dusky Sound (Beer 2011). Males are sedentary and defend a loosely defined territory with 3 to 5 resident females (Beer 2011; Cole et al. 2000; Gebbie 2014). Francis (2012) suggests that sex inversion from female to male occurs primarily between ages 6 and 11 years old, but female sex change can occur at any age and is triggered by the death or removal of large dominant males (Beentjes and Carbines 2005; Beer 2011). Adults live to be 32 years old, with males growing to a maximum size of 60 cm SL and females growing to 40 cm SL (Francis 2012; Johnson and Struthers 2015), although Beer (2011) reports that females may grow to 54 cm.

Like many protogynous hermaphrodites, blue cod are highly vulnerable to fishing practices that target the largest fish in a population. Intense harvesting of large males stimulates many females to change sex, creating a male-dominated population structure (Beentjes and Carbines 2005; Beer 2011). These changes dramatically reduce the reproductive potential of the population, especially as the oldest females that contribute disproportionately large quantities of eggs when they spawn are the most likely fish to invert sex (Beer 2011). Establishing marine reserves helps allow body size distributions to recover (Davidson 2001; Pande et al. 2008). However, protected areas do not necessarily contribute towards population size recovery because blue cod are highly sedentary and territorial, which prevents high population densities from forming in any marine reserves, and the fish that leave are quickly harvested (Pande et al. 2008). Furthermore, blue cod populations in nearshore areas are probably subsidized from spawning sources further out on the continental shelf, which are often not protected from harvesting (Beer 2011).

Implications for Little Ice Age Populations

There is little information available about the relationships between environmental factors and blue cod demographics. Blue cod are more abundant at higher latitudes in cooler waters, but the mechanism behind this pattern is not understood. It is possible that the delayed maturation of southern populations affords them more spawning opportunities and greater fecundity, but these sorts of trade-offs are usually only beneficial where the stocks with delayed maturation also grow to larger sizes and have longer life spans (Trip et al. 2011a). Regardless, decreasing water temperature in the LIA may have allowed northern blue cod populations to increase. There is no known latitudinal gradient in growth rates, so body size distributions probably did not change, and it is unlikely that their range shifted in any way.

Family Gempylidae

<u>Barracouta (*Thyrsites atun*)</u>

Barracouta are widespread in coastal waters of the southern hemisphere from temperate to subantarctic zones. They prefer temperatures of 10°C to 13°C, up to a maximum of 18°C. In Aotearoa, they are more abundant to the south than in the north (Griffiths 2002, 2003; Hurst and Bagley 1989; Stewart 2015b). They are highly mobile schooling fish that range from the surface to the seabed up to 550 m depth (Griffiths 2002; Stewart 2015b).

Spawning takes place in large offshore aggregations between 30 m and 115 m depth according to Crawford et al. (1990), and 150 m to 400 m depth according to

Griffiths (2002). Horn (2002) observed spawning across four different locations in southern Aotearoa. Langley and Bentley (2002) also note that spawning fish are present in all South Island fisheries and observed a discrete spawning season from August to October in the western South Island stock, which includes fish that migrate from Taranaki and the Tasman Bay to spawn. Energetic demands associated with spawning are higher for females than males. Barracouta eggs are transported to nursery areas by prevailing currents, and hatch two days after fertilization. Young of the year may also follow schools of clupeid prey inshore, and then move further offshore when the clupeid schools migrate away. In South Africa, larval abundances are greatest in spring and summer (Griffiths 2002), though a subsequent study noted two separate pulses of egg and larvae in winter and spring (Griffiths 2003).

Juvenile barracouta are widespread in Aotearoa coastal waters above 150 m depth, with higher concentrations in Tasman Bay, Hauraki Gulf, and the South Island and fewer juveniles observed in Southland (Horn 2002; Langley and Bentley 2002). Growth rates appear highly variable across populations, which may relate to differences in the timing of spawning events for individual cohorts. Southland barracouta also show interannual variation in growth rates, especially among juveniles, making it difficult to determine their age based on size alone (Horn 2002). In South Africa, they mature between 3 and 4 years of age and probably join adult stocks as they return northward after spawning (Crawford et al. 1990). Adults grow to a maximum size of 150 cm SL, though they normally only reach lengths of 100 cm in Aotearoa (Stewart 2015b).

Adult barracouta make large migrations while maintaining distinct stocks. Griffiths (2002) found that female barracouta in South Africa move inshore between spawning events to find higher densities of prey. Aotearoa barracouta also move inshore over summer and autumn to feed in surface waters (Stewart 2015b). Tagging experiments show that longer migrations are mostly directional and seasonal, with Aotearoa barracouta moving up to ~925 km northwards in 188 days between February and September (Hurst and Bagley 1989). Qualitative patterns in barracouta populations suggest there are at least three separate stocks along the west coast of Aotearoa (South Island, Tasman Bay, western Cook Strait, and Taranaki), the east coast, and Southland, with limited population exchange between eastern South Island and western North Island schools (Langley and Bentley 2002).

Implications for Little Ice Age Populations

Barracouta are present throughout Aotearoa today, but northern North Island populations risk exposure to temperatures that are well above their preferred thermal range or potentially beyond their thermal tolerances. Decreasing temperatures associated with the LIA could very likely have ameliorated these thermal challenges, allowing their populations to grow and increasing their encounter rates with human fisheries as they would be able to spend more of the year in coastal waters. Although Southland stocks may have experienced some environmental stress if water temperatures dropped substantially there, it's not clear that there would have been any change in the range of barracouta, especially in the northern North Island. There is not enough information available on the factors that control barracouta growth rates to determine whether the LIA would have affected body size distributions.

Family Scombridae

Blue Mackerel (*Scomber australasicus*)

Blue mackerel are widely distributed in temperate and subtropical waters across the Red Sea, the Persian Gulf, the Indo-Pacific, north to Japan, south to Australia and Aotearoa, Hawaii, and east to Socorro Island (Francis 2012; Roberts 2015b; Schmaar et al. 2011; Smith et al. 2005; Taylor 2002). Schmaar et al. (2011) found differences in mitochondrial DNA between blue mackerel from West Australia, Queensland, and Aotearoa that suggest there is no gene flow between these populations. They are abundant in Aotearoa coastal waters, forming large surface schools during summer in Northland, Bay of Plenty, South Taranaki Bight, and Kaikoura. In winter they move to deeper waters and commercial catch rates drop off substantially (Ballara 2016; Francis 2012; Taylor 2002). Studies from the Great Australian Bight found that blue mackerel are largely captured at 50 m to 150 m depth with no observed relationship between length and depth (Stevens et al. 1984), while blue mackerel in the East China Sea show a preference for waters between 17°C and 25°C, though Sassa and Tsukamoto (2010) caution that different populations probably have different optimum temperatures. In Aotearoa, they are captured above 250 m depth (Smith et al. 2005).

Spawning occurs serially over spring and summer in Aotearoa (Francis 2012; Roberts 2015b; Rogers et al. 2009), and from summer through autumn in New South Wales (Schmaar et al. 2011). Reproduction in Australian blue mackerel is closely tied to temperature, with no spawning taking place below 17°C (Neira and Keane 2008). Blue mackerel from Aotearoa may be able to spawn at lower temperatures, as some studies have identified active gonads during July when SST would be below 15°C (Taylor 2002). Spawning events take place every 2 to 11 days.

For the most part, blue mackerel eggs are only found from spring to summer at water temperatures of 15°C to 23°C in Aotearoa (Ballara 2016; Taylor 2002), and they are exclusively captured in waters between 18°C and 22°C in southeast Australia. In Tasmania, eggs are notably absent from water between 16°C and 17°C (Neira and Keane 2008). Neira and Keane (2008) also observed that the preferred spawning areas of blue mackerel are associated with upwelling hotspots within ~18 km shoreward of the continental shelf-break at 100 m to 125 m depth. Aotearoa blue mackerel have at least three separate spawning areas in Northland and the Hauraki Gulf, western Bay of Plenty, and the South Taranaki Bight, and a possible fourth concentration in Tasman Bay (Ballara 2016; Smith et al. 2005; Taylor 2002).

Egg and larval development are thought to be closely dependent on temperature (Ballara 2016; Taylor 2002). In the closely related species *Scomber japonicus*, which is more tolerant of cold water, eggs fail to hatch below 14°C (Neira and Keane 2008). In the East China Sea, blue mackerel larvae are predominately distributed in waters of 20°C to 23°C. However, they substantial variation in growth has also been observed despite very slight differences in temperature (0.1°C to 0.5°C change), suggesting that higher than normal prey abundances can increase growth rates. Eggs and larvae are passively transported by pelagic currents until 3 to 4 weeks after fertilization when larvae reach about 2 cm SL and they begin swimming and schooling (Sassa and Tsukamoto 2010). Between North Cape and East Cape on the North Island, the greatest concentrations of eggs are found in the Hauraki Gulf and in western Bay of Plenty in December and April, though they are probably present throughout summer (Taylor 2002).

Juvenile blue mackerels show a more northerly distribution than adults, with few juveniles present south of the North Island or Golden Bay and Tasman Bay. Yearlings are usually collected from bottom trawls of shallow water, and their inshore distributions may be related to prey abundances (Ballara 2016; Francis 2012; Taylor 2002). They display rapid but variable growth, with individuals in Aotearoa reaching between 17 cm and 35 cm FL by their first year of age. While otolith aging methods have not been validated, making aging attempts very difficult and variable, the mean FL at age shows large differences between regions: 26 cm at 1 year and 31.9 cm at 3 years in Aotearoa, 20.9 cm at 1 year and 29.4 cm at 3 years in the Great Australian Bight, and 31 cm at 1 year and 34 cm at 3 years in Taiwan (Stewart and Ferrell 2001).

Blue mackerel are thought to reach sexual maturity between 23 cm and 30 cm FL and grow to a maximum size of 44 cm FL (Francis 2012; Roberts 2015b; Stevens et al. 1984; Taylor 2002), though Rogers et al. (2009) state they mature at a mean size of 31.8 cm. Differences in aging methods make it difficult to determine their maximum age. While one Bay of Plenty study found that they live to 24 years with a mode of 8 to 10 years (in Ballara 2016), Roberts (2015b) states they only live to 7 years. They form large schools over continental shelves mixed with jack mackerel, kahawai, skipjack tuna, and trevally (Ballara 2016). Smaller, younger fish are more likely to be found closer to the coast (Taylor 2002), and fish form schools according to size (Schmaar et al. 2011). It is still unclear whether blue mackerel follow any migratory patterns or whether they maintain connections with particular spawning areas (Ballara 2016; Taylor 2002).

Implications for Little Ice Age Populations

While there is some ambiguity in the literature, blue mackerel spawning and early life history appear to be closely controlled by SST. As the Aotearoa stocks appear largely unable to reproduce below 15°C, the onset of LIA conditions could have impacted blue mackerel populations. However, if primary productivity increased in this period any increases in prey availability might have ameliorated these climate drivers. As blue mackerel are at the southern extent of their range in Kaikoura, and juveniles are not found south of Tasman and Golden Bays, the decreases in SST might have also caused their range to retreat northwards, but it’s likely this range shift would have been observed in northern Aotearoa. Given the wide variation in blue mackerel growth rates and a poor understanding of the factors that control growth, there is not enough information to make predictions about changes in body size distributions.

Order Pleuronectiformes

In a global review of flatfish recruitment patterns, van der Veer (1994) found no evidence for starvation or density-dependent population growth in flatfishes. Year-class strength in temperate species is clearly established during the planktonic or early demersal stages of flatfish life histories. While juvenile somatic growth rates are affected by population density, temperature, and prey density, growth rates and size-selective mortality do not explain variability in interannual abundances (van der Veer et al. 1994).

Family Bothidae

Witch (*Arnoglossus scapha*)

Witch is an endemic species of lefteye flounder that is widespread across Aotearoa continental shelves (Munroe 2015a). They inhabit coarse sand and muddy substrata in shallow water, harbours, embayments, and to 737 m depth, but they are mostly found between 30 m and 300 m depth (Francis 2012; Munroe 2015a). Witches have a varied diet that suggests they may also predate in midwater at night as well as from the seabed (Francis 2012).

Spawning takes place on the continental shelf up to 100 m depth from August to April (Francis 2012; Munroe 2015a). Larvae remain in a prolonged pelagic stage for several months, and juveniles smaller than 11 cm SL are also pelagic at depths of 30 m to 350 m where bottom depth is 1700 m to 2100 m. Adults grow to a maximum size of 35 cm SL. Munroe (2015a) notes their flesh is thin and water with many fine bones.

Implications for Little Ice Age Populations

There is very little information available on the effects of changing climate on witch populations. However, their wide distribution across Aotearoa suggests they can tolerate a wide range of conditions, and it is unlikely that they would have been impacted in the northern North Island. There is not enough information on witch growth to determine if body size distributions would have changed.

Family Rhombosoleidae

Rhombosoleidae was previously considered one of five subfamilies in Pleuronectidae, which contained all Northern and Southern hemisphere righteye flatfishes (Munroe 2015b). Chapleau and Keast (1988; Chapleau, 1993) raised each of these subfamilies to family status by contrasting their morphological characteristics. However, the taxonomic classifications of righteye flatfishes requires additional work, as some species of Rhombosoleidae more closely resemble members of Soleidae than their own family (Munroe 2015b).

New Zealand Turbot (*Colistium nudipinnis*)

Turbot are endemic and widespread from Northland to the southern South Island, though their distribution is patchy and they are most commonly captured off the west coast of the South Island (Hickman et al. 2002; Munroe 2015b; Stevens et al. 2005; Tait and Hickman 2001). They are common in nearshore and subtidal waters over sand and mud, and also on the inner continental shelf to 50 m depth. Turbot are occasionally found in bays and estuary mouths (Munroe 2015b), but older individuals may have lower tolerances for the fluctuations in salinity in those habitats (Hickman et al. 2002).

Spawning takes place from July to August, though ovaries remain enlarged and at least a few fish spawn through January (Munroe 2015b; Tait and Hickman 2001). Ovulation and spawning occur primarily in the late afternoon and early evening, with one study showing that 92% of eggs produced in a given day are released in within two hours of sunset. Low semen production in males suggests that spawning takes place in close proximity, possibly in pairs (Tait and Hickman 2001). While experimentally raising turbot in laboratory conditions to test their suitability for aquaculture, Tait and Hickman (2001) observed 60% mortality in eggs and larvae before first feeding at 3 to 4 days after hatching, and more than 80% mortality in larvae by 10 days. Eggs hatched 84 hours after fertilization at 14°C. Larvae initially measured an average length of 2.2 mm and immediately rose to the surface. After 36 hours most larvae moved deeper in the water column. Larvae grew to 14 mm in 20 to 22 days, and 31 mm in 57 days.

Juvenile turbot are present inshore and can be captured with push-nets from shallow sandy bays, suggesting they may be able to tolerate salinity fluctuations (Hickman et al. 2002). Hickman et al. (2002) experimentally reared juveniles in laboratory conditions and found that optimum growth conditions were achieved at moderate salinity levels (23 g/L), but only when tanks used recycled water with 2x to 3x the bacterial load of fresh water. Length frequencies of wild turbot from Lyall Bay near Wellington indicate there may be as many as four recruitment episodes in a single year, with strong recruitment in January, July, and October, and a weaker episode in March. Juveniles initially settle at 2 cm to 4 cm TL and then grow rapidly over the next 6 months (Stevens et al. 2005).

Measurements of juvenile turbot growth suggest that optimum growth is achieved at around 16°C. Hickman and Tait's (2001) growth experiments found that growth was much faster around temperatures of 16°C compared to warmer temperatures of 20°C or 22°C to 24°C, though they also observed substantial variation in growth rates within each treatment. Fish kept in water at 24°C experienced 61% mortality over 10 days, and mortality rates dropped when the temperature was lowered to 22°C (Hickman and Tait 2001). Stevens et al. (2005) observed that growth in Lyall Bay was almost twice as fast in summer and fall compared with winter or spring. They also found that females grow much faster and larger than males, with females growing to 48 cm TL in 5 years while males only reach 40 cm. Growth slows substantially after 7 years (Stevens et al. 2005).

Adult turbot are the largest Aotearoa flounder, and grow to a maximum size of 97.5 cm SL, but they are more commonly caught between 25 cm and 63 cm length (Munroe 2015b; Tait and Hickman 2001). In a survey of turbot from the west South Island, the oldest male was >13 years old, and the oldest female was >16 years old. Over 80% of the catch in both sexes was younger than 10 years (Stevens et al. 2005). According to Thomson and Anderton (1921 in Tait and Hickman 2001), turbot is a "fine fish."

Implications for Little Ice Age Populations

Most of the research on this species has been conducted in the South Island or Cook Strait, and no specific information is available about the smaller northern North Island populations. However, if the higher abundances of turbot to the south are related to the cooler water temperatures there, decreasing SST may have allowed turbot abundances to increase in the north. It is unclear whether the changes in water temperature would have enhanced turbot growth rates, or only caused the seasonality of enhanced growth rates to change. It is unlikely that there would have been any change in the range of turbot.

Lemon Sole (*Pelotretis flavilatus*)

Lemon sole is endemic and found throughout Aotearoa, though it is most common between Cook Strait to the north and Dunedin to the south (Munroe 2015b; Rapson 1940). Rapson (1940) reported negligible lemon soles in Bay of Plenty, widely distributed but uncommon catches in Hauraki, and no catches north of Whangarei on the east side of Northland and none north of Ahipara on the west side. They prefer sand and mud seabeds on the continental shelf from 20 m to 150 m depth, but they are also found as shallow as 4 m and as deep as 618 m (Francis 2012; Munroe 2015b; Rapson 1940). Lemon sole is an ambush predator that buries itself in mud and sand before gulping its benthic prey (Francis 2012).

Spawning takes place from winter through spring, with larger soles beginning by July and smaller soles beginning as late as the end of August (Francis 2012; Rapson 1940). More fish spawn in the afternoon than in the morning, and spawning probably occurs over of several days with only a small number of eggs ripening at once. Larvae hatch from the pelagic eggs about 4 days after fertilization, and remain suspended without directional movement for a further 3 days (Rapson 1940). Larvae initially measure 1.9 mm to 2.8 mm in length and settle in sheltered bays when they have grown to 3 cm SL (Munroe 2015b; Rapson 1940).

Juvenile lemon soles are found in shallower water than adults. They mature at about 20 cm, and most fish mature and begin spawning by their second year when they measure 23 cm (Francis 2012; Rapson 1940). Adults can grow to a maximum size of 50 cm SL, but they usually measure 25 cm to 35 cm (Munroe 2015b). Observations from offshore sites in Blueskin Bay, Otago show there is a strong relationship between size and depth (Roper and Jillett 1981). Adults congregate in shallow water for spawning between July and September, with peak aggregations in August (Munroe 2015b). Females leave the spawning grounds in October and November (Rapson 1940).

Implications for Little Ice Age Populations

There is very little information available on the relationships between lemon sole life histories and climatic conditions. However, if the higher abundances of lemon soles to the south are related to the cooler water temperatures there, decreasing SST may have allowed lemon sole abundances to increase in the north. There is not enough information on lemon sole growth to determine if body size distributions would have changed. Lemon sole is already distributed throughout Aotearoa, and I do not expect that their range would have changed.

New Zealand Sole (*Peltorhamphus novaezeelandiae*)

New Zealand sole is endemic to Aotearoa and widespread from Northland to Southland. It is the most abundant Aotearoa flatfish, but it is more common in the South Island than in the north (Munroe 2015b). This sole inhabits sand and mud substrata in estuaries, harbours, bays, and the inner continental shelf from subtidal areas to 55 m depth, and sometimes up to 100 m to 274 m depth as well (Francis 2012; Munroe 2015b). They are easy to approach on the seabed where they are very well camouflaged, and they may swim in the midwater as well (Francis 2012).

Spawning has been observed in the South Island from July to October, peaking in August and September (Francis 2012; Munroe 2015b). Planktonic larvae are present in small quantities in Otago Harbour (Roper and Jillett 1981), while juveniles are abundant in nearshore bays and estuaries (Munroe 2015b). Maturity is reached around 16 cm SL, and adults grow to a maximum size of 52.5 cm SL. They are more commonly only 25 cm to 45 cm SL, with similar sizes in males and females (Munroe 2015b). There is a strong relationship between size and depth offshore in Blueskin Bay, Otago (Roper and Jillett 1981).

Implications for Little Ice Age Populations

There is very little information available on the relationships between New Zealand sole life histories and climatic conditions. However, if the higher abundances of New Zealand soles in the South Island are related to the cooler water temperatures there, decreasing SST may have allowed New Zealand sole abundances to increase in the north. There is not enough information on New Zealand sole growth to determine if body size distributions would have changed. New Zealand sole is already distributed throughout Aotearoa, and I do not expect that their range would have changed.

Yellowbelly flounder (*Rhombosolea leporina*)

Yellowbelly flounder is endemic and abundant to the coasts of mainland Aotearoa (though one individual has been recorded in south Australia) (Munroe 2015b), and one of only two flounder species that is abundant in the Hauraki Gulf (Colman 1972). They prefer sheltered, muddy areas in estuaries, harbours, and coastal bays from subtidal habitats to 25 m. They are also sometimes found in brackish bays and lowland rivers – but never in freshwater – and as deep as 50 m (Francis 2012; Munroe 2015b).

Adults move offshore to spawn in winter or spring. Francis (2012) writes that spawning takes place at 30 m to 40 m depth, but Colman (1973) and Munroe (2015b) report spawning at 12 m to 30 m. Analysis of ovary condition in yellowbelly flounder catches from the Hauraki Gulf shows that females are predominately ripe in September and October, and they are mostly spent from October through December (Colman 1973). Based on this evidence, all fish are assigned an analytic birthday of 1 October (Colman 1974a). Spent fish largely relocated to shallower waters in the Firth of Thames before they were captured. Planktonic surveys found that flounder eggs of indeterminate species were heavily concentrated in the area between the Coromandel Peninsula and Waiheke Island (Colman 1973). Colman (1973) notes that the factors controlling spawning onset and duration are unclear and hypothesizes that spawning only occurs with rising temperatures. He also suggests spawning at depth where temperature and salinity fluctuations are minimal may enhance egg and larval survival.

Juveniles recruit to shallow-water nurseries from July to December and gradually move to deeper water with age (Munroe 2015b). Only a few 0+ year-old individuals have ever been captured, and they were all from shallow marine/estuary waters (Colman 1974a). There are conflicting reports for size-at-maturity. Colman (1972) found that 100% of males were mature at 15 cm, and 50% of females were mature at 26 cm to 27 cm. According to Francis (2012), males mature between 15 cm and 2 cm, and females mature at 26 cm. Munroe (2015b) writes that 50% of males are mature at 24 cm TL and females are 50% mature at 30 cm TL.

Males grow to a mean length of 24 cm by their second year. Females grow to a mean length of 28 cm by their second year, and to 39 cm by their third year (Colman 1974b; Francis 2012). Colman (1974b) observed that few males live longer than two years, while adult females have bimodal size-frequencies reflecting two size categories: two-year-olds and three- to 4+ year-olds. If Colman's findings are accurate, Munroe's size-at-maturity estimates may be incorrect. Adults grow to a maximum size of 45 cm SL (Munroe 2015b).

Colman (1974a) also conducted a tagging study, which showed that yellowbelly flounders tagged in the Firth of Thames moved into deeper water for spawning in October and November, and they returned to the mouth of the Waihou River by

December. The principle flounder fisheries of the Hauraki Gulf are located in the Firth of Thames, and most yellowbelly flounders are captured in the Waihou River, at the river mouth, and in shallow coastal waters between November and March (Colman 1973, 1974a). Similar offshore-onshore migrations have also been reported for yellowbelly flounders in Tasman Bay (Colman 1974a).

Implications for Little Ice Age Populations

There is very little information available on the relationships between yellowbelly flounder life histories and climatic conditions. However, because they are distributed across a wide latitudinal range, it seems unlikely that they would be negatively impacted by decreasing SST in the north. There is not enough information on yellowbelly flounder growth to determine if body size distributions would have changed. Yellowbelly flounder is already distributed throughout Aotearoa, and I do not expect that their range would have changed.

<u>Sand Flounder (*Rhombosolea plebeia*)</u>

Sand flounder is endemic and widespread in Aotearoa from Northland to Rakiura (Munroe 2015b), and they are the second of the only two flounders that are abundant in the Hauraki Gulf (Colman 1972). They are found on soft seabeds of sand, mud, clay, and eelgrass, but also over pebble and ravel bottoms in inshore tidal flats, harbours, estuaries, and over the continental shelf to 100 m depth. They are most commonly between 20 m and 70 m depth (Francis 2012; Munroe 2015b). During the day they cover themselves in sand or mud, and they are more active while feeding at night (Francis 2012).

Spawning takes place year-round inshore and offshore to 40 m depth, with peak activity between June and December when adults move offshore (Colman 1973; Munroe 2015b), but to in the south spawning is confined to spring (Francis 2012; Roper and Jillett 1981). In the Hauraki Gulf, spawning predominately takes place in the area between the Coromandel Peninsula and Waiheke Island, where disproportionately high ovary weights indicate spawning activity takes place in two pulses from July through November. Artificially fertilized sand flounder eggs raised under laboratory conditions hatch after 4 to 5 days at 15°C (Colman 1973). Planktonic larvae are common in Otago Harbour from late winter through early summer (Roper and Jillett 1981).

Juveniles settle on the seabed and move inshore to mudflats in bays, harbours, estuaries, and rivers, where they remain for two years before migrating to deeper waters (Colman 1974a; Francis 2012; Munroe 2015b). Juveniles are present in Papanui Inlet and Hoopers Inlet in Otago throughout the year, with large numbers of small fish arriving in spring and peaking over summer then becoming rare in winter (Roper and Jillett 1981). In the Hauraki Gulf, Colman (1973) reports that more juveniles can be found in the Firth of Thames than in the area between Waiheke Island and Great Barrier Island.

There is disagreement about the size-at-maturity for sand flounders, which may be a result of the different definitions of maturity that authors use. Francis (2012) writes that males are mature at 10 cm, and females at 16 cm to 20 cm. According to Munroe (2015b), males mature between 11 cm and 12 cm TL and that females are mature at 23 cm TL. Colman (1972) reports that 50% of males are mature at 18 cm, while 50% of females are mature at 18 cm and 95% are mature at 23 cm.

Males grow to 17 cm TL by the end of their second year, and females grow to 24 cm in two years and to 30 cm after 3 years (Francis 2012; Munroe 2015b). Sand flounders can grow to a maximum size of 45 cm SL, though they rarely grow larger than 30 cm (Colman 1972; Munroe 2015b). Few fish live longer than 4 years (Francis 2012). Adults reportedly migrate between shallow waters in spring and summer, and deeper spawning grounds in autumn and winter, with similar patterns also observed in Tasman Bay and in Canterbury (Colman 1974a; Francis 2012).

Implications for Little Ice Age Populations

There is very little information available on the relationships between sand flounder life histories and climatic conditions. However, because they are distributed across a wide latitudinal range, it seems unlikely that they would be negatively impacted by decreasing SST in the north. There is not enough information on sand flounder growth to determine if body size distributions would have changed. Sand flounder is already distributed throughout Aotearoa, and I do not expect that their range would have changed.

Black Flounder (*Rhombosolea retiaria*)

Black flounder is endemic to Aotearoa and widespread in coastal waters (Munroe 2015b), though Colman (1973) reports they are not present in the Hauraki

Gulf. They are common in harbours, river mouths, and estuaries at up to 50 m depth, with a preference for soft mud, sand, vegetated areas, and gravel and cobble bottoms. They are also common up to 250 km upstream in freshwater, coastal and lowland lakes, and they can navigate gravelly rapids to make winter migrations to marine coasts. Spawning takes place in marine habitats and the eggs are pelagic. Young-of-the-year 1 cm to 1.5 cm SL arrive in rivers and coastal lakes in spring. Black flounders grow rapidly compared to other Rhombosoleids. Maturity is reached in the second or third year, and adults grow to a maximum size of 45 cm SL, though they are usually only found at 20 cm to 25 cm SL (Munroe 2015b).

Implications for Little Ice Age Populations

There is very little information available on the relationships between black flounder life histories and climatic conditions. However, because they are distributed across a wide latitudinal range, it seems unlikely that they would be negatively impacted by decreasing SST in the north. There is not enough information on black flounder growth to determine if body size distributions would have changed. Black flounder is already distributed throughout Aotearoa, and I do not expect that their range would have changed.

Order Tetraodontiformes

Family Monacanthidae

<u>Leatherjacket (*Meuschenia scaber*)</u>

Leatherjacket is widespread along the southern half of Australia, throughout Aotearoa from Kermadec Islands sea mounts to Rakiura and the Chatham Islands (Stewart and Roberts 2015; Visconti et al. 2017). The species was widely recorded as *Parika scaber*, but that genus is now considered junior to *Meuschenia* (Stewart and Roberts 2015). There are two other species of leatherjackets – smooth leatherjacket (*Aluterus monoceros*) and darkvent leatherjacket (*Thamnaconus analsi*) – that are present but rarely sighted along mainland coastal Aotearoa (Kingsford and Milicich 1987; Stewart and Roberts 2015). *Meuschenia scaber* is common on rocky reefs, above sand and mud, and in midwater from the surface to 300 m depth, though it is mainly found from 10 m to 40 m (Francis 2012; Stewart and Roberts 2015; Visconti et al. 2017).

Visconti et al. (2017) provide a thorough overview of leatherjacket spawning behaviour. Spawning takes place from August to December, with a peak in activity from September to November. Analysis of ovaries shows that female gonad weight – a proxy for reproductive activity – is negatively correlated with temperature. Spawning only appears to occur between 14°C and 16°C, which would mean it is triggered by the coldest water temperatures of Hauraki Gulf winter conditions at a time when prey abundances are highest for larvae and juveniles. Spawning behaviour has been observed at Goat Island Bay in December, where males court a female, who digs a nest in the male's territory and then rapidly lays eggs while the male nudges her. Afterwards, the female departs and the male remains in the vicinity to guard his territory, but no parental care is given to the nest. Leatherjackets may spawn daily over the course of the season like some other Monacanthids, though it is unusual for teleosts with protracted spawning seasons (Visconti et al. 2017).

Larvae are planktonic and they quickly disperse after hatching (Francis 2012; Kingsford and Milicich 1987). Kingsford and Milicich (1987) provide a thorough overview of leatherjacket early life history. Notochord flexion begins at 6.5 mm and adult pigmentation and fin counts develop by 8 mm to 9 mm length. Presettlement juveniles congregate around drift algae inshore and offshore from October through January. Most algal fish are 40 to 50 days old in November, with a range of 22 to 66 days at any given time. Fish in drift algae measure 6.8 mm to 34.6 mm long, and in tethered algae they measure between 8 mm and 24 mm long.

By late summer or early autumn, juveniles begin settling into kelp forests on reefs at 1.6 cm to 7.6 cm length, even though any algal fish are capable of settling into rocky reefs (Francis 2012; Kingsford and Milicich 1987; Stewart and Roberts 2015; Visconti et al. 2017). Kingsford and Milicich (1987) write that juveniles settle at 32 to 73 days old, but Visconti et al. (2018) put them at 86 to 153 days old by January and February. Growth rates are rapid in juveniles, growth is fastest in January, and leatherjackets reach 14 cm SL at the end of their first year (Kingsford and Milicich 1987; Stewart and Roberts 2015). Growth in juveniles that were raised experimentally under laboratory conditions was strongly correlated with food abundance, but there was no relationship between growth rates and temperature (Milicich and Choat 1992). Males and females have virtually identical growth patterns, though males grow to a slightly larger mean length (27.6 cm) than females (27.1 cm) (Visconti et al. 2017).

Estimates of maturity suggest 50% of males and females are mature at about 19 cm TL, and 95% are mature at 22 cm to 23 cm TL by 2 years of age (Visconti et al. 2017, 2018), though Stewart and Roberts (2015) write that leatherjackets mature at 26 cm SL and 2 years of age. Adults grow to a maximum size of 33 cm SL (Stewart and Roberts 2015), males live to just under 10 years old, and females live to 17 years (Visconti et al. 2018).

Implications for Little Ice Age Populations

Leatherjacket reproduction appears to be sensitive to water temperature, but as they spawn in the coldest modern conditions of the Hauraki Gulf it is unlikely that decreasing water temperature would negatively impact spawning in the northern North Island. As leatherjacket growth rates are not affected by water temperature, the onset of LIA conditions would not cause any direct impacts to body size distributions. Leatherjackets are distributed across a wide latitudinal range, and I do not expect their range would have shifted.

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